University of Alberta

An adaptive approach to endangered species recovery based on a management experiment: reducing moose to reduce apparent competition with woodland caribou

by

Robert David Serrouya

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

Doctor of Philosophy

in

Ecology

Department of Biological Sciences

Fall 2013
Edmonton, Alberta

ABSTRACT

Species that are rare yet widely distributed are among the most challenging to conserve. The mountain ecotype of woodland caribou (*Rangifer tarandus*) is declining because of apparent competition with non-caribou ungulates (NCU) such as moose (*Alces alces*). I experimentally assessed whether reducing NCU could facilitate caribou recovery by taking advantage of a government policy to reduce moose abundance with increased hunting. First, I used microsatellite markers to evaluate the evolutionary significance of the mountain ecotype, and determined whether previously identified subpopulations were demographically distinct. I found that subpopulation structure was mainly caused by genetic drift in small populations. The demographic isolation of many subpopulations suggests that they are appropriate as management units for recovery planning. I then developed an ecological target for recovering caribou by estimating the abundance of moose that would have occurred in the absence of forest harvesting. I incorporated this target into predator-prey equations to make predictions about the risks and benefits to caribou. Predictions suggest that reducing NCU without reducing predators could negatively impact caribou. The predicted impact was greater if there was a time lag of the predators' numerical response, but gradually reducing NCU could mitigate this impact. Once the moose reduction was initiated in the field, the decline in moose numbers was greater than could be explained by the hunting treatment alone. I contrasted several hypotheses to explain the rate of decline, including density dependent, depensatory, or compensatory predation by wolves (*Canis lupus*). I found that depensatory predation best explained the moose decline, but hunting was the catalyst. Reducing moose appeared to reduce wolf numbers, with dispersal the likely mechanism. Remaining wolves spent more time in caribou habitat, but based on scat and kill-site investigations, there was no evidence that wolves shifted their diet to caribou. In the treatment and reference areas, the caribou response was mixed, with the larger subpopulations stabilizing but smaller ones continued to decline. By combining theoretical predictions with empirical manipulations I conclude that reducing NCU and predators concurrently is a prudent approach to recover caribou. Few broad-

scale manipulations exist to recover endangered species, but are needed to evaluate recovery options.

ACKNOWLEDGEMENTS

I very much enjoyed interacting with an advisory committee from diverse backgrounds that include working for government and academia. These people choose to conduct science under different umbrellas but share the goal of creating knowledge. My supervisor, Stan Boutin, was always available for discussion, even when those little chats stretched on. Feedback was quick, always honest, and most of all helped to focus my thinking (not an easy task). Bruce McLellan has been a mentor for a decade and a half, and the level of support he's provided has been astounding – scientifically, financially, and philosophically. I look forward to more of the same. Mark Lewis, Scott Nielsen, and Dale Seip were genuinely interested in this project, and caught a few key errors – thanks! I also thank Erin Bayne for insightful comments on the final draft. I encourage students interested in broad-scale conservation and ecological theory to seek out these people for advice and guidance.

I am indebted to the many field assistants who worked in often difficult but sometimes pleasant conditions. These people included Corey Bird, Gary Pavan, Mandy Kellner, Saakje Hazenberg, Kelsey Furk, Pat McMechan, Jacob Bapty, John Townley, Shawn McFarland, Cory Legebokow, Cornelius Suchy, Brian Glaicar, Stan Smith, Diane Millar, Miles Howard, Sabina Wodak, Charlie McLellan, Melanie Plett, Bill Beard, Patrick Stent, Janis Hooge, and John Flaa from Parks Canada. Laura Gastor, Don Munro, and other members of the Columbia Forest District fire crew helped with pellet transects. Among thousands of other things, Gary Pavan also provided skilled GIS assistance. Thank you all for dealing with devil's club!

From the British Columbia Ministry *du jour* (it changed three times), I'd like to thank Kurt Huettmeyer, Dave Raven and Ken Talbot for supporting this research by allowing us to use the Columbia Forest District compound, office space, and equipment. All the staff in the Columbia Forest District are also thanked for putting up with various odours seeping out from freezers in the warehouse. I'd also like to thank Shannon Stotyn who provided the wolf data from 2004-2005. Good thing you were with us early on to collect those data! Debbie Jenkins, Mitch Campbell, Mathieu Dumont, Keri Zittlau, Leo Degroot and Nicola Freeman provided genetic samples for Chapter 2. Dave Paetkau, Chapter 2 was your push, and thanks for the glimpse into population genetics. John Simms helped to program the GIS bootstrapping code for Chapter 3 (and forges knives with my son – thanks for that). Meike Wittmann was instrumental in helping with Chapter 4, the ideas for which grew in a class taught by Mark Lewis. Michelle McLellan conducted the scat analyses and I am grateful that she took this on. Patrick Jones helped to train Michelle. Michelle and Meike will be authors on the corresponding chapters when they are submitted for publication. Kyle Artelle was a partner for a class project when I worked on Chapter 5 and I thank him for his feedback. Kim Poole taught me how to count moose, which is greatly appreciated.

I value the many fruitful discussions I had with colleagues and friends including Doug Heard, Harry van Oort, Heather McPhee, Seth Cherry, Mandy Kellner, Gary Pavan, Corey Bird, Kelsey Furk, Heiko Wittmer, Kyle Knopff, Chris Johnson, Michael Proctor, Jamie Gorrell, Aaron Shaffer, Garth Mowat, Shawna Pelech, Craig Demars, Mark Hebblewhite, Nick DeCesare, Nate Webb, Dave Latham, Amy Nixon, Lara Roorda, and Randy Wright. Sadly, Randy recently passed away.

A special thanks to Dave Mair of Silvertip Aviation for piloting in some of the most difficult mountain weather on the continent. He knows more about the animals than any of us, and always put safety first. Clay Wilson of Bighorn Helicopters captured animals in a safe and professional manner and I am greatly indebted to his contribution. Paul Tigchelaar from Glacier Helicopters, Matt Callaghan from Arrow Helicopters, and the crew at Selkirk Mountain Helicopters provided excellent piloting during wolf, caribou, and moose censuses.

Gary, Harry, Mandy, Corey and Kelsey were also key at leading cluster investigations, and wolf and caribou censuses – you folks formed the core of our caribou team and I sincerely appreciate every effort you undertook. Without your guidance, collaboration, and friendship this project would not have happened. Thanks also to my lab mates for many valuable discussions; lab meetings are one of the best ways to share information and get roasted, so I hope Stan and Erin Bayne keep that format going.

Funding for this thesis was provided by the now defunct Research Branch of the British Columbia Ministry of Forests, the BC Forest Science Program, the Forest Investment Account, Habitat Conservation Trust Foundation, Fish and Wildlife Compensation Program (Columbia Basin), Parks Canada, Downie Timber, Louisiana Pacific, Bell Pole, and the Revelstoke Community Forests Corporation. The Selkirk College Geospatial Research Centre provided the GPS collars for moose collaring. Thanks to Dieter Offermann (Downie Timber), Peter Gribbon and Colin Pike for initiating some of the early funding. Personal support was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), Alberta Ingenuity, the Bill Shostak Wildlife Award, the Provost Doctoral Entrance Award, and the Andrew Stewart Memorial Graduate Prize. Garth Mowat, John Krebs, Tara Szkorupa and Chris Ritchie also helped ensure that the money kept flowing for important aspects such as wolf and moose censuses. Garth and Tara also helped with pellet transects. I have invited Garth and Harry to be authors on Chapter 6a, and Shannon on 6b. Doug Jury, John Surgenor, and Chris Proctor helped with logistics and information relevant to the reference area.

Families are extremely important. I'd like to thank my parents, Nadine and Marc Serrouya, and my sister Lillian and brother Danny for their unwavering support. Most importantly, I'd like to thank my wife, "saint" Sylvia Wood (Sylvia, I'm on dishes and dinner for the next four and a half years), and my kids Ruby (the Destroyer) and Carlos ("you said six months, six months ago…"). I will forgive just about anything from now on – so dig this sentence out any time! The love and dedication I've experienced from my wife and children is something I cherish deeply. Rubes, thanks for holding the ladder steady for those camera checks, and 'Los, next time, I won't miss your hockey finals – congrats again on the 2013 playoff win. Let's all go ski touring now.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

PERSPECTIVES ON FACTORS LIMITING WOODLAND CARIBOU ABUNDANCE AND HOW TO ATTEMPT RECOVERY

How does one approach the recovery of an endangered species? Clearly there is no one-size-fits-all approach because the factors limiting population growth can vary enormously among species and ecosystems. Yet, Graeme Caughley reminded us that there are certain basic principles that can be applied when a species is in decline (Caughley 1994). The iterative steps of determining the agent(s) of decline, removing the agent(s), transplanting if necessary, and monitoring the population response, have intuitive appeal because of their simplicity. The medical community understands this approach implicitly when attempting to cure a patient. Such a simple recipe, however, almost trivializes the difficulties involved at each step, although this was not the intent of Caughley's review. By his own admission, there had been few successes implementing these steps, and they were most easily applied to small-scale island systems (Caughley 1994). For large mammals that may be naturally rare and dispersed at a continental scale, obtaining the necessary evidence to discriminate among competing hypotheses to explain a population decline is seldom trivial. Entire essays are devoted to the topic of how to identify limiting factors, with methodological debates about the merits and shortfalls of studies based on time-series, observation, natural spatial comparisons, or manipulations (Hurlbert 1984, Underwood 1990, Walters and Holling 1990, Boutin 1992, Carpenter et al. 1995, Roush 1995, Beckmann 2011, van Oort et al. 2011).

Fortunately, for the organism I study my predecessors did much of the heavy lifting when it came to identifying the agent of decline. This knowledge allowed me to focus on the subsequent steps: testing recovery options for an endangered ecotype of woodland caribou (*Rangifer tarandus caribou*), while investigating many associated components of the ecosystem including their predators, sympatric cervids, and the vegetation that influences their abundance and distribution. The agent of decline for many woodland caribou populations across North America appears to be excessive predation (Festa-Bianchet et al. 2011) through a process that is termed apparent competition (Holt 1977). Apparent competition describes a situation where two or more prey species appear to compete for a resource, but their interactions are mediated through a shared predator. Predictions from this hypothesis are that prey species with a lower reproductive rate or higher vulnerability to predation can have a lower equilibrium or will go extinct. The reason this can occur is that predator numbers are mainly influenced by the more abundant primary prey that are more fecund or resilient to predation, so as the secondary prey decline, there is little or no feedback to predator numbers. Because caribou tend to be less fecund (Shackleton 1999) or more vulnerable to predation relative to other cervids (Haber 1977), they are often the victim of apparent competition.

A historical account of how the evidence accumulated for predation as the agent of decline is especially relevant because it helps contextualize the difficulties in achieving scientific consensus for the first step in the recovery process. Early caribou researchers in British Columbia (BC) and elsewhere focused on bottom-up processes, specifically how reducing the amount and distribution of lichens, an important caribou forage, must be limiting caribou abundance. Lichens regenerate slowly so there was intuitive appeal that disturbing them must negatively affect caribou. This reasoning was especially pertinent for arboreal lichens that grow primarily on old conifers in the BC interior, trees that are highly valued by environmental groups but also by the timber industry. From work done in the area of Wells Gray Park in the 1950s, Edwards et al. (1960) wrote “Survival of caribou in this area, therefore, depends in part upon the availability of *Alectoria* [arboreal lichens] in winter….The abundance of lichen must be an additional factor enabling caribou survival.” Predation was not mentioned as a limiting factor, even though major changes to the large mammal community had been occurring for 2 – 3 decades (Seip 2008). Wildfires and human disturbance were considered to negatively affect caribou because they can reduce food supply and displace individuals from prime habitat (Edwards 1954, Klein 1971). But there was another mechanism that may have been overlooked at the time. Wildfires and a warming or drying climate can also favour moose (*Alces alces*) and deer (*Odocoileus* spp.) abundance (Schwartz and Franzmann 1991, Dawe 2011), which in turn increases predator numbers (Fuller et al. 2003). Many large wildfires occurred in the central portion of mountain caribou range in the 1920s (McLellan 2010). Seip (2008) quotes early settlers in BC as stating that when moose increased the caribou declined, but the process confused them because: "…they don't even eat the same kind of food, and yet the caribou did start going down hill shortly after the moose arrived (Boudreau 1998 cited in Seip 2008)." Similar patterns were emerging elsewhere in BC (McLellan 2010, Santomauro et al. 2012), but the process remained unclear.

Tom Bergerud was among the first wildlife biologists to argue that predation could have a major limiting role on wildlife populations, particularly on caribou, and he began to challenge the bottom-up disturbance hypothesis (Bergerud 1974, Bergerud et al. 1984). This idea represented a major shift in wildlife management because there was a belief that predation tended to remove the "doomed surplus" (Errington 1946, Mech 1970). Bergerud also argued that in some regions, overhunting played a major role in woodland caribou declines (Bergerud 1974, Bergerud et al. 1984), and McLellan's (2010) review of historic caribou hunting allocations supports this hypothesis. In one of Bergerud's most well-known studies, he compared caribou density on the predator-free Slate Islands of Ontario, to nearby Pukaskwa National Park on the mainland where bears and wolves existed. Caribou density on the Slate Islands was 100-fold greater (Bergerud et al. 2007). He also used a meta-analysis to determine that 6.5 wolves per 1000 km^2 represented the maximum wolf density where caribou recruitment would equal or exceed caribou mortality (Bergerud and Elliot 1986).

However, this work was not universally accepted. Prominent ecologists referred to Bergerud's evidence as "circumstantial" (Krebs 1985, 1994, 2001). At a gathering of managers and scientists in Vancouver, Canada in 1978 (Bunnell et al. 1978) there were "400 people arguing against one" (Seip pers. comm.), because these ideas represented a new paradigm in wildlife management. Some of this skepticism may have been justified. For example, Bergerud's graph linking predation to caribou population trends in BC was necessarily approximate (Bergerud et al. 1984). Much of the province was surveyed for caribou in 1978, producing reliable estimates, but the estimates from *c*. 1960 and 1970 were less reliable (Bergerud 1978). These data did not meet the standards of experimental ecologists. Nonetheless, he was the seed for many important ideas including the notion that forestry roads could alter a predator's functional response by improving its foraging efficiency (Bergerud et al. 1984), which has been supported by subsequent empirical studies (James and Stuart-Smith 2000; McKenzie et al. 2012). Over time, his data, and those of others, increasingly supported his hypotheses.

The primary follow-up to Bergerud's work occurred when Seip (1992) used a natural spatial comparison and a wolf removal experiment to show that caribou were limited by wolves because of the apparent competition process. A subpopulation of caribou with year-round overlap with moose and wolves was declining, with wolf predation the primary cause of mortality. An adjacent caribou subpopulation migrated to a mountainous summer refuge in Wells Gray Park, where moose and thus wolves were rare. These caribou were increasing in number with higher adult survival and recruitment rates. Caribou recruitment improved following two years of wolf removal in the area where caribou were sympatric with wolves year-round. Yet, this approach to science was still criticized for not addressing underlying mechanisms (Krebs 2002). Since that study was done, even the Wells Gray subpopulation has declined (Wittmer et al. 2005a).

Other studies have continued to contribute evidence regarding the role of predators in limiting caribou populations. In Alberta, wolves were the major source of caribou mortality (McLoughlin et al. 2003), and wolves were more likely to be found near human disturbances such as seismic lines (James and Stuart-Smith 2000). In Saskatchewan, Rettie and Messier (1998) found that adult caribou survival and recruitment was low, and speculated that wolves were limiting the population. They reasoned that at $0.05/km^2$, caribou were too rare to sustain wolves within the study area (Messier 1985), so wolves must be supported by more abundant primary prey that may be linked to early seral forests (Rettie and Messier 1998). Again in British Columbia, Wittmer et al. (2005b) used a hypothetico-deductive approach to discern among three hypotheses causing observed caribou declines: food regulation, predator-sensitive forging (PSF), and predation as an outcome of apparent competition. The latter hypothesis predicts a density independent per capita growth rate (r), with predation as the major agent of mortality. The food regulation and PSF hypotheses both predict density dependent growth rates, with the difference being malnutrition as the dominant mortality source caused by food regulation, but predation the primary source in the case of predator-sensitive foraging. Based on a meta-analysis of population growth (r) among 18 caribou subpopulations, they found that subpopulations with the most food per individual declined at the fastest rate, which supported the apparent competition hypothesis. McLellan et al. (2012) addressed lingering concerns from Wittmer et al.'s (2005b) work by asking whether caribou killed by predators had less marrow fat, or whether the amount of food per caribou influenced marrow. If food were the limiting agent, then there should be a positive relationship between food per caribou and marrow fat, whereas if caribou were taking greater risks to forage because of logging, those killed by predators should be in worse condition. None of these hypotheses was supported, with the variance in marrow fat best explained by gender: males in the rut were in the worst condition. Body condition did not make caribou more vulnerable to predation and there appeared to be enough forage to support populations that were 2 – 5 times more abundant only 15 years prior. In an elegant natural experiment, Latham et al. (2011) used a time-series approach by comparing caribou growth rates before and after the invasion of white-tailed deer in northern Alberta. Deer increased 17-fold and both the distribution and abundance of wolves in caribou range increased. Caribou were stable then began to decline coincident with these changes. Collectively, these studies encompassed a range of scientific methods including mensurative, experimental, and time-series approaches, and arrived at the conclusion that apparent competition with other cervids was the proximate cause of woodland caribou declines.

In 2009, Bergerud's primary results were reproduced within Krebs' textbook (Krebs 2009), along with figures from other studies of predator-mediated apparent competition and woodland caribou (Wittmer et al. 2005b). If we use this "textbook" measure as a yardstick, it has taken three decades to achieve consensus on this topic. However, some skepticism remains (Brown et al. 2007, Theberge and Walker 2011, Wasser et al. 2011, 2012), which is a healthy component of the scientific process.

THESIS OBJECTIVES

Conserving a species that is rare and declining, but that also covers a broad geographic area, is extremely challenging. Woodland caribou range across most of Canada's boreal forest, and a large portion of Canada's temperate and montane forests. Their survival is linked to large tracks of undisturbed, older forests, primarily because these areas contain fewer non-caribou ungulates, but also because lichens are most abundant in these stands (Serrouya et al. 2007, Wittmer et al. 2007).

My thesis was focussed specifically on mountain caribou in British Columbia and Idaho, which are considered a distinct ecotype of woodland caribou (Heard and Vagt 1998). These animals are divided into 18 subpopulations (Wittmer et al. 2005a), with two recently having gone extinct and 11 subpopulations numbering under 100 individuals. The term "mountain caribou" is misleading however, because many caribou herds live in the mountains, but not all are exposed to deep snow (2 – 5 m snowpack) that distinguishes this ecotype (Fig. 1.1). The deep snow means that they forage almost exclusively on arboreal hair lichens of the genus *Alectoria* and *Bryoria* because ground forage is buried, and the snowpack provides the lift needed to access these lichens that are most abundant in the tree canopy (Serrouya et al. 2007). I refer to these caribou as deep-snow or mountain caribou interchangeably in this thesis. The

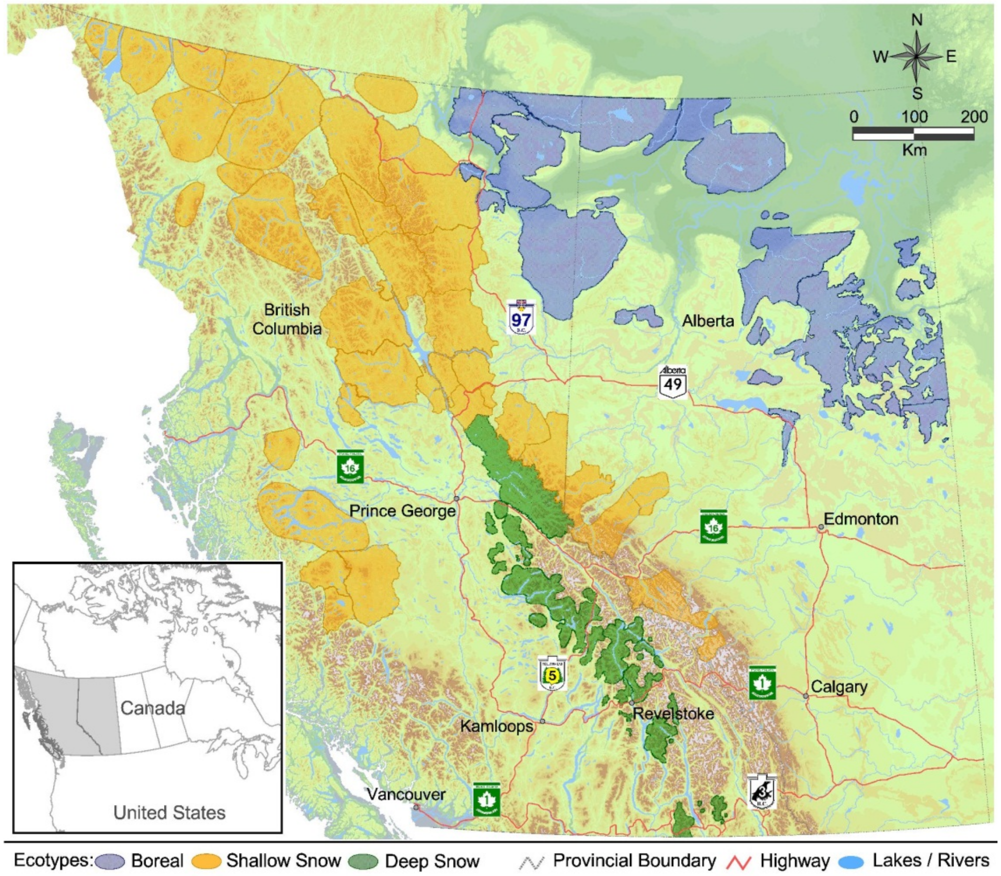


Figure 1.1. Map of the three ecotypes of woodland caribou in British Columbia and Alberta. I use deep-snow and mountain caribou synonymously in this thesis.

work of Edwards (1954), Seip (1992), Wittmer et al. (2005a, b), McLellan et al. (2012), and many others, all occurred on this caribou ecotype.

The primary hypothesis I tested was whether the apparent competition mechanism could be reversed by reducing moose abundance as a means of indirectly reducing wolf abundance, and in turn reduce the rate of caribou decline. Moose have become more abundant in southern BC, and landscape disturbance is likely a contributing factor (Chapter 3). The key to testing this hypothesis was that the BC Government implemented a program to reduce moose abundance across a broad area to increase recreational opportunities for hunters and to reduce damage to cedar plantations (D’Eon et al. 2003). The opportunity arose to transform this new policy into an experiment, allowing evaluation of this strategy as a recovery option for mountain caribou. My approach was to combine concepts from adaptive management along with

Caughley's recipe to recover a declining population. Many essays have been written on the successes and challenges with implementing adaptive management (Walters 1986, Walters and Holling 1990, Gregory et al. 2006, Gunderson and Light 2006), so I will not review these issues here. I will however highlight some of the key principles my colleagues and I tried to implement. First, adaptive management involves using management actions to learn, and for most natural resource challenges this means applying treatments at a broad scale. The management action(s) can't be arbitrary however, and must be set up to clearly test the hypotheses most relevant to the problem. To do this properly, one must get into the habit of linking managers and researchers early on in the process. As the change in policy was being discussed, in 2004 I gathered a dozen managers and researchers from southern BC to an initial meeting with the goal of identifying the primary hypotheses, the scales to investigate, and attempted to standardize the response metrics. This opened the door for collaboration, funding, and regular communication.

I attempted to use active adaptive management, which means using a perturbation to test a hypothesis and comparing the outcome to other areas where other policies are implemented. I did this by using a spatial reference area where a moose reduction was not initiated. This design is considered an improvement over passive adaptive management where the approach is based on a time series with no reference area, but is often the only option (Walters and Holling 1990). I also made use of computer simulations to predict outcomes of treatments, because the opportunity for replication or to correct errors is severely constrained when experimental units encompass large areas. Another key piece of advice I gleaned from Walters and Holling (1990) was to use a nested design whenever possible, because a factorial approach is impractical when experimental units are limited. For example, in the treatment area I took advantage of variations in moose density and linked this to wolf diets and recruitment.

By combining the advice from Walters and Holling (1990) and Caughley (1994), I describe six steps to implement a recovery program for woodland caribou:

1. determine the cause of decline,
2. identify the scales and subpopulations to implement recovery,
3. set ecological targets for recovery,
4. make quantitative predictions based on these targets,
5. remove the limiting factors, and
6. monitor the outcome.

Steps 2 to 6 roughly correspond to the chapters in this thesis. Although these steps are presented in an ideal order, in reality moose were being reduced (step 5) before I could finalize steps 2 to 4. Nonetheless, it was useful to present these steps to help frame the problem, to use for subsequent iterations of the cycle, or to apply in other situations. In Chapter 2, I established caribou demographic units for conservation using population genetics. I evaluated whether the mountain caribou ecotype was distinct based on neutral genetic markers (Ryder 1986), and whether existing subpopulation bounds were appropriately defined as demographic units. This was a critical step because several subpopulation bounds corresponded to the boundaries of the experimental units, and if caribou movement occurred between these areas then any response to the experimental treatment would be confounded. Next, I established an ecological target to recover caribou, by asking the question: How many moose would have been in the ecosystem had it not been logged (Chapter 3)? This value can be used as a target for both moose and wolves under the assumption that these historic conditions were more suited to caribou persistence. In the fourth chapter I used the target from Chapter 3 to make quantitative predictions using Rosenzweig and MacArthur's (1963) theoretical predator-prey model represented as a system of ordinary differential equations (ODEs). I used the ODEs to predict the population response of caribou by varying the rate and magnitude of reducing primary prey, as well as the intensity of reducing predators. In the fifth chapter I described how the change in government policy was used to reduce moose abundance, but the resulting moose decline occurred more rapidly than could be explained simply due to the increased hunter harvest. To find out why this happened, I used the hypothetico-deductive method by developing alternative hypotheses based on predator-prey theory, and used the moose data as the arbiter to distinguish among them (Hilborn and Mangel 1997). The hypotheses were that predation was compensatory, density dependent, independent, or depensatory. In the last two chapters (6a and 6b), I evaluated the degree that reducing moose encouraged recovery of caribou. In Chapter 6a I determined how increasing the number of hunting permits reduced moose abundance, and in turn whether this resulted in fewer wolves and more caribou. These metrics represented the numerical response to the treatment. In the final data chapter (6b), I focussed on the wolves' functional or behavioural response to the manipulation. I argue that both aspects were needed to understand why the system responded in the manner it did, and why monitoring abundance alone may overlook important mechanisms that led to the observed patterns (Krebs 2002).

LITERATURE CITED

Beckmann, J. P. 2011. Understanding the role of behavioral mechanisms and impacts of habitat fragmentation on structuring small declining populations. Animal Conservation **14**:229-230.

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

Bergerud, A. T. 1978. The status and management of caribou in British Columbia. British Columbia Ministry of Environment, Fish & Wildlife Branch, Victoria, BC.

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 J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology **64**:1515-1529.

Bergerud, A. T., W. J. Dalton, H. Butler, L. Camps, and R. Ferguson. 2007. Woodland caribou persistence and extirpation in relic populations on Lake Superior. Rangifer Special Issue **27**:57-78.

Boutin, S. 1992. Predation and moose population dynamics - a critique. Journal of Wildlife Management **56**:116-127.

Brown, G. S., L. Landriault, D. J. H. Sleep, and F. F. Mallory. 2007. Comment arising from a paper by Wittmer et al.: hypothesis testing for top-down and bottom-up effects in woodland caribou population dynamics. Oecologia **154**:485-492.

Bunnell, F. L., D. S. Eastman, and J. M. Peek. 1978. Symposium on natural regulation of wildlife populations, Vancouver, BC. Forest, Wildlife, and Range Experiment Station, University of Idaho.

Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science **269**:324-327.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**:215-244.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada. University of Alberta, Edmonton.

D'Eon, R.G., R. Serrouya, G. Pavan. 2003. Moose damage on cedar seedlings in the Lake Revelstoke Valley: Year 2 summary. Report for the BC Forest Investment Account.

Edwards, R. Y. 1954. Fire and the decline of a mountain caribou herd. Journal of Wildlife Management **18**:521-526.

Edwards, R. Y., J. Soos, and R. W. Ritcey. 1960. Quantitative observations on epidendric lichens used as food by caribou. Ecology **41**:425-431.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology **21**:144-177.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. Coté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Canadian Journal of Zoology **89**:419-434.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161-191 *in* D. L. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

Gregory, R., D. Ohlson, and J. Arvai. 2006. Deconstructing adaptive management: criteria for applications to environmental management. Ecological Applications **16**:2411-2425.

Gunderson, L. and S. S. Light. 2006. Adaptive management and adaptive governance in the Everglades ecosystem. Policy Sciences **39**:323-334.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. University of British Columbia, Vancouver.

Heard, D. C. and K. L. Vagt. 1998. Caribou in British Columbia: a 1996 status report. Rangifer **18**:117-123.

Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

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

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187-211.

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.

Klein, D. R. 1971. Reaction of reindeer to obstructions and disturbances. Science **173**:393-398.

Krebs, C. J. 1985. Ecology: the experimental analysis of distribution and abundance. 3rd edition. Harper & Row, New York.

Krebs, C. J. 1994. Ecology: the experimental analysis of distribution and abundance. 4th edition. HarperCollins College Publishers, New York, NY.

Krebs, C. J. 2001. Ecology: the experimental analysis of distribution and abundance. 5th edition. Benjamin Cummings, San Francisco.

Krebs, C. J. 2002. Beyond population regulation and limitation. Wildlife Research **29**:1-10.

Krebs, C. J. 2009. Ecology: the experimental analysis of distribution and abundance. 6th edition. Benjamin Cummings, San Francisco, Calif. ; London.

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.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus **2**:205-216.

McLellan, B. N. 2010. An historic perspective of mountain caribou distribution and abundance. BC Ministry of Forests, Research Branch, Victoria, British Columbia.

McLellan, M., R. Serrouya, B. N. McLellan, K. Furk, D. Heard, and H. Wittmer. 2012. Implications of body condition on the unsustainable predation rates of endangered mountain caribou. Oecologia **169**:853-860.

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

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, NY.

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

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.

Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist **97**:209-223.

Roush, W. 1995. When rigour meets reality. Science **269**:313-315.

Ryder, O. A. 1986. Species conservation and systematics - the dilemma of subspecies. Trends in Ecology & Evolution **1**:9-10.

Santomauro, D., C. J. Johnson, and G. Fondahl. 2012. Historical-ecological evaluation of the long-term distribution of woodland caribou and moose in central British Columbia. Ecosphere **3**. http://dx.doi.org/10.1890/ES11-00371.1

Schwartz, C. C. and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs **113**:1-58.

Shackleton, D. 1999. Hoofed mammals of British Columbia. UBC Press and the Royal Bristish Columbia Museum.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Seip, D. R. 2008. Mountain caribou interactions with wolves and moose in central British Columbia. Alces **44**:1-5.

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.

Theberge, J. and G. Walker. 2011. Managing for caribou and ecological integrity: reply to Serrouya and Wittmer 2010. Conservation Biology **25**:858-859.

Underwood, A. J. 1990. Experiments in ecology and management - their logics, functions and interpretations. Australian Journal of Ecology **15**:365-389.

van Oort, H., B. N. McLellan, and R. Serrouya. 2011. Metapopulation or predictable pattern of extinction? Animal Conservation **14**:231-232.

Walters, C. J. 1986. Adaptive management of renewable resources. Macmillan ; Collier Macmillan, New York, London.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Wasser, S. K., J. L. Keim, M. L. Taper, and S. R. Lele. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. Frontiers in Ecology and the Environment **9**:546-551.

Wasser, S. K., J. L. Keim, M. L. Taper, and S. R. Lele. 2012. To kill or not to kill - that is the question. Frontiers in Ecology and the Environment **10**:67-68.

Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, G. S. Watts, and D. Hamilton. 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. R. E. Sinclair, and B. N. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology **76**:568-579.

CHAPTER 2

POPULATION SIZE AND MAJOR VALLEYS EXPLAIN MICROSATELLITE VARIATION BETTER THAN TAXONOMIC UNITS FOR CARIBOU IN WESTERN CANADA[1]

In the current era of rapid loss of biological diversity (Sala et al. 2000), designating population units for conservation below the species level continues to gain importance (Moritz 1994, Crandall et al. 2000, Fraser and Bernatchez 2001, Green 2005), particularly when decision-makers are forced to prioritize which units to conserve (Schneider et al. 2010). The Evolutionarily Significant Unit (ESU) is a common term used to describe groups of organisms that have undergone sufficient genetic divergence from conspecifics to represent unique and significant adaptive potential relative to the species as a whole (Ryder 1986). How to designate these units continues to be debated (Moritz 1994, Paetkau 1999, Fraser and Bernatchez 2001), yet recognized subspecies, varieties, and ecotypes (*sensu* Turesson 1922) are often candidates for unique recognition.

Although existing taxonomic units can act as a basis for listing, in most cases there is incomplete genetic information to validate these designations. To deal with this uncertainty, additional criteria were developed to define units, including demographic or geographic isolation, bio-geographic uniqueness, and conservation status (Green 2005). Variants of these criteria have been reflected in several legal frameworks (Green 2005). Given the diverse approaches used to define intra-specific units, it has become increasingly important to understand the geographic and ecological factors that influence population genetic structure, so that population units and corresponding conservation status can be appropriately defined. By contrasting the relative influence of geographic features (mountain ranges, valleys, or distance) with existing taxonomic

---

[1] A version of this chapter has been published as: Serrouya, R., D. Paetkau, B. N. McLellan, S. Boutin, M. Campbell, and D. A. Jenkins. 2012. Population size and major valleys explain microsatellite variation better than taxonomic units for caribou in western Canada. Molecular Ecology **21**:2588-2601.

designations, we can learn whether current classifications are appropriate, or whether new ones should be considered.

Gauging the importance of existing taxonomy and landscape features is complicated by population size, a factor that is particularly relevant when dealing with endangered species. Among larger populations, where the rate of genetic drift is low, classical genetic methods would not be sensitive to connectivity declines in the last two or three generations, but in smaller populations one might encounter significant changes in allele frequencies from one generation to the next (Wright 1931). The high rate of genetic drift in small populations might mask the historic contributions of taxonomic boundaries or landscape features to population structure. To date, most landscape genetics studies have incorporated factors that are limited to geographic correlates (Manel et al. 2003) and may not have considered how population size could affect these interpretations.

Caribou (*Rangifer tarandus*) in North America are a good example of the challenges faced when identifying conservation units. They have multiple subspecies designations, are broadly distributed across a variety of ecosystems, and exist in subpopulations that range in abundance over five orders of magnitude, many of which are in rapid decline (Wittmer et al. 2005a, Festa-Bianchet et al. 2011). Caribou are distributed from treeless deserts of the high arctic (<20 cm precipitation/yr), to temperate rainforests where precipitation exceeds 200 cm/yr, with most falling as snow (14 m/yr). These climatic extremes are matched by differences in foraging and antipredator behaviour (Bergerud et al. 2008) and influenced their taxonomic classification. Subspecies in North America include migratory Peary (*R. t. pearyi*) and barren ground (*R. t. groenlandicus*; Banfield 1961), animals that spend at least part of the year north of treeline, and woodland caribou (*R. t. caribou*), which live in forested ecosystems. In addition, there are three recognized ecotypes of woodland caribou in western North America (Heard and Vagt 1998): 1) boreal caribou, which are found across the boreal forest and dig through shallow snow to access terrestrial lichens during winter, 2) shallow-snow mountain caribou, which spend most of the year in mountains and also dig through shallow snow for terrestrial lichens, either on mountain ridges or adjacent dry forests, and 3) deep-snow mountain caribou, which remain high on the mountains during winter where they walk on top of a very deep snowpack (2 – 5 m) to access arboreal lichen in the canopy of conifers (Seip and McLellan 2008). The latter group's exclusive use of arboreal lichens has led to their designation as a unique ecotype (Edwards 1960), but it remains unknown if there is genetic support for this classification. This ecotype is the most endangered of the three, where 20 yr of radio-telemetry has revealed 18 subpopulations (Wittmer et al. 2005a), two having recently been extirpated and another 11 numbering < 100 individuals.

My goal with this chapter was to present caribou as case study to evaluate existing taxonomy using microsatellite markers, but to contrast the magnitude of this pattern with population size, a mechanism that can clearly influence spatial structure. My specific objectives were threefold. The first was to assess existing classifications of subspecies and ecotypes using microsatellite alleles and to contrast taxonomy with landscape features that were independent of taxonomic designation. If allele frequencies corroborate the taxonomy, then assessing conservation status for each of these groupings is supported. The second objective was to investigate the relationship between genetic differentiation (F_{ST}) and population size. I expected that smaller populations would be more genetically distinct relative to their neighbours compared to pairs of populations that were large, while controlling for geographic distance. If this result was confirmed, then population size would be of importance to incorporate into estimates of spatial population structure. The final objective was to determine if the structure estimated by microsatellite markers was supported by tracking a large proportion of the endangered deep-snow ecotype using radio telemetry. Comparing estimates of movement using marked individuals relative to indirect estimates of gene flow (e.g., Ehrlic 1975, Slatkin 1987) can be revealing because indirect estimates will lag behind contemporary barriers to movement, particularly for larger populations where the rate of drift is lower. Yet, if the population genetics confirm the structure identified using radio-telemetry, the implication is that the structure is older, perhaps predating recent anthropogenic landscape changes. Thus, contrasting the two approaches provides more complete understanding of the timing and thus mechanisms governing population structure (Boulet et al. 2007, McDevitt et al. 2009).

METHODS

Sample collection

The samples encompassed three of the world's eight recognized caribou/reindeer subspecies (Flagstad and Røed 2003): Peary, barren ground, and woodland. These samples represented a broad diversity of ecosystems in western North America, ranging from northern Idaho, USA, to Bathurst Island, Nunavut, Canada, spanning a distance of > 3000 km. This area included wet, old-growth forests of the Columbia Mountains where natural disturbances are rare, drier forests from the Rocky Mountains where fires are relatively common, boreal forests where fires are also frequent but the topography is subdued, and areas north of treeline to the high Arctic.

Blood and tissue samples were collected during caribou live-capture as part of previous research on deep-snow caribou (e.g., Wittmer et al*.* 2005a). Additional fecal samples were collected during winter within 48 hr of deposition by swabbing the surface with cotton swabs. Samples from northern and western British Columbia and barren ground caribou were from tissues collected during hunter harvest, and samples from Peary caribou were from antler sheds. Samples from the boreal ecotype and the Purcells were provided by McLoughlin et al. (2004) and Zittlau (2004), but I increased the number of genotyped markers to 18.

DNA was extracted using DNeasy kits from QIAGEN using their specified methods. Fecal swabs were clipped and treated as other tissue samples. Hair samples were processed by clipping roots from up to 10 hairs and then analysed following standard protocols (Paetkau 2003). Analysis of microsatellites used ABI's detection system on 310 automated sequencers, while genotypes were scored using Genotyper software (ABI). Genotype profiles were assigned a low-confidence score if they failed to satisfy thresholds for legibility and strength. The use of these thresholds has been shown in other studies from both hair and fecal samples to produce initial rates of genotyping error well below 1% per locus (Kendall et al. 2009, Poole et al. 2011). As per Paetkau (2003), samples that produced low-confidence scores for > 50% of markers on the first attempt at analysis were culled from the dataset based on the logic that their low DNA concentration would elevate rates of genotyping error (Taberlet et al. 1996). In other cases, low-confidence scores were re-analyzed to confirm the weak initial result, using 60% more template DNA than during the first attempt. Samples that still had low-confidence scores for > 1 marker after this phase of re-analysis were also culled from the dataset, once again eliminating the most error-prone samples. Eight PCR reactions were used to amplify the 18 loci. Markers used were Rt1, Rt5, Rt6, Rt7, Rt9, Rt24, Rt27 (Wilson et al. 1997), BL42, BM4513, BM6506 (Bishop et al. 1994), BMS1788, BMS745 (Stone et al. 1995), CRH (Moore et al. 1992), FCB193 (Buchanan and Crawford 1993), NV16, NV30 (Røed and Midthjell 1998), OhemD, and OhemQ (Jones et al. 2000). We tested each marker for deviations from Hardy-Weinberg equilibrium and for linkage disequilibrium using Genepop v. 4.0.10 (Raymond and Rousset 1995).

Genetic structuring among subspecies and ecotypes

I conducted population genetic analyses at several spatial scales. The broadest scale included samples from all three caribou subspecies and the three ecotypes of the woodland subspecies. The program FITCH (Fitch and Margoliash 1967) within the PHYLIP 3.69 package (Felsenstein 2005) was used to represent a matrix of F_{ST} values as a bifurcating, hierarchical 'tree'. Within the tree I differentiated subspecies and ecotypes, and along with a map this enabled broad comparisons of genetic and geographic distances in relation to subspecies and ecotypes (Appendix 2.1 represents F_{ST} divided by geographic distance). I included all available Peary and barren ground subpopulations within the sample area, but selected a subset of woodland subpopulations that were representative of their geographic area (i.e. centre of the range or geographic endpoints) to reduce complexity in the tree. Therefore, this analysis included one Peary caribou subpopulation (Bathurst Island), three barren-ground subpopulations (Southampton, Dolphin & Union, and Qamanirjuaq), six deep-snow mountain subpopulations (Hart, Cariboo, Wells Gray, Columbia North, Columbia South, Purcells), five shallow-snow mountain subpopulations (Jasper, Graham, and Kennedy/Quintette/Moberly [the latter three were grouped; McDevitt et al. 2009, and see Results]), and five boreal subpopulations. Jasper samples have been classified as separate herds (Tonquin and Maligne) but were treated as one because they were similar based on microsatellite markers (McDevitt et al. 2009). The Southampton samples were from a caribou population restricted to an Island in Hudson Bay that was founded from 48 caribou that were transplanted from Coates Island (also *R.t. Groenlandicus*) in 1968. We excluded two deep-snow subpopulations that received transplants (Monashee South and South Selkirk) because they originated from different ecotypes and therefore may confound interpretation.

My second scale of investigation was restricted to one subspecies, woodland caribou from British Columbia and Alberta, but included samples from all putative subpopulations for which data existed, including those from the previous analysis. The additional subpopulations included 12 shallow-snow mountain herds (Atlin, Horseranch, Level-Kawdy, Rabbit, Muskwa, Frog, Tsenaglode, Pink Mountain, Wolverine, Spatsizi, Tweedsmuir, Itchas-Ilgatchuz), and five deep-snow mountain subpopulations (Barkerville, Frisby-Queest, Groundhog, Kinbasket, Central Selkirks/Duncan, South Selkirks), totalling 12 of the 18 deep-snow subpopulations identified by Wittmer et al. (2005a). To increase sample size, Horseranch and Level-Kawdy were grouped, as were Spatsizi and Tsenaglode (these were large herds with contiguous ranges).

I used the program STRUCTURE (Pritchard et al. 2000), which assumes no a-priori group membership, to identify groups of individuals. STRUCTURE runs had a burn-in of 100,000, a Markov Chain of 800,000, and were based on the admixture model. I tested for K (the number of populations) from 1 – 10, and repeated these 15 times. I used the methods of Evanno et al. (2005) to estimate the number of populations (K) that best describes the system under study. I then plotted the population membership of each individual on a map that outlined previously assumed ecotype designations. For each individual, STRUCTURE provides the estimated proportion of ancestry in each putative population (‘q’), so I categorized individuals based on their mean value of q (0-0.6, 0.6-

0.8, >0.8) and report the proportion of assignments in each cluster where $q > 0.8$, as an index of cluster strength.

I used Mantel analyses to test the hypothesis that ecotypes within the woodland subspecies were genetically distinct units, while controlling for geographic distance. This test measures the variance of alleles among subpopulations relative to the total variance (similar to F_{ST} variance). Rousset's (1997) genetic distance ($F_{ST}/(1-F_{ST})$) was the response metric. Major landscape features were included as covariates and included the North Thompson Valley, the Peace River Valley, the Fraser River Valley and the Rocky Mountains (Table 2.1). All analyses involving landscape features or ecotype membership were based on a matrix created for each covariate, with 1s indicating pairs of subpopulations that were on the same side of a landscape feature or ecotype membership, and 0s indicating pairs of populations that did not share that feature. This coding ensured that if a feature was stronger than the effect of geographic distance (if distance was indeed a factor), the Mantel r value would be negative. I combined the Mantel analyses with multiple regressions (Legendre et al. 1994) to clarify the importance of individual factors, and present r^2 estimates using Legendre et al.'s (1994) method. Mantel and regression analyses were performed using the ecodist package (Goslee and Urban 2007) in R (R Development Core Team 2008). I also used Program Arlequin version 3.11 (Excoffier et al. 2005) because this software partitions variance within subpopulations (F_{ST}), among ecotypes (F_{CT}), and subpopulations within ecotypes (F_{SC}). As a post-hoc test, I used Arlequin and grouped caribou by landscape features (instead of ecotype) identified as important from the Mantel and MR analyses. This was done to act as a check of the Mantel and MR analyses, but also to compare the AMOVA-based variance explained from the ecotype (F_{CT}) grouping, to groupings based on landscape features (F_{CT}). Arlequin was also used for F_{ST} estimates with 1000 permutations for significance tests, and all values presented are significant ($p < 0.05$) unless specified (p-values are in Appendix 2.2). If subpopulations contained fewer than five samples they were not included in Mantel or Arlequin analyses (McDevitt et al. 2009).

Table 2.1. Description of landscape features within the study area and included in the Mantel, multiple regression, and AMOVA analyses.

Landscape feature	Description of features within the study area bounds
Rocky mountains	Mountain range that varies from 874 m to 3954 m in elevation, with adjacent valleys as low as 600 m.
North Thompson Valley	Broad valley surrounded by mountains and includes the North Thompson river, Highway 5, a railway and several settlements with <10,000 people.
Fraser Valley	Broad valley surrounded by mountains and includes the Fraser river, Highway 16, a railway and several settlements with <10,000 people.
Peace River Valley	Broad valley including the Peace River, with a major dam and reservoir in British Columbia, free flowing in Alberta but with extensive agriculture.

Effects of population size on differentiation and heterozygosity

I conducted two analyses using population size to predict genetic patterns. First, I investigated how population size could affect differentiation among neighbouring subpopulations. For each subpopulation, I selected the subpopulation that was its nearest geographic neighbour, and calculated Rousset's F_{ST} divided by the geographic distance between population centres and used this index of geography-adjusted genetic distance as the dependent variable. The independent variable was the harmonic mean population size between pairs, which is commonly used in genetics because it weighs smaller populations more heavily (Hartl and Clark 2007). I did a permutation test by treating the subpopulation as the sample unit (because it may occur in >1 nearest-neighbour comparisons), similar to a Mantel test, to estimate the uncertainty of this relationship. The second analysis was to quantify the relationship between expected heterozygosity (H_E) and population size. I used the nls function (non-linear regression) in R, weighting each subpopulation by the inverse of the H_E variance, and bootstrapped subpopulations to estimate if the slope was different from 0. Both analyses used data from all subspecies and ecotypes within the sampling area, except those that received transplants (Monashee, South Selkirk, Southampton) or those with few samples (< 5). In cases where the sample collection covered a period of time when population size changed rapidly, the mid-point of the subpopulation size was used.

Genetic structuring and migrant estimation within deep-snow mountain caribou

To determine if population genetics supported the population structure of deep-snow caribou estimated by Wittmer et al. (2005a) using telemetry, I used program STRUCTURE with the same simulation parameters as above but included one neighbouring outgroup for comparison (Jasper, a shallow-snow ecotype that occurs adjacent to the deep snow range). I also sought to estimate the number of first-generation migrants using an assignment test (Paetkau et al. 2004) with Geneclass 2.0 (Piry et al. 2004) to determine the chance of demographic rescue of smaller and declining subpopulations. This analysis was limited to estimating movement from the larger northern populations to the smaller southern populations of this ecotype of woodland caribou. However, such an analysis was only possible if there was sufficient genetic structuring to assign individuals to their natal population, so I conducted this analysis post-hoc after the STUCTURE analyses, and if there was structure between more abundant northern and less abundant southern subpopulations.

To clarify the population structure of caribou at the ecotone between the deep- and shallow-snow ecotypes of mountain caribou in British Columbia, I used factorial correspondence analysis (FCA) with program Genetix (Belkhir 1999). FCA is similar to principal components analysis, and provides an objective depiction of groupings of similar individual genotypes with no a-priori assumptions of group membership. I included four shallow-snow subpopulations (Burnt, Graham, Quintette, Moberly and Kennedy) that were nearby or adjacent to the northern distribution of deep-snow mountain caribou (Wells Gray, N. Cariboo Mountains, and Hart subpopulations).

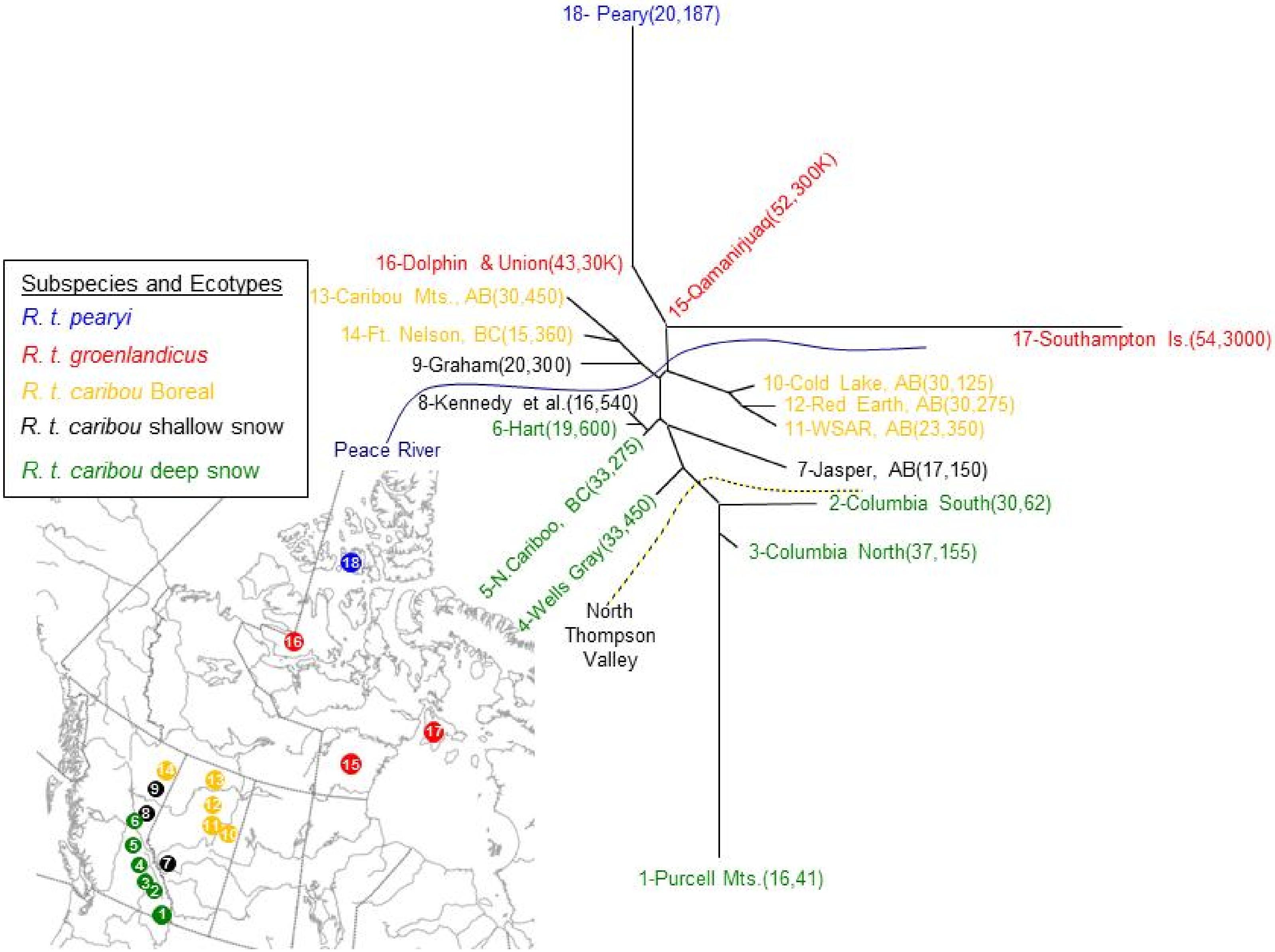

Subspecies and Ecotypes
R. t. pearyi
R. t. groenlandicus
R. t. caribou Boreal
R. t. caribou shallow snow
R. t. caribou deep snow
18- Peary(20,187)
15-Qamanirjuaq(52,300K)
16-Dolphin & Union(43,30K)
13-Caribou Mts., AB(30,450)
14-Ft. Nelson, BC(15,360)
9-Graham(20,300)
8-Kennedy et al.(16,540)
6-Hart(19,600)
17-Southampton Is.(54,3000)
10-Cold Lake, AB(30,125)
12-Red Earth, AB(30,275)
11-WSAR, AB(23,350)
7-Jasper, AB(17,150)
2-Columbia South(30,62)
3-Columbia North(37,155)
5-N.Cariboo, BC(33,275)
4-Wells Gray(33,450)
North Thompson Valley
Peace River
1-Purcell Mts.(16,41)
18
16
17
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1

Figure 2.1. Classification tree based on genetic distance of pre-defined caribou subpopulations in western Canada. Legend shows colour for three caribou subspecies, and three ecotypes within the woodland subspecies. Map shows collection locations, highlighting major departures of geographic vs. genetic distances. The North Thompson Valley and the Peace River are highlighted (see Table 2 for significance of these features). The F_{ST} value between the Purcells and Peary was 0.22. Southampton samples were founded based on transplants from 48 barren ground caribou. Sample size, followed by population size (K = × 1000) are shown in brackets.

RESULTS

A total of 606 unique genotypes were identified, 590 from blood or tissue, and 16 from scat (all scat samples were from the deep-snow ecotype). I had 20, 149, and 437 genotypes from Peary, barren ground, and woodland samples, respectively. Sample sizes from each subpopulation are listed in each figure where appropriate. None of the 18 markers showed significant deviation from HWE. There were 127 cases of linkage disequilibrium out of 2753 comparisons (4.6%; 18 markers across subpopulations) which is expected by chance at a critical value of 0.05.

Genetic structuring among subspecies and ecotypes

At the broadest scale of analysis, only the Peary subspecies formed a distinct clade (F_{ST} = 0.07 with its nearest neighbour) in the phylogenetic tree; all other subspecies and ecotypes were interleaved (Fig. 2.1). The genetic distance between some adjacent deep-snow mountain caribou subpopulations was much larger than differences among ecotypes and even among subspecies (Fig. 2.1). For example, the genetic distance of the Purcell subpopulation to its neighbours < 250 km away (F_{ST} = 0.15) was greater than between some of the tundra/taiga herds that were separated by >1000 km (i.e., Peary to Qamanirjuaq F_{ST} = 0.07; Fig. 2.1). Even the directly adjacent deep-snow mountain subpopulations of Columbia North and Columbia South (5 km of separation, F_{ST} = 0.04) were more genetically distinct than large migratory herds separated by almost 1000 km (e.g. Qamanirjuaq vs. Dolphin & Union, F_{ST} = 0.02). Furthermore, the difference between Columbia North and Columbia South was of the same magnitude as differences between subspecies (e.g. Graham vs. Qamanirjuaq; F_{ST} =

0.04; Fig. 2.1). Similarly, the genetic distance between Wells Gray and Columbia North subpopulations, which live as close as 5 km apart, was large relative to differences among ecotypes and subspecies. Populations south of the North Thompson Valley were relatively distinct from those to the north ($F_{ST} \geq 0.04$, Appendix 2.2). The Peace River was also associated with population differentiation, regardless of whether caribou were separated by the portion flooded by the WAC Bennett Dam in British Columbia (shallow-snow mountain ecotype) or the undammed portion in Alberta (boreal ecotype).

The finer-scale analysis was restricted to woodland caribou, and program STRUCTURE suggested that the optimal number of clusters was five (Fig. 2.2), though some subpopulations were not well classified in any of these clusters, e.g. Jasper and South Selkirks. Four of 11 samples from the South Selkirks contained highly admixed individuals ($q<0.6$); this deep-snow subpopulation received transplants in the 1990s from the shallow-snow ecotype. The five clusters represented boreal caribou from north of the Peace River, boreal caribou from south of the Peace River, shallow-snow mountain caribou samples from north of the Peace River, the mix of shallow-snow and

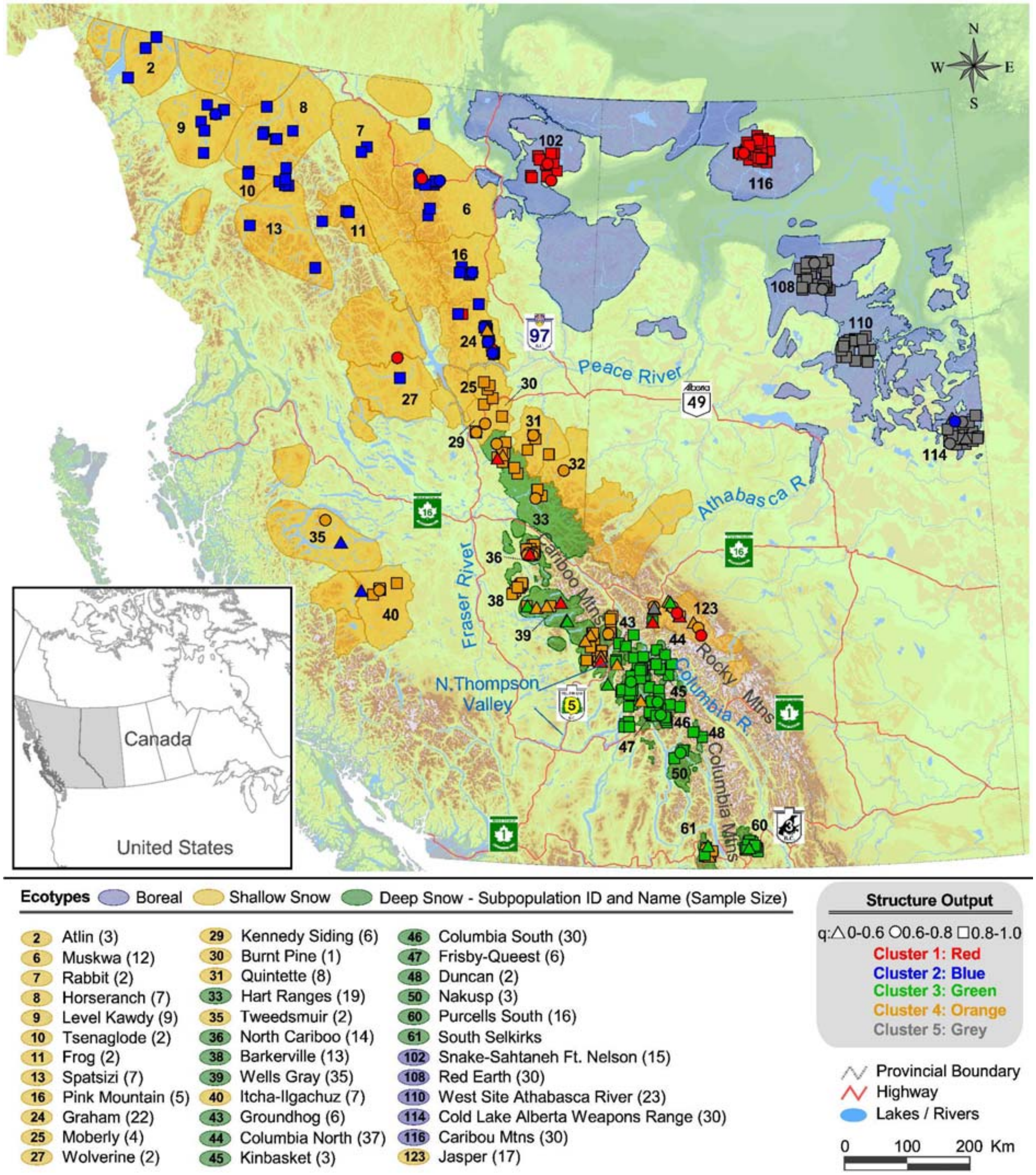


Figure 2.2. Genetic clusters of individual woodland caribou samples from British Columbia and Alberta using program STRUCTURE. Cluster membership is shown by colour, and classification uncertainty is shown by symbols. Also shown are a-priori defined ecotypes (colour-shaded polygons), and subpopulation names of woodland caribou. For reference, the FST value for cluster 2 vs. cluster 3 is 0.07 (see Appendix 2.3). Sample sizes are shown in brackets.

deep-snow mountain caribou between the Peace River and the North Thompson Valley, and the deep snow mountain caribou to the south of the North Thompson Valley (Fig. 2.2). The proportion of samples that were strongly assigned ($q > 80\%$) to their respective clusters was always ≥ 70% (70, 78, 92, 72, and 92% for Clusters 1 – 5, respectively). However, two of 15 runs provided a moderately different clustering pattern because iterations converged to a different (lower) local maximum on the likelihood surface. In these runs 3 clusters were unaffected, but boreal samples north of the Peace River in Alberta (Cluster 1) were lumped with shallow-snow mountain caribou samples from north of the Peace River in British Columbia, and samples from Wells Gray formed a distinct cluster (Appendix 2.3). Because these alternate outcomes occurred in <15% of the runs and produced lower likelihoods, I used average q-values from the runs that produced the more common pattern, as shown in Figure 2.2. The F_{ST} values for these clusters ranged from 0.09 between cluster 3 and 5, to 0.03 for between cluster 1 and 2 (Fig. 2.2 and Appendix 2.4). At this scale the boreal ecotype of woodland caribou was clearly separated into two clusters, on either side of the Peace River, consistent with the phylogenetic tree (Fig. 2.1). The shallow-snow mountain ecotype of woodland caribou was also separated into two clusters, again with an apparent break associated with the flooded portion of the Peace River in British Columbia. Samples from western British Columbia (the Itcha-Ilgatchuz and Tweedsmuir) more closely resembled the shallow-snow ecotype south of the Peace River. The Wells Gray deep-snow mountain subpopulation contained animals from both the southern and northern cluster. The main discontinuity in the deep-snow mountain caribou was the North Thompson Valley. A significant break appeared at this location, despite adjacent subpopulations having < 5 km of separation. F_{ST} values for all woodland subpopulations defined *a priori* are provided in Appendix 2.2.

Mantel analyses within woodland caribou revealed that the ecotype designation of deep-snow mountain was weak ($r^2=0.13$) but significant (Mantel r = -0.36, CI = -0.55 to -0.27; Table 2, Model 12). When corrected for geographic distance, the correlation was weaker than its independent effect (Mantel r = -0.26, Model 10), but the CIs between the two models overlapped. Neither the boreal nor shallow-snow ecotype designations of woodland caribou were significant (Mantel r overlapping 0, Models 6 and 7, r^2=0). When geographic distance was accounted for, the r^2 for these models (Table 2.2, Models 3 and 4) was similar to the r^2 for geographic distance alone (r^2 = 0.17), so boreal and shallow-snow ecotype designations did not add any explanatory power. The effect of the Fraser River Valley was almost identical to caribou classified as the deep-snow ecotype (Model 11), even though this valley transected the northern 20% of deep-snow caribou range (see Fig. 2.2). In contrast to the ecotype designations, the North Thompson Valley had the clearest influence on allele variation within all woodland caribou from sampled subpopulations. The Mantel correlation value (r) remained negative even when corrected for geographic distance, and the r^2 was 0.44, suggesting that a high proportion of allelic variation was explained by this valley. This valley splits the range of deep-snow caribou into northern and southern halves, although *c.* 80% of the current population of this ecotype live north of this valley. Finally, the Rocky Mountains were associated with population structure but the amount of variation explained was minimal (Table 2.2). The variance partitioning from the AMOVA suggested that 2.68% of the allelic variance was explained by the ecotype designations (F_{CT}) for woodland caribou. This value compared to 91.33 % for variance within subpopulations (F_{ST}), and 5.98% for among subpopulations but within ecotypes ($F_{SC;}$ all values significant at $p < 0.001$). With caribou grouped by landscape feature (south of the North Thompson, between the North Thompson and the Peace River, and N of the Peace River), 41% more variation was explained compared to ecotype grouping (F_{CT} = 3.80%).

Table 2.2. Factors affecting the genetic distance ($F_{ST}/(1-F_{ST})$) among woodland caribou subpopulations in BC and Alberta. Analyses were conducted using both Mantel and multiple regressions (Legendre et al. 1994). Mantel analyses are represented by the r-value (with 95% CIs), whereas Legendre et al.'s (1994) multiple regression was used to calculate r^2 (MR r^2). Asterisks denote significance of independent factors based on the multiple regression approach. The effect of caribou ecotype is contrasted with major landscape features (described in Table 2.1). For partial Mantel tests (e.g. when geographic distance was included as a covariate) the interpretation is the effect of 'X' while controlling for geographic distance.

No.	Model		Mantel r	Lcl[a]	Ucl[a]	MR r^2
1	Geo_dist**		0.41	0.29	0.53	0.17
2	Peace_riv*	Geo_dist**	0.27	0.18	0.33	0.23
3	Boreal_ecot	Geo_dist**	0.14	-0.02	0.25	0.18
4	Shallow_ecot	Geo_dist**	0.10	0.01	0.23	0.18
5	Peace_riv		-0.02	-0.16	0.06	0.00
6	Boreal_ecot		-0.03	-0.17	0.05	0.00
7	Shallow_ecot		-0.03	-0.20	0.08	0.00
8	Rockies**		-0.16	-0.32	-0.04	0.03
9	Fraser_riv*	Geo_dist*	-0.21	-0.48	-0.02	0.20
10	Deep_ecot**	Geo_dist**	-0.26	-0.48	-0.10	0.22
11	Fraser_riv**		-0.36	-0.53	-0.19	0.13
12	Deep_ecot**		-0.36	-0.55	-0.27	0.13
13	Nt_valley**	Geo_dist**	-0.57	-0.68	-0.48	0.44
14	Nt_valley**		-0.60	-0.71	-0.54	0.36

*p< 0.05, ** p <0.01

[a] Upper and lower 95% CIs (Ucl and Lcl)

Geo_dist, geographic distance; Peace_riv, the Peace River; Rockies, the Rocky Mountains; Nt_valley, the North Thompson Valley; Fraser_riv, Fraser River Valley; Deep_ecot, deep snow mountain ecotype; Shallow_ecot, shallow-snow mountain ecotype; Boreal_ecot, boreal ecotype

Effects of population size on differentiation

Using data from all subpopulations including the three subspecies and ecotypes, there was a negative exponential relationship between the harmonic mean abundance of adjacent pairs of subpopulations, and genetic distance (Fig. 2.3; r = 0.74, CIs 0.72 – 0.77). The outlier at the bottom left was from a population pair that van Oort et al. (2011) found was connected based on telemetry (Groundhog and Columbia North, i.e. updated data from Wittmer et al. 2005a), so excluding this data point would increase the r-value to 0.91. Population size (N) positively affected heterozygosity (Fig. 2.4), where H_E = 0.014 × ln(N) + 0.68, and the 95% CI of the slope was 0.010 – 0.023 (genetic diversity data by subpopulation are in Appendix 2.5).

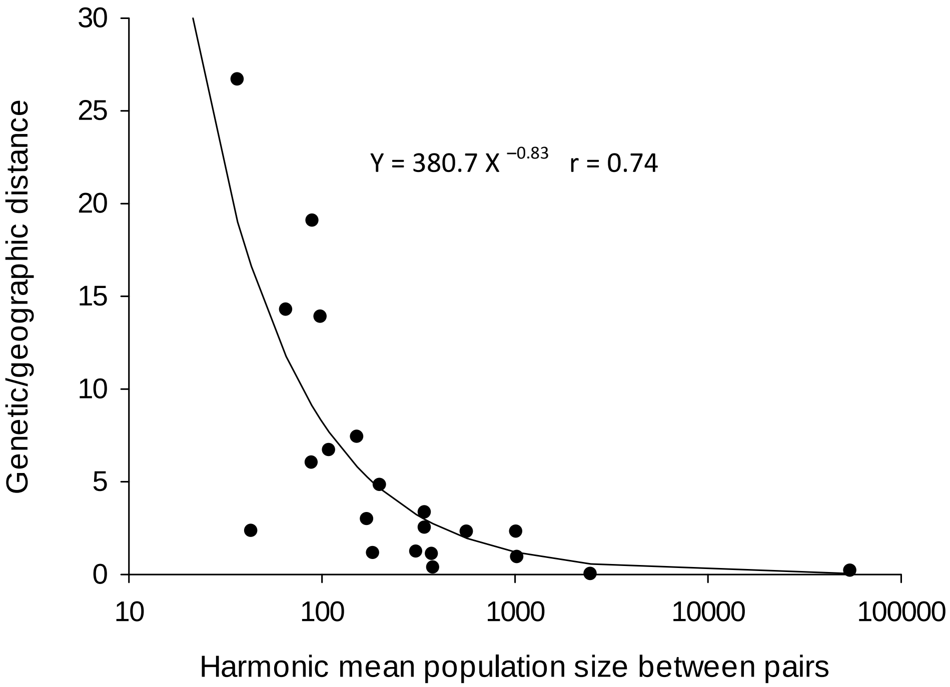


Figure 2.3. Genetic distance, adjusted for geographic distance, as a function of the harmonic mean population size between pairs of caribou subpopulations. Pairs of subpopulations were based on their nearest geographic neighbour from sampled populations in western Canada.

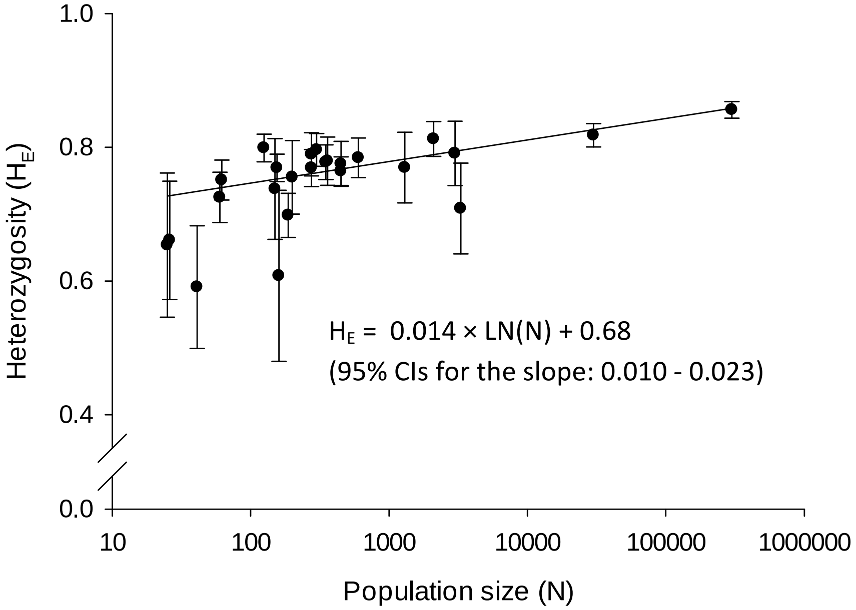


Figure 2.4. Expected heterozygosity (HE) as a function of population size for caribou in western Canada. Parameters were estimated using non-linear regression, weighted by the inverse of the HE variance. The subpopulations were bootstrapped (n = 1000) to estimate uncertainty. Error bars are 95% CI.

Genetic structuring and migrant estimation within deep-snow mountain caribou

Program STRUCTURE suggested six clusters within this ecotype of woodland caribou, with Jasper, a shallow-snow ecotype included as an outgroup, adding a seventh cluster (Fig. 2.5). Program STRUCTURE grouped the 10 separate subpopulations estimated by Wittmer et al. (2005a) using radio telemetry into six clusters. No meaningful genetic differentiation was detected between the Hart Ranges and the North Cariboo, nor among the Columbia North, Groundhog, Frisby-Queest, and Nakusp/Duncan subpopulations, but in the remaining cases the genetic analysis supported the population structure estimated by Wittmer et al. (2005a).

I again expressed the strength of each cluster as a proportion of individuals that were strongly ($q > 0.8$) assigned to their own cluster. Cluster 2 (Barkerville, 87%) was the strongest, followed by Cluster 3 (Jasper, 84%), whereas Cluster 4 (Columbia

North/Groundhog/Frisby-Queest/Nakusp, 42%) and Cluster 7 (Columbia South, 54%) had fewer individuals that were strongly assigned to their own cluster.

The structure within deep-snow caribou confirmed that the North Thompson Valley was a barrier to gene flow (Fig. 2.5). The post-hoc analysis was used to estimate the migration rate across and to the south of this valley (i.e. from the Wells Gray subpopulation), where caribou are declining more rapidly (Wittmer et al. 2005a). Out of 48 samples collected from subpopulations south of the North Thompson Valley (i.e., Groundhog, Columbia North, and Frisby-Queest), only one potential first-generation migrant originated from Wells Gray during this 17-year time span (1992 – 2008; p = 0.002, all other p > 0.50).

My analysis of the ecotone between deep and shallow-snow subpopulations revealed that the Graham subpopulation, north of the Peace River, was distinct from populations to the south. South of the Peace River, several subpopulations appear indistinguishable, and these include both deep (Hart Ranges, North Cariboo) and shallow-snow ecotypes (Kennedy, Quintette, Moberly). To the south of these, the Wells Gray subpopulation was distinct (Fig. 2.6).

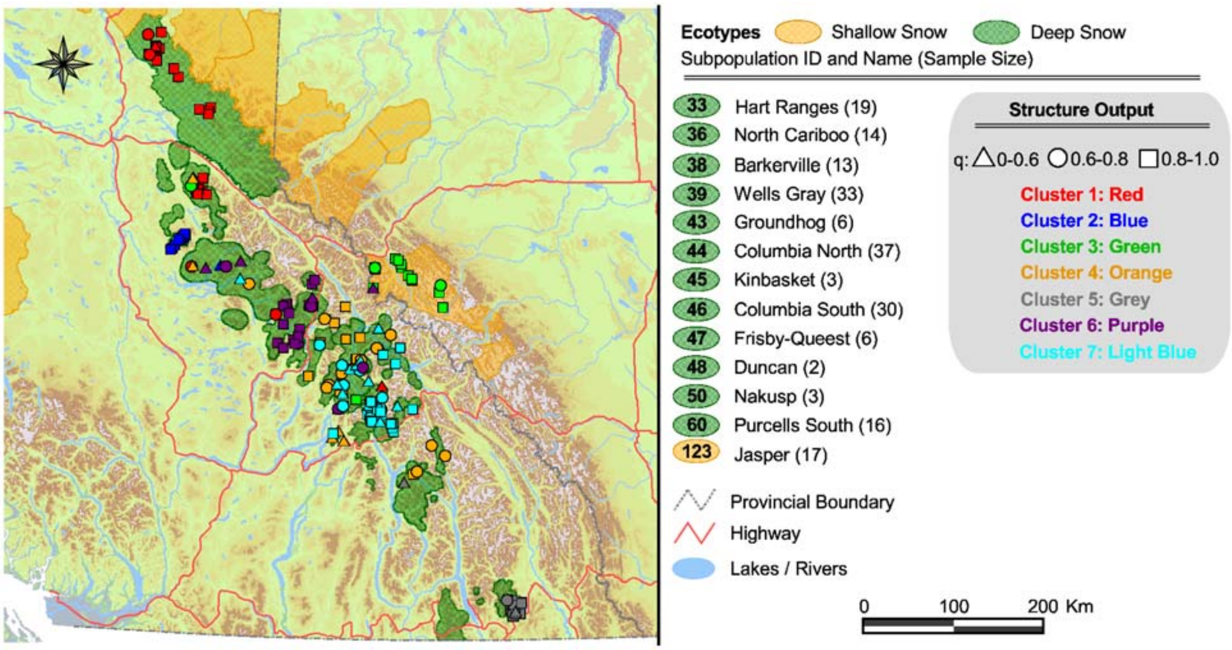


Figure 2.5. Genetic clusters of individual woodland caribou samples from the deep-snow ecotype, including one outgroup subpopulation from Jasper, AB. Program STRUCTURE

assuming no a-priori group membership. Cluster membership is shown by colour, and classification uncertainty is shown by symbols.

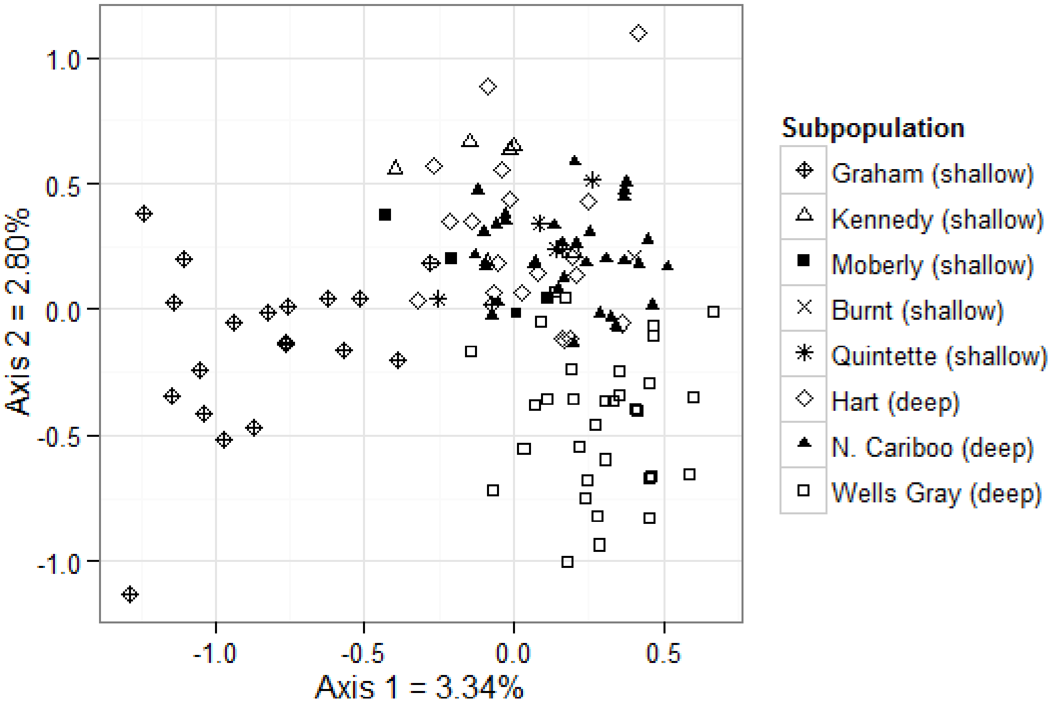


Figure 2.6. Ecotone between deep and shallow-snow mountain caribou. All subpopulations are on the edge of the deep and shallow-snow ecotypes (see Fig. 2.2 for population locations). The Peace River lies between the Graham subpopulation and those to the south.

DISCUSSION

There appears to be little support for ESU designation using current taxonomic definitions for caribou below the species level. With the exception of Peary caribou, branches within the phylogenetic tree did not correspond to existing taxonomic designations, as branch lengths among units were often shorter than lengths within units. This lack of pattern was most pronounced at the level of ecotype within the woodland subspecies, whereby genetic differentiation (F_{ST}) indicated less demographic isolation than expected for populations with independent evolutionary trajectories. Additional analyses suggested that landscape features and in particular major valleys explained variation better than ecotype designation. The AMOVA, Mantel, and multiple regression approaches all support this conclusion. Finally, a visual inspection of the STRUCTURE outputs (Fig. 2.2, Appendix 2.3) reveals breaks at two major valleys, and less so at ecotype boundaries.

Mitochondrial analyses of caribou DNA suggest two main lineages, northern and southern, roughly corresponding to the barren ground and woodland caribou subspecies (Cronin et al. 2005), and both lineages have been documented within subpopulations (Cronin et al. 2005, McDevitt et al. 2009). These lineages probably reflect refugia north and south of continental ice sheets present during the Pleistocene (Flagstad and Røed 2003). Although I sampled fewer subpopulations across subspecies relative to ecotype, Weckworth et al.'s (2012) recent analyses at the mtDNA and nDNA level support my findings that little differentiation occurs among some of the woodland and adjacent barren ground subpopulations. Furthermore, there is little evidence that ecotype designations within the woodland caribou subspecies evaluated herein are supported by mitochondrial analyses (McDevitt et al. 2009; Weckworth et al. 2012). Behavioural differences in foraging and seasonal migration patterns between ecotypes (Jones 2007) are likely too recently derived and genetically complex to be manifested through mtDNA, and may be rooted in phenotypic plasticity.

Population size and landscape features

In contrast to existing taxonomy, population size and specific landscape features were strongly associated with genetic variation among subpopulations. That population size had a non-linear influence on population structure is a predictable result based on the theory of genetic drift (Wright 1931). Although the relationship may vary among species due to possible differences between census and effective population sizes, there appears to be a threshold with caribou. Below a census population size of approximately 150 animals, the magnitude and variation of differentiation greatly increases between pairs of adjacent subpopulations. The fact that H_E was also affected by population size further suggests that drift was the mechanism that led to spatial structuring among neighbouring populations (and see Côté et al. 2002). These results demonstrate a genetic outcome of ecological factors affecting woodland caribou since at least the early 20th century (Seip 1992; Bergerud et al. 2008). Many subpopulations have and continue to decline from unsustainable predation because of apparent competition (Holt 1977) with moose (*Alces alces*) and deer (*Odocoileus* spp.) (Seip 1992). Continued declines are anticipated (Wittmer et al. 2010) because predator numbers are not linked to the abundance of caribou. The resulting small populations of caribou suffer more rapid genetic drift and populations become increasingly structured. Therefore, these results demonstrate a link between community-level ecological processes and genetic population structure within caribou.

It is well established that heterozygosity is affected by population size (Frankham 1996; Courtois et al. 2003). However, the effect of small population size on population structure is an important consideration, particularly when estimating the relevance of factors such as highways and valleys settled by people that are often highlighted in landscape genetic research (Manel et al. 2003). Including population size as an explanatory factor may have broad applicability in the field of landscape genetics, particularly when dealing with endangered species. This approach could explain variation that was unaccounted for and more importantly, unmask spurious correlations that may have been erroneously attributed to landscape-level factors. For example, if formerly contiguous populations contracted and became isolated due to overharvest, predation, or competition, a retrospective landscape analysis may conclude that landscape features such as human development caused the population fragmentation by reducing movement, when in reality the mechanism was simply reduced abundance and distribution (Gaston et al. 2000). Another consideration is that effects of population size on genetic distance are likely to be complicated by time, because the longer a population has been isolated, the greater the differentiation. Time at a given population phase was not accounted for in my analysis, yet the results seemed robust to this omission.

The effect of population size on genetic structuring helps contextualize other ecological factors affecting differentiation. Arguments of uniqueness are ubiquitous in the conservation literature and are often used to assign conservation priority to certain population units. Based on their unique behaviour among all Cervids of walking on top of the > 2 m snowpack to access a food source that is otherwise out of reach (Serrouya et al. 2007), deep-snow mountain caribou were an interesting candidate to determine if there was a genetic correlation with this foraging strategy as there is likely selective pressure on an ungulate living under such extreme conditions. These animals must respond not only to snowfall events outside the normal range for temperate ungulates, but also to snow texture and consolidation when deciding to migrate to high elevations in winter. Their limited dispersal behaviour and philopatry (van Oort et al. 2011), plus living in rugged mountains that may naturally fracture populations and restrict gene flow, provided intuitive support for taxonomic distinction. Yet, my results suggest that deep-snow mountain caribou as a group were not genetically unique, particularly when geographic distance and landscape features are accounted for. The southern-most subpopulations such as the Purcells did stand out as unique (*sensu* Zittlau 2004), but this is likely due to their very small population size and consequent rapid drift.

Two major river valleys were associated with genetic discontinuities. The effect of the North Thompson Valley was reflected across a variety of spatial scales and analyses. The Peace River was also associated with differentiation, similar to what McLoughlin et al. (2004) documented. Population fractures at major valleys is likely a result of these caribou generally preferring higher elevations (Apps et al. 2001) for foraging as well as avoiding predation at lower elevations where deer, moose, and their predators are more abundant (Stotyn 2008).

Historic vs. contemporary movement: demographic rescue within the deep-snow ecotype

Although there was little support for taxonomic subdivision in our dataset, results suggest isolation of many subpopulations. By using an assignment test to directly identify putative migrants and validate contemporary telemetry information with longer-term measures of gene flow estimated by indirect methods, deep-snow caribou exhibit structure consistent with little movement among subpopulations. These subpopulations can therefore be considered separate management units as defined by

Palsbøll et al. (2007). Furthermore, this structure suggests that fragmentation preceded telemetry studies which began in the early 1990s.

While direct and indirect genetic methods can be used to show relative demographic independence, a lack of genetic differentiation cannot be interpreted as proof of demographic integration. For example, the subpopulations of Frisby-Queest and Columbia North appear genetically similar, but van Oort et al. (2011) documented no interchange of individuals, despite intensive sampling (over time, > 40% of the standing population size had been radio-tagged). A telemetry data set from the early 1980s, however, found 4 of 9 collared animals moved between these two subpopulations (unpublished data from Simpson and Woods 1987). Therefore, the lack of genetic differentiation probably reflects a time lag resulting from a contemporary barrier to gene flow (van Oort et al. 2011). This contrast between genetic data and telemetry based movement is consistent with comparatively recent fragmentation. In a second case, at the ecotone between deep and shallow-snow caribou, several populations of both ecotypes appear genetically indistinguishable. In this area Jones (2007) found that individual caribou exhibited both foraging strategies (terrestrial and arboreal) depending upon local and annual snow conditions, suggesting a degree of plasticity in foraging behaviour.

The population structuring among deep-snow mountain subpopulations has immediate implications for conservation. The genetic structuring, radio-tagged dispersal estimates (van Oort et al. 2011) and the assignment test all suggest insufficient movement to provide demographic rescue. From 1992 to 2008, 48 caribou adjacent to but south of the North Thompson Valley were sampled, yet only one potential immigrant was identified across this barrier from the large population (Wells Gray) immediately north of this valley, for an immigration rate of 2.1%. During the same time period, the populations south of the North Thompson Valley declined from 272 to 170 (Wittmer et al. 2005a; McLellan and Serrouya unpubl. data). Therefore, the immigration rate estimated from the assignment test is approximately 1/17th the level needed to provide sufficient movement to stabilize the smaller populations directly south of this barrier. Our genetic results support van Oort et al. (2011) in concluding that deep-snow mountain caribou are in a non-equilibrium metapopulation and narrow the range of management options to transplants and addressing the proximate cause of unsustainable predation (Wittmer et al. 2005b). A risk with transplants is that any undetected adaptation to deep-snow conditions would be jeopardized, however, this argument is academic when faced with the imminent extinction of many subpopulations (Serrouya and Wittmer 2010; Wittmer et al. 2010). While the specific fitness consequences are unknown, a previous transplant to the deep-snow ecotype (South Selkirks) appeared to stabilize a population decline (Warren et al. 1996), with alleles from the shallow-snow ecotype apparently persisting in subsequent generations (Fig. 2.2, Appendix 2.3).

In conclusion, neutral genetic data from microsatellite markers suggest that two of three subspecies, and all three ecotypes of the woodland subspecies, lack the cohesion and uniqueness of ‘evolutionarily significant’ groups, suggesting that current classifications are inappropriate. By contrast, there was support in the genetic data for the demographic independence of many of the deep-snow mountain subpopulations that were originally defined using radio telemetry data, confirming that it is appropriate to treat these groups as demographically independent for management purposes. Finally, moving beyond the caribou perspective, samples covered a large range of population sizes, revealing the importance of population size in explaining the degree of differentiation among subpopulations. This finding may be of broad interest to landscape genetic studies seeking to understand population structure of endangered species in particular.

LITERATURE CITED

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.

Banfield, A.W.F. 1961. A revision of the reindeer and caribou, genus *Rangifer*. National Museum of Canada Bulletin **177**: 1–137.

Belkhir, K., P. Borsa, L. Chikhi, N. Raufaste and F. Bonhomme. 1996-2004. GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France).

Bergerud, A. T., S. N. Luttich, and L. Camps. 2008. The return of caribou to Ungava. McGill-Queen's University Press, Montreal.

Buchanan F.C., and A.M Crawford. 1993. Ovine microsatellites at the OarFCB11, OarFCB128, OarFCB193, OarFCB266 and OarFCB304 loci. Animal Genetics **24**:145.

Bishop, M. D., S. M. Kappes, J. W. Keele, R. T. Stone, S. L. F. Sunden, G. A. Hawkins, S. S. Toldo, R. Fries, M. D. Grosz, J. Y. Yoo, and C. W. Beattie. 1994. A genetic-linkage map for cattle. Genetics **136**:619-639.

Boulet, M., S. Couturier, S. D. Côté, R. D. Otto, and L. Bernatchez. 2007. Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. Molecular Ecology **16**:4223-4240.

Côté, S. D., J. F. Dallas, F. Marshall, R. J. Irvine, R. Langvatn, and S. D. Albon. 2002. Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. Molecular Ecology **11**:1923-1930.

Courtois, R., L. Bernatchez, J. P. Ouellet, and L. Breton. 2003. Significance of caribou (*Rangifer tarandus*) ecotypes from a molecular genetics viewpoint. Conservation Genetics **4**:393-404.

Crandall, K. A., O. R. P. Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology & Evolution **15**:290-295.

Cronin, M. R. A., M. D. MacNeil, and J. C. Patton. 2005. Variation in mitochondrial DNA and microsatellite DNA in caribou (*Rangifer tarandus*) in North America. Journal of Mammalogy **86**:495-505.

Edwards, R.Y., J. Soos, and R.W. Ritcey. 1960. Quantitative observations on epidendric lichens used as food by caribou. Ecology **41**, 425-431.

Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechnie, and L. E. Gilbert. 1975. Checkerspot butterflies - historical perspective. Science **188**:221-228.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology **14**:2611-2620.

Excoffier L., G. Laval, and S. Schneider. 2005. Arlequin ver. 3.0: an integrated software package for population genetic data analysis. Evolutionary Bioinformatics Online. **1:** 2611–2620.

Felsenstein, J. 2005. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by the author. Department of Genome Sciences, University of Washington, Seattle.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. Cote, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Canadian Journal of Zoology **89**:419-434.

Fitch, W.M., and E. Margoliash. 1967. Construction of phylogenetic trees. Science **155:** 279–284.

Flagstad, Ø, and K. H. Røed. 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. Evolution **57**:658-670.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology **10**:1500-1508.

Fraser, D. J. and L. Bernatchez. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology **10**:2741-2752.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. Journal of Applied Ecology **37**:39-59.

Green, D. M. 2005. Designatable units for status assessment of endangered species.

Conservation Biology **19**:1813-1820.

Goslee, S.C., and D.L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software **22**, 1-19.

Hartl, D.L., and A.G. Clark. 2007. Principles of population genetics, fourth ed. Sinauer Associates, Sunderland.

Heard, D. C. and K. L. Vagt. 1998. Caribou in British Columbia: a 1996 status report. Rangifer **18**:117-123.

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

Jones, E. S. 2007. Use, selection, and winter foraging patterns among woodland caribou herds in central British Columbia. M.Sc. Thesis, University of Northern British Columbia.

Jones, K. C., K. F. Levine, and J. D. Banks. 2000. DNA-based genetic markers in black-tailed and mule deer for forensic applications. California Fish and Game **86**:115-126.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and Genetic Structure of a Recovering Grizzly Bear Population. Journal of Wildlife Management **73**:3-17.

Legendre, P., F. J. Lapointe, and P. Casgrain. 1994. Modeling brain evolution from behavior - a permutational regression approach. Evolution **48**:1487-1499.

McDevitt, A. D., S. Mariani, M. Hebblewhite, N. J. DeCesare , L. Morgantini, D. Seip, B. V. Weckworth, and M. Musiani. 2009. Survival in the Rockies of an endangered hybrid swarm from diverged caribou (*Rangifer tarandus*) lineages. Molecular Ecology **18**:665-679.

McLoughlin, P. D., D. Paetkau, M. Duda, and S. Boutin. 2004. Genetic diversity and relatedness of boreal caribou populations in western Canada. Biological Conservation **118**:593-598.

Manel, S., M.K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology &

Evolution **18:**189-197.

Moore, S. S., W. Barendse, K. T. Berger, S. M. Armitage, and D. J. S. Hetzel. 1992. Bovine and Ovine DNA microsatellites from the Embl and Genbank databases. Animal Genetics **23**:463-467.

Moritz, C. 1994. Defining evolutionarily-significant-units for conservation. Trends in Ecology & Evolution **9**:373-375.

Paetkau, D. 1999. Using genetics to identify intraspecific conservation units: a critique of current methods. Conservation Biology **13**:1507-1509.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. Molecular Ecology **12**:1375-1387.

Paetkau, D., R. Slade, M. Burden, and A. Estoup. 2004. Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Molecular Ecology **13**:55-65.

Palsbøll, P. J., M. Bérubé, and F. W. Allendorf. 2007. Identification of management units using population genetic data. Trends in Ecology & Evolution **22**:11-16.

Piry, S., A. Alapetite, J. M. Cornuet, D. Paetkau, L. Baudouin, and A. Estoup. 2004. GENECLASS2: A software for genetic assignment and first-generation migrant detection. Journal of Heredity **95**:536-539.

Poole, K. G., D. M. Reynolds, G. Mowat, and D. Paetkau. 2011. Estimating Mountain Goat Abundance Using DNA From Fecal Pellets. Journal of Wildlife Management **75**:1527-1534.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics **155**:945-959.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raymond, M. and F. Rousset. 1995. GENEPOP (VERSION-1.2) - Population-genetics software for exact tests and ecumenicism. Journal of Heredity **86**:248-249.

Røed, K. H. and L. Midthjell. 1998. Microsatellites in reindeer, *Rangifer tarandus*, and their use in other cervids. Molecular Ecology **7**:1773-1776.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics **145**:1219-1228.

Ryder, O. A. 1986. Species conservation and systematics - the dilemma of subspecies. Trends in Ecology & Evolution **1**:9-10.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Biodiversity - Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Schneider, R. R., G. Hauer, W. L. Adamowicz, and S. Boutin. 2010. Triage for conserving populations of threatened species: The case of woodland caribou in Alberta. Biological Conservation **143**:1603-1611.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Seip D.R., and B.N. McLellan. 2008. Mountain caribou. *In*: Caribou and the North: A Shared Future (eds M. Hummel and J. Ray), pp. 240–255. Dundurn Press, Toronto, Ontario.

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 H. U. Wittmer. 2010. Imminent Extinctions of Woodland Caribou from National Parks. Conservation Biology **24**:363-364.

Slatkin, M. 1987. Gene flow and the geographic structure of natural-populations. Science **236**:787-792.

Stone, R. T., J. C. Pulido, G. M. Duyk, S. M. Kappes, J. W. Keele, and C. W. Beattie. 1995. A small-insert Bovine genomic library highly enriched for microsatellite repeat sequences. Mammalian Genome **6**:714-724.

Stotyn, S. 2008. Ecological interactions of mountain caribou, wolves and moose in the north Columbia Mountains, British Columbia. University of Alberta, Edmonton.

Taberlet, P., S. Griffin, B. Goossens, S. Questiau, V. Manceau, N. Escaravage, L. P. Waits, and J. Bouvet. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research **24**:3189-3194.

Turesson, G. 1922. The genotypical response of the plant species to the habitat. Hereditas **3**:211-350.

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.

Warren, C. D., J. M. Peek, G. L. Servheen, and P. Zager. 1996. Habitat use and movements of two ecotypes of translocated caribou in Idaho and British Columbia. Conservation Biology **10**:547-553.

Weckworth, B. V., M. Musiani, A. D. McDevitt, M. Hebblewhite, and S. Mariani. 2012. Reconstruction of caribou evolutionary history in Western North America and its implications for conservation. Molecular Ecology **21**:3610-3624.

Wilson G.A., C. Strobeck, L. Wu, and J.W. Coffin. 1997. Characterization of microsatellite loci in caribou *Rangifer tarandus*, and their use in other Artiodactyls. Molecular Ecology **6:** 697-699.

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, G. S. Watts, and D. Hamilton. 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. R. E. Sinclair, and B. N. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16**: 97-159.

Zittlau, K.A. 2004. Population genetic analyses of North American caribou (*Rangifer tarandus*). PhD Thesis, University of Alberta, Canada.

APPENDIX 2.1. MATRIX OF GEOGRAPHICALLY ADJUSTED GENETIC DISTANCE ($F_{ST}/(1-F_{ST})$) CORRESPONDING TO SUBPOPULATIONS SHOWN IN FIGURE 2.1. TOP 5% OF VALUES ARE HIGHLIGHTED IN RED.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1- Caribou Mts, AB																	
2- Cold Lake	1.2																
3- Columbia North	1.2	1.7															
4- Columbia South	1.1	1.9	**5.8**														
5- Hart	1.0	0.7	1.7	1.7													
6- Ft. Nelson	0.8	0.6	1.1	1.2	0.9												
7- Graham	1.1	0.6	1.5	1.6	1.7	1.1											
8- Jasper	1.2	1.3	**7.4**	**5.6**	1.5	1.1	1.5										
9- N. Cariboo	0.8	0.7	2.1	2.3	0.7	0.8	1.2	1.9									
10- Purcell	1.7	3.1	**3.6**	**7.8**	2.7	1.9	2.2	**5.8**	2.5								
11- Red Earth	**4.0**	0.5	1.9	1.7	1.1	1.4	1.4	1.4	0.9	2.6							
12-Kennedy/Quintette	1.1	0.8	1.6	1.6	1.1	1.0	2.9	1.6	0.5	2.4	1.3						
13- Wells Gray	0.9	1.1	2.8	3.2	1.6	0.8	1.3	**4.8**	2.5	3.7	1.4	1.1					
14- WSAR	2.2	1.2	2.0	2.0	1.0	1.1	1.0	1.8	0.9	3.0	1.2	1.0	1.5				
15- Qamanirjuaq	0.5	0.3	0.4	0.4	0.3	0.3	0.2	0.4	0.2	0.9	0.5	0.2	0.3	0.4			
16- Dolphin & Union	0.5	0.3	0.4	0.5	0.4	0.4	0.3	0.5	0.3	0.7	0.5	0.3	0.4	0.5	0.2		
17- Southampton	1.3	1.0	1.0	0.9	0.9	1.1	1.0	1.0	0.9	1.5	1.1	1.0	1.0	1.1	2.3	1.3	
18- Peary	0.7	0.6	0.7	0.7	0.6	0.7	0.6	0.8	0.5	0.9	0.8	0.6	0.6	0.7	0.5	1.1	2.1

APPENDIX 2.2. F_{ST} VALUES (BELOW DIAGONAL, P-VALUES ABOVE DIAGONAL) FOR PAIRS OF SUBPOPULATIONS EXAMINED WITHIN WOODLAND CARIBOU.

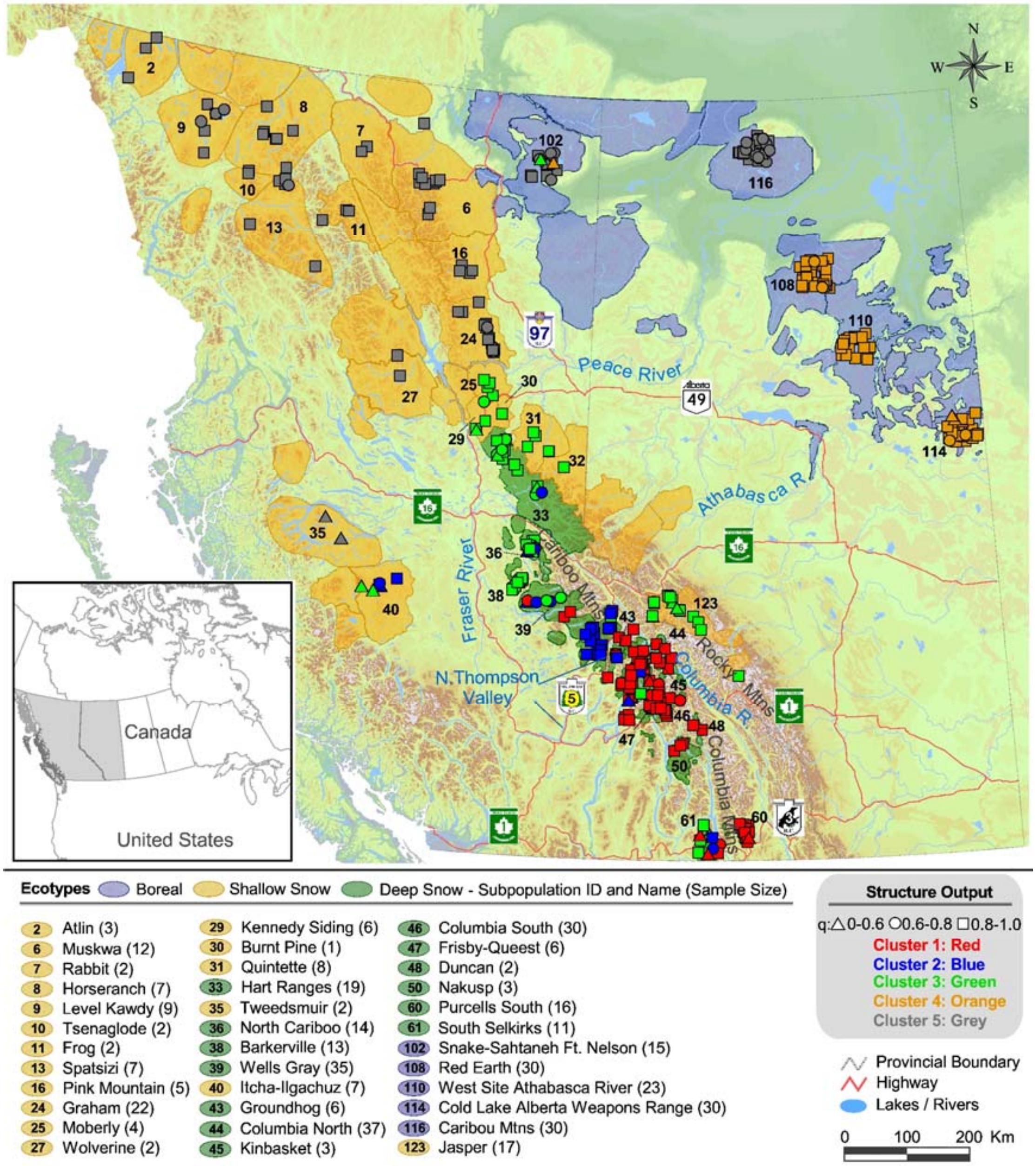
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 – Groundhog		0.000	0.000	0.000	0.000	0.145	0.003	0.000	0.000	0.072	0.000	0.000	0.000	0.002	0.000
2 – Wells Gray	0.062		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3 – N. Cariboo	0.068	0.022		0.273	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.077	0.540
4 – Hart	0.084	0.041	0.004		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.325
5 – Columbia South	0.063	0.061	0.063	0.071		0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
6 – Columbia North	0.010	0.041	0.049	0.058	0.039		0.000	0.000	0.000	0.086	0.000	0.000	0.000	0.000	0.000
7 – Central Selkirk_Dunca	0.131	0.081	0.092	0.116	0.101	0.089		0.000	0.000	0.002	0.000	0.001	0.000	0.002	0.001
8 – Purcell	0.126	0.136	0.134	0.154	0.152	0.098	0.163		0.000	0.000	0.000	0.000	0.000	0.000	0.000
9 – Barkerville	0.104	0.088	0.061	0.078	0.103	0.088	0.168	0.191		0.000	0.000	0.000	0.000	0.000	0.000
10 – Frisby	0.026	0.073	0.076	0.070	0.041	0.014	0.131	0.138	0.108		0.000	0.000	0.000	0.003	0.000
11 – Jasper	0.097	0.074	0.044	0.047	0.081	0.068	0.122	0.178	0.106	0.082		0.000	0.000	0.000	0.000
12 – Tweedsmuir_Itchas	0.108	0.064	0.054	0.063	0.121	0.082	0.109	0.163	0.113	0.126	0.104		0.000	0.003	0.002
13 – Graham	0.107	0.059	0.036	0.035	0.092	0.079	0.123	0.162	0.088	0.107	0.073	0.070		0.000	0.000
14 – Kennedy	0.116	0.066	0.016	0.029	0.093	0.091	0.143	0.200	0.097	0.108	0.070	0.080	0.060		0.015
15 – Quintette	0.082	0.038	0.002	0.005	0.078	0.060	0.106	0.148	0.050	0.086	0.056	0.053	0.036	0.027	
16 – Ft. Nelson	0.124	0.060	0.047	0.042	0.094	0.086	0.131	0.174	0.103	0.112	0.074	0.097	0.033	0.073	0.037
17 – Caribou Mtns, AB	0.114	0.065	0.054	0.057	0.087	0.086	0.136	0.148	0.111	0.104	0.076	0.102	0.048	0.085	0.052
18 – Red Earth	0.151	0.083	0.054	0.053	0.105	0.108	0.157	0.178	0.120	0.137	0.071	0.119	0.063	0.085	0.055
19 – WSAR	0.132	0.082	0.052	0.057	0.107	0.104	0.152	0.177	0.114	0.124	0.080	0.114	0.060	0.068	0.054
20 – Cold Lake, AB	0.128	0.071	0.045	0.049	0.104	0.095	0.144	0.171	0.113	0.120	0.065	0.106	0.047	0.066	0.058
21 – Horseranch_Level	0.110	0.073	0.051	0.066	0.097	0.086	0.121	0.166	0.108	0.106	0.083	0.084	0.046	0.067	0.056
22 – Muskwa	0.115	0.078	0.053	0.059	0.110	0.094	0.142	0.176	0.109	0.114	0.089	0.084	0.038	0.080	0.054
23– Pink Mountain	0.128	0.081	0.063	0.059	0.120	0.102	0.154	0.200	0.116	0.147	0.079	0.088	0.026	0.091	0.051
24 – Spatsizi_Tsenglode	0.102	0.072	0.043	0.056	0.101	0.081	0.115	0.180	0.114	0.102	0.083	0.075	0.042	0.061	0.056

APPENDIX 2.2 Continued

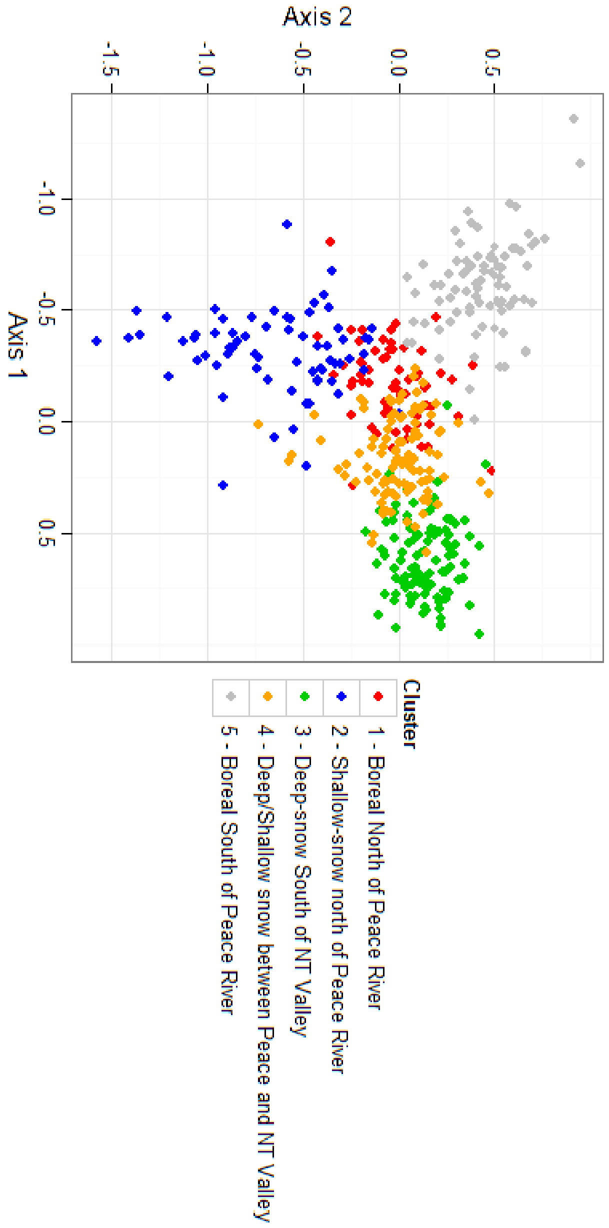
Population	17	18	19	20	21	22	23	24
1 – Groundhog	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000
2 – Wells Gray	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3 – N. Cariboo	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4 – Hart	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5 – Columbia South	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6 – Columbia North	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
7 – Central Selkirk_Dunca	0.000	0.000	0.000	0.000	0.000	0.001	0.009	0.001
8 – Purcell	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9 – Barkerville	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
10 – Frisby	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000
11 – Jasper	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
12 – Tweedsmuir_Itchas	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
13 – Graham	0.000	0.000	0.000	0.000	0.000	0.000	0.018	0.000
14 – Kennedy	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.001
15 – Quintette	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000
16 – Ft. Nelson	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000
17 – Caribou Mtns, AB		0.000	0.000	0.000	0.000	0.000	0.000	0.000
18 – Red Earth	0.055		0.000	0.000	0.000	0.000	0.000	0.000
19 – WSAR	0.071	0.021		0.000	0.000	0.000	0.000	0.000
20 – Cold Lake, AB	0.060	0.020	0.024		0.000	0.000	0.000	0.000
21 – Horseranch_Level	0.072	0.075	0.060	0.055		0.000	0.000	0.558
22 – Muskwa	0.049	0.080	0.080	0.062	0.036		0.156	0.001
23– Pink Mountain	0.040	0.068	0.067	0.044	0.046	0.013		0.001
24 – Spatsizi_Tsenglode	0.070	0.078	0.061	0.055	0.000	0.033	0.042	

APPENDIX 2.3. GENETIC CLUSTERS OF INDIVIDUAL WOODLAND CARIBOU SAMPLES FROM BRITISH COLUMBIA AND ALBERTA USING PROGRAM STRUCTURE.

This image shows the alternate clustering pattern that occurred in <15% of the STRUCTURE runs. Dominant runs are shown in Figure 2.2. Cluster membership is shown by colour, and classification uncertainty is shown by symbols. Also shown are a-priori defined ecotypes (colour-shaded polygons), and subpopulation names of woodland caribou. Sample sizes are shown in brackets.



APPENDIX 2.4. FACTORIAL CORRESPONDENCE ANALYSIS REPRESENTING THE RESULTS FROM PROGRAM STRUCTURE AT THE SCALE OF WOODLAND CARIBOU IN BRITISH COLUMBIA AND ALBERTA, CANADA



Factorial Correspondence Analysis using the program Genetix (Belkhir 1999) representing the results from program STRUCTURE at the scale of woodland caribou in British Columbia and Alberta, Canada. For reference, the F_{ST} value for cluster 2 vs. cluster 3 is 0.068, for cluster 3 vs. cluster 5 is 0.087, and for cluster 3 vs. cluster 4 is 0.039.

APPENDIX 2.5. EXPECTED HETEROZYGOSITY (H_E; STANDARD DEVIATION; SD) AND MEAN ALLELES PER LOCUS (APL) FOR SUBPOPULATIONS USED IN ANALYSIS OF POPULATION SIZE (FIGURES 2.3 AND 2.4).

Subpopulation	Population size	H_E	SD	APL	n (sample size)
Groundhog	25	0.65	0.13	4.4	6
Frisby_Queest	26	0.66	0.11	4.3	6
Purcell	41	0.59	0.19	4.8	16
Barkerville	60	0.73	0.07	5.4	13
Columbia South	62	0.75	0.08	7.1	30
CLAWR	125	0.79	0.06	8.3	30
Jasper	150	0.74	0.07	6.5	17
Kennedy	150	0.74	0.09	5.6	6
Columbia North Central	155	0.77	0.06	8.2	37
Selkirk_Duncan	160	0.61	0.15	4.0	5
Peary (Bathurst)	187	0.70	0.08	5.3	20
Quintette	200	0.76	0.08	6.3	8
N. Cariboo Mtn	275	0.79	0.06	7.6	14
Red Earth	275	0.77	0.08	8.6	30
Graham	300	0.80	0.06	8.5	22
WSAR	350	0.78	0.06	7.2	23
Ft. Nelson	360	0.78	0.07	7.7	15
Wells Gray	450	0.76	0.06	8.2	33
Caribou Mts Alberta	450	0.78	0.09	9.3	30
Hart	600	0.78	0.07	8.5	19
Muskwa	1300	0.77	0.09	7.4	12
Horseranch_Level Kawdy	2100	0.81	0.05	8.8	16
Spatsizi_Tsenglode	3000	0.79	0.07	7.3	7
Itchas Ilgatchus	3300	0.71	0.10	5.3	9
Dolphin & Union	30000	0.82	0.06	10.0	43
Qamanirjuaq	300000	0.86	0.05	14.1	52

CHAPTER 3

DEVELOPING A POPULATION TARGET FOR AN OVERABUNDANT UNGULATE FOR ECOSYSTEM RESTORATION[2]

Restoring ecosystems after broad-scale alteration by humans poses a tremendous challenge to scientists and managers seeking to retain components of community composition and structure (Dobson and Bradshaw 1997). When forested ecosystems with rare natural disturbance (e.g. rainforests) are harvested, it can take centuries for succession to achieve former levels of structure and biomass (Franklin et al. 2002). Yet, ecosystem restoration has typically focussed on re-establishing vegetation with the assumption that processes at higher trophic levels will follow. This approach is critical for the long-term restoration of ecosystems but may not prevent extinctions in the short term. Interim action at higher trophic levels may be necessary to maintain key processes and species until conditions at lower trophic levels recover.

Temperate forested ecosystems with high precipitation (> 100 cm/yr) produce climax stands of large, old trees. These ecosystems are highly productive (Meidinger and Pojar 1991) and there is a substantial shift in structure when they are logged, as forests with closed canopies and little understorey are replaced by openings with dense shrubs. Consequently, harvested landscapes gain organisms that thrive in early-seral conditions but lose those adapted to late-successional forests. One such ecosystem is the inland temperate rainforest found from Idaho, USA, to central British Columbia (BC), Canada.

The mammal of greatest conservation concern in this system is the mountain caribou (*Rangifer tarandus caribou*), which is an endangered ecotype of woodland caribou. Their numbers have been declining for many decades and were recently found in 18 subpopulations; six have < 20 animals and two are now extinct (Wittmer et al. 2005a). Currently, the proximate cause of their decline appears to be apparent

---

[2] A version of this chapter has been published as: Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. Journal of Applied Ecology **48**:935-942.

competition (Holt 1977) with other ungulate species (Seip 1992, Wittmer et al. 2005b). When shrubs become abundant after forest harvesting, moose (*Alces alces*) and deer (*Odocoileus* spp.) increase in number (Rempel et al. 1997, Latham et al. 2011). Wolves (*Canis lupus*) are strongly dependent on ungulate biomass (Fuller et al. 2003) so their numbers correspondingly increase. Because caribou have lower fecundity than other ungulates (Shackleton 1999), the incidental predation on caribou can cause population decline without influencing predator abundance since they depend on other prey species (Seip 1992, Wittmer et al. 2005b). This apparent competition mechanism is consistent with many woodland caribou population declines across North America (Bergerud and Elliot 1986, Schaefer 2003, James et al. 2004, Courtois et al. 2007), as well as other species in other ecosystems (Norbury 2001, Courchamp et al. 2003, DeCesare et al. 2010).

Given that most caribou populations will continue to decline or go extinct before old growth forests are restored (Serrouya and Wittmer 2010, Wittmer et al. 2010), maintaining caribou over the short term is reliant on managing at higher trophic levels where there are two plausible recovery options (Seip 2008). The first option is to directly reduce predators until their primary prey (non-caribou ungulates) decline as existing early seral habitats transition to older forests that have few preferred shrub species. The second option is to reduce primary prey by sport hunting to indirectly reduce predator abundance. Although predator reductions positively affect caribou recruitment and in some cases abundance (Bergerud and Elliot 1986, Orians et al. 1997, Hayes et al. 2003), predators quickly recover once control has stopped, and predator control is much less acceptable to the public than it once was (Orians et al. 1997, but see Boertje et al. 2010). Given the social and ecological constraints, the best solution may be to reduce both predators and primary prey concurrently (Courchamp et al. 2003). A critical management question is to what level should these populations be reduced? Eliminating predators and primary prey to allow recovery of mountain caribou is one extreme but is not socially acceptable (Orians et al. 1997). An alternative target would be to reduce primary prey and predators to the number expected before alteration of the system by human activities.

My objective was to estimate the number of moose that would have occurred in an ecosystem prior to it being heavily modified by forest harvesting. This estimate could be used to set targets for both moose and wolf abundance so a more natural predator-prey system can be re-established, helping maintain caribou populations until the vegetation recovers to a state where moose forage is less abundant. My ultimate hypothesis was that these targets would be compatible with caribou persistence because they are more likely to represent historic conditions in this rainforest ecosystem.

METHODS

Study area

The study was located in BC, Canada, near the city of Revelstoke (51° 32’, -118° 31’). The Monashee Mountains to the west and the Selkirk Mountains to the east attain heights of ≈ 3400 m. Between these mountains at 600 m is the Revelstoke Reservoir, a portion of the Columbia River that was dammed in 1983, flooding 114 km^2 of low-elevation forest. The overall study area was 6368 km^2 and includes Revelstoke National Park (Appendix 3.1). Average annual valley-bottom snowfall was 396 cm (n = 100 yr, SD = 120), and 1,427 cm (n = 39 yr, SD = 263, Parks Canada files) at 1,875 m (i.e. caribou late-winter habitat; Apps et al*.* 2001). Total precipitation is 200 cm/yr, and plant communities were described by Apps et al*.* (2001). Deep snow restricted the winter range of moose to 1,050 km^2 at low elevations, but in summer moose dispersed to higher elevations, covering about three times the area (R. Serrouya, unpublished telemetry data). Mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), mountain goat (*Oreamnos americanus*) and mountain caribou are present at low densities, and carnivores include wolves, a few cougars (*Puma concolor* ; n<6, van Oort et al. 2010), and bears (*Ursus americanus* and *U. Arctos*), which are more common. Beginning in 2003, moose numbers were reduced using sport hunting to increase hunting opportunity and to reduce apparent competition with caribou, although no population target was developed.

Four of 16 remaining subpopulations of mountain caribou are in the study area. From 1994 to 2009, these subpopulations declined from 117 (105–130; 90% CI) to 10 (Columbia South), 232 (203–272) to 142 (142–200; Columbia North), 34 (27–47) to 12 (Frisby-Boulder), and 17 to 3 (Central Rockies) (Wittmer et al*.* 2005a, McLellan et al. 2008).

During the study, the vegetation within the harvestable forest (areas outside parks and economically viable to log) consisted of 46% primary (> 250 year-old) forest, 33% regenerating cutblocks, 6% "mid seral" (30-80 years old), and 6% was 140 to 250 year-old forest. The remaining 9% included natural openings such as avalanche paths and marshes. Additionally, forests that contain old trees but are uneconomical to harvest covered 35% of the study area. Above these forests are alpine areas, glaciers and rocky peaks that cover 27% of the study area. As a result of legally-binding land-use plans, 67% of the remaining old harvestable forest is protected for mountain caribou, which corresponds to 48,000 ha in the study area (RHLPO 2005).

Analysis

My analyses were based on creating a habitat-based population estimate for moose (Boyce and McDonald 1999). I used 1994 to 2010 moose censuses using stratified-random block (SRB) surveys and pellet transects to estimate the abundance of moose under current, human-altered landscapes (see Appendix 3.1 for detailed methods used to monitor moose abundance). I then created a resource selection function (RSF; Manly et al*.* 2002) using these censuses and ecological covariates thought to be important to moose habitat selection. Covariates were represented as spatial databases in a geographic information system (GIS). I validated the RSF using independent data from moose fitted with radio collars in the same area but collected from 2004 to 2010. I then simulated a landscape in the same area that excluded human-caused early-seral vegetation (cutting units and hydro-electric powerlines), which I termed the 'pristine' landscape. The final step was to apply the RSF to the pristine landscape to estimate the change in moose habitat quality and thus moose population size, by using the ratio of RSF values of the pristine to the current landscape (*sensu* Patthey et al. 2008).

Moose abundance in the harvested landscape

To back-calculate moose numbers for the pristine landscape, I used the 2003 population estimate to represent the ecological carrying capacity under current landscape conditions. The 2003 estimate was based on a SRB aerial census, with a sightability correction factor based on a radio-marked sample of moose (Quayle et al. 2001). I defined ecological carrying capacity as an abundance that is limited by a combination of food and natural predation. I provide three indications that moose were near ecological carrying capacity in 2003. First, moose had been lightly hunted (< 4%, males only) for at least 12 years and were rapidly increasing prior to 2003. Secondly, I compared moose recruitment in the study area after 2000, to earlier periods and other areas because recruitment should decline near carrying capacity (Nicholson 1933). I also compared recruitment to 65 other moose surveys in BC. Thirdly, I compared moose densities in my system to those from other areas in BC.

Moose habitat model

I used logistic regression to model the RSF based on habitats selected by moose in winter. The binary response was moose locations recorded during winter aerial population censuses and random locations were considered “available” (i.e. Design I, Manly et al. 2002). Random locations were distributed throughout the study area (Appendix 3.1) and I increased their number until the proportions of habitat types varied by <1% as new random locations were added. The RSF model can be summarized using the equation:

$$W(x) = e^{(\beta_1 x_1 + \beta_2 x_2 \ldots + \beta_n x_n)} \qquad \text{eqn 3.1}$$

where $W(x)$ is the relative probability of occurrence as a function of the covariates x_1, x_2, . .x_n, and $\beta_1 . . . \beta_n$ are the respective parameter estimates obtained from logistic regression. There is no intercept or asymptote to this function because it is considered to predict the relative probability of occurrence, not an absolute probability (Boyce and McDonald 1999).

I developed RSF models for the winter season. Although annual energy budgets may limit ungulate populations (Parker et al. 1996), winter is considered the limiting season in mountainous ecosystems because deep snow restricts their distribution and movements and forage is least available (Poole and Stuart-Smith 2006). In summer and autumn, moose can remain in valleys or spread out into the mountains where there is abundant forage.

I considered seven factors as potential predictors of moose habitat selection. Two were human-caused early seral habitats: cutting units (< 30 yr old) and hydro-electric transmission lines, which were combined into one variable called "human seral." Three factors represented natural types of early seral vegetation: marshes, avalanche paths and wildfires < 30 yr old. I also considered age of the forest stand, and closest distance to any early seral vegetation. The distance variable was included because moose often forage in early-seral areas but move in and out of adjacent forest. Finally, I considered elevation because this variable influences many ecological processes in mountainous ecosystems (Apps et al. 2001). I developed nine *a priori* candidate models but did not include factors that were highly correlated ($r > |0.7|$). To assess model fit I presented the area under the receiver operating curve (ROC). Although this metric can be biased due to the use-available design employed (Boyce et al. 2002), biases would not compromise comparisons between models. To rank the relative weight of evidence for each model, I used Akaike's information criteria (AIC; Burnham and Anderson 2002).

I also validated the models with independent data by using locations from moose fitted with GPS and VHF collars from 2004 – 2010 in the study area during the late winter season (12 January to 22 April; Apps et al. 2001). I accounted for biases in GPS collar fix success using D'Eon et al.'s (2002) equation, which was derived in the same ecosystem as this study. For each late-winter moose location I extracted the RSF value from the census-based model, then binned the RSF scores into 10 equal categories, and plotted the sum of the RSF value in each bin against the area-corrected frequency distribution of the telemetry locations. Then I calculated the Spearman correlation between the RSF scores and the frequency distribution as the index of validation (Boyce et al. 2002). I also used the telemetry data to summarize the proportion of locations that were within or 200 m from human-caused early seral vegetation, as a comparison to the census-based proportions.

To create the simulated 'pristine' landscape, I converted human-caused seral habitat (cutting units and transmission lines) to mature forest by assigning the age of adjacent stands using a 'nearest neighbour' algorithm from Hawth's tools (Beyer 2004). I also calculated relevant GIS layers for the pristine landscape such as distance to seral edge, to be able to apply the RSF to the pristine landscape. The RSF value was calculated for each pixel, using the logit back-transformation of the sum of the linear predictor from eqn 3.1. This process was done for both the 2003 and the pristine landscape. I then compared the sum of the RSF values for all pixels for the 2003 landscape to the pristine landscape and the corresponding pristine population estimate using

$$N_{pristine} = \left(\frac{\sum_{i=1}^{j} W(x_{pristine,j})}{\sum_{i=1}^{j} W(x_{2003,j})} \right) \times N_{2003} \qquad \text{eqn 3.2}$$

where N is the moose population size, j is each pixel in the study area, and 2003 and pristine denote the two landscapes being compared. To obtain robust confidence intervals (CIs) of the relative change between both landscapes, I bootstrapped the 2003 census data 500 times. At each iteration of the bootstrap I obtained parameter estimates from logistic regression, calculated the RSF for both landscapes, and finally calculated the ratio between the pristine and the 2003 landscape as per eqn 3.2. I then used the percentile method to report 95% CIs and the mean $N_{pristine}$ of the bootstrapped values. These steps were programmed in R (version 2.11.1, R Core Team 2006; GIS-RSF linked bootstrapping R code is provided in Appendix 3.2).

RESULTS

Moose population trends

Recent (2003 – 2009) aerial censuses and pellet transects indicate that moose declined from 1650 to 447 individuals (Fig. 3.1). Aerial censuses from the 1990s suggest lower moose numbers relative to the apparent peak in 2003. Adult male to female ratios in 2003 were 77:100 (66–89, 90% CI).

The calf per adult female ratio in 2003 was 22:100 (18–27), compared to 69:100 (66–72) in 1994, when the moose population was increasing rapidly (Fig. 3.1). The 2003 census also revealed a low calf ratio relative to 65 other surveys in BC summarized by Hatter (1999), where only four of these studies had calf ratios lower than 25:100 females. Calf per female ratios remained low in 2006 and 2007 (Fig. 3.1). Finally, at 1.58/km^2, moose densities in 2003 were more than twice that of the next highest in Hatter's (1999) summary of 65 surveys (mean = 0.30/km^2, SD = 0.22, range 0.26 – 0.73).

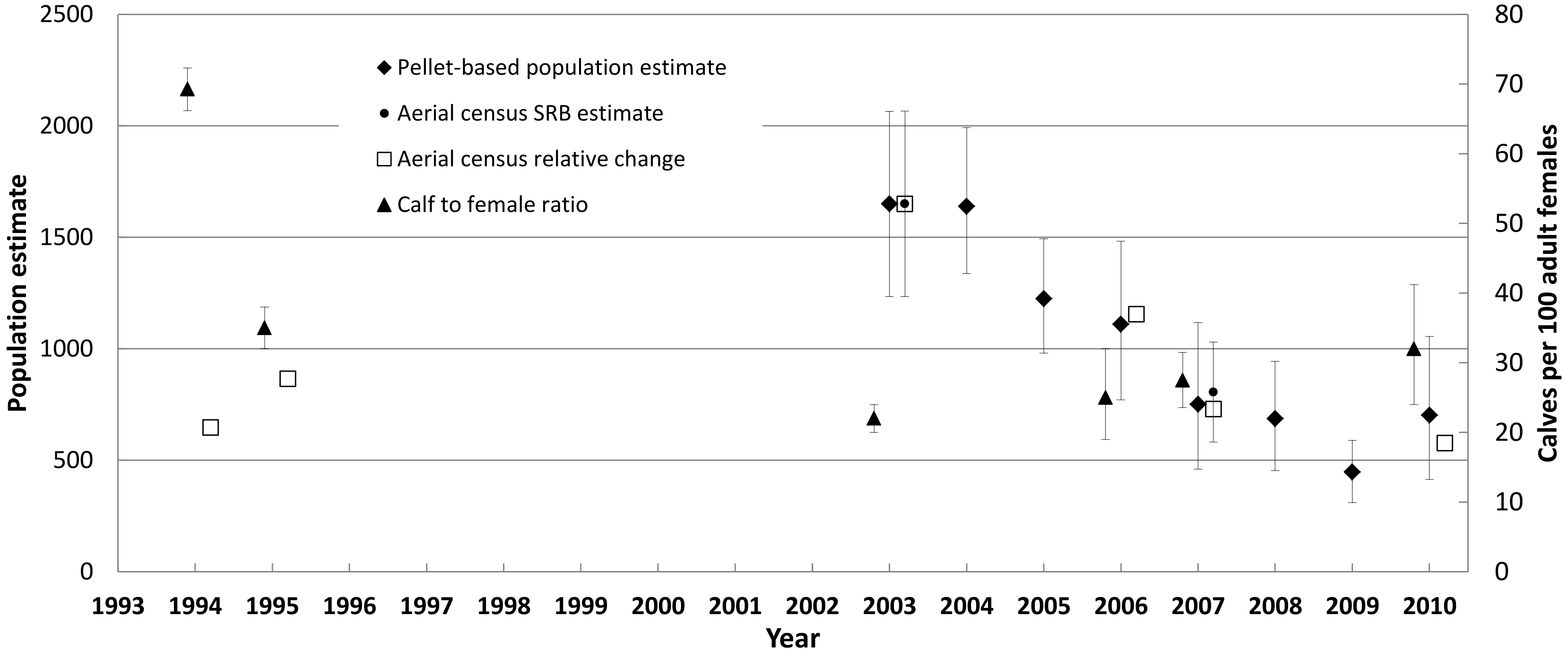


Figure 3.1. Changes in moose abundance in the Lake Revelstoke Valley from 1994 – 2010. Three different methods are presented (see Appendix 3.1): 1) Abundance estimates using a stratified random block design aerial census (SRB; circles); 2) relative change based on aerial counts of moose from a sample of 5 survey blocks (open squares); 3) Relative change based on 17 pellet transects (diamonds). Both relative indices were set to the 2003 SRB estimate as the initial value. Also shown are calf to adult female ratios (triangles; secondary y-axis). Error bars are 90% CIs**.**

Moose habitat model

During the 2003 SRB census I observed 337 groups of moose, ranging from 1 to 10 individuals (mean = 1.9, median = 1, SD = 1.3). Once I accounted for the number of moose per group and corrected for sightability (Quayle et al. 2001), 67.0 % of moose were found in cutting units despite only accounting for 20.3 % of the study area. Comparing moose to random locations revealed that moose were positively associated with early seral vegetation created by humans, low elevations and marshes, but negatively associated with avalanche chutes and increasing distance from all forms of early seral vegetation (Table 3.1). Based on AIC weights, the most influential of these factors were human-created early seral vegetation, distance to early seral vegetation, elevation, and avalanche chutes, whereas marsh areas were less important (Table 3.1b). Both top models had high ROC scores (0.95), indicating a reliable discrimination between used and random locations.

There were sufficient winter telemetry data from 28 moose (20 GPS and 8 VHF collars) for independent model validation. The census-based RSF bins and the area-adjusted frequency of telemetry locations were highly correlated (Spearman *r* = 0.93; Fig. 3.2). During winter, 59.8% of the telemetry locations were in 'human seral,' and 18.5% were < 200 m from these young stands, thus 78.3% of the moose locations were in 20.3% of the landbase associated with human-created early seral conditions.

Table 3.1a. Logistic regression results for top models (0 – 2 AIC units) for factors predicting moose habitat selection, based on census data from the Lake Revelstoke Valley, January 2003.

Model structure[a]	ROC	AIC	k	LogL	ΔAIC	AICω
Human_seral+Seral_distance + Avalanche_path + Elevation	0.95	835.86	5	-412.9	0.00	0.54
Human_seral+Seral_distance+Marsh+ Avalanche_path+Elevation	0.95	837.85	6	-412.9	1.99	0.20

Table 3.1b. AIC weights (AICω) for each variable present in the top model, weighted parameter estimates, and 95% confidence intervals (CIs; based on 500 bootstrap iterations).

Variable*	Parameter estimate**	95% CIs**	AICω
Elevation	-0.81	-0.72 to -0.93	1.00
Seral_distance	-0.65	-0.38 to -1.19	0.98
Human_seral	40.77	116.30 to -12.05	0.88
Avalanche_path	-80.84	1.28 to -179.62	0.87
Marsh	0.53	34.71 to -30.14	0.37

* ROC is the area under the receiver operating curve, AIC are Akaike Information Criteria units, k is the number of parameters, LogL is the log likelihood, ∆AIC is the difference in AIC units between the top model and the ith model, and AICω are Akaike weights; Human_seral is any early seral vegetation caused by humans; Seral_distance is the distance to any early seral vegetation; Marsh is open meadows or marshes; Avalanche_path is where snow avalanches occur regularly, maintaining early seral vegetation; Elevation is elevation a.s.l.

** x 100.

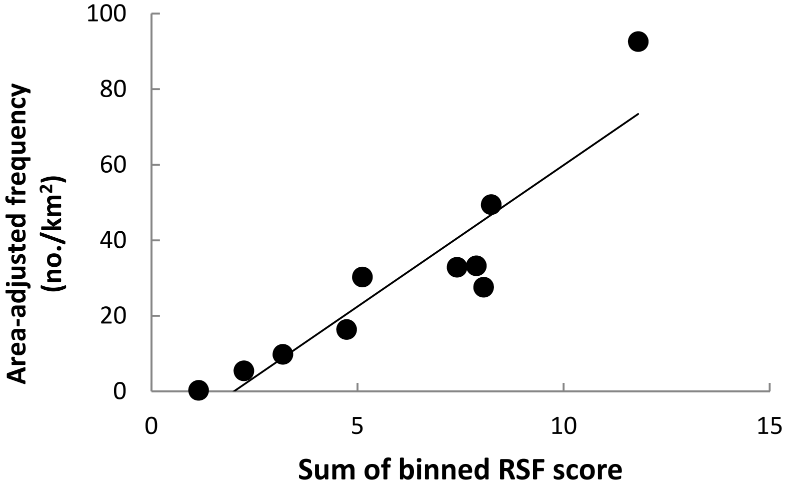


Figure 3.2. Independent validation of the moose winter habitat model. The winter model was based on 2003 aerial census data (corrected for sightability) and the validation was conducted using radio-telemetry data from 2004 – 2010. Spearman *r* = 0.93.

When I applied the census-based model to the current landscape (Fig. 3.3a), the sum of the RSF values for all pixels was 13074. The sum of RSF values for the pristine landscape (Fig. 3.3b) was 2401, suggesting a decline in habitat quality of 81.6%. Bootstrapping the 2003 census data resulted in 95% confidence intervals of 71.0 to 89.9%. Assuming a linear relationship between RSF values and population size (eqn 3.2; *sensu* Boyce and McDonald 1999), and using 2003 as the approximate ecological carrying capacity under current landscape conditions, then the pristine landscape was predicted to have 303 (167 – 478; 95% CI) moose.

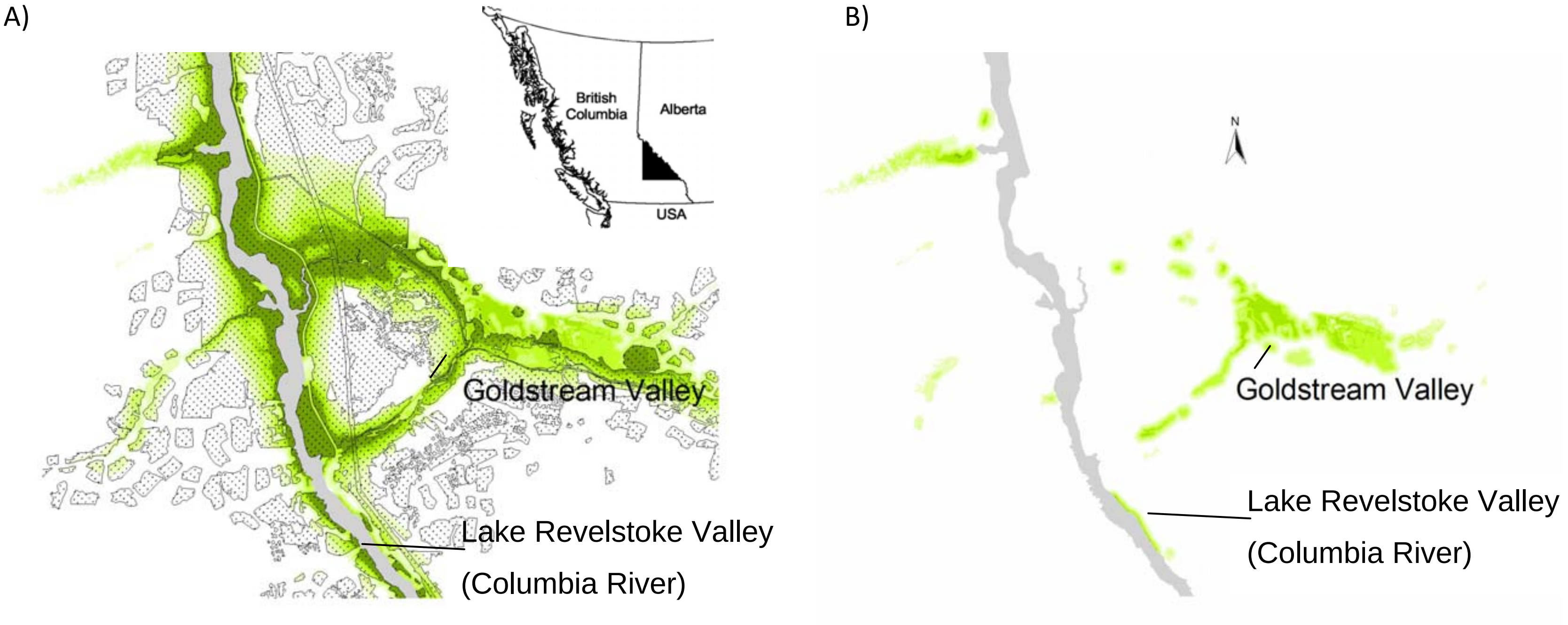


Figure 3.3. Resource selection function (Table 3.1) for moose in a small portion of the study area (the Goldstream Valley is a tributary of Lake Revelstoke) for: A) current (2003) logged landscape and B) a simulated pristine landscape. Darker green indicates higher habitat quality, and speckled polygons are human-caused early seral vegetation (clearcuts and hydroelectric transmission lines). The effects of removing this vegetation can be seen by comparing the two maps. The moose habitat that remains in the pristine landscape is from natural openings such as marshes and wetlands. Note how habitat quality decreases with increasing distance from early seral vegetation and increasing distance from valley bottoms (i.e. elevation; Table 3.1).

DISCUSSION

Restoration efforts benefit from having clear goals with associated targets to help estimate achievement (Margules and Pressey 2000), yet there continues to be a debate on how to develop these targets. Some argue for landscape conditions set to a specific time period (Loh et al. 1998), whereas others suggest use of protected areas as benchmarks (Arcese and Sinclair 1997). In this case I simulated a landscape free from human-caused disturbance and applied a model derived under current conditions to estimate a target for restoration. Although the model was robust to independent validation, I recognize that it is being extrapolated beyond the range of conditions from its development. A substantial change in moose foraging behaviour in a landscape dominated by old forests would change the selection coefficients I presented here and thus affect the pristine estimate. However, alternative approaches to deriving targets also have shortcomings. Protected areas in mountainous systems are often biased to high-elevation, scenic sites with less productive ecosystems (Margules and Pressey 2000, Scott et al. 2001) compared to the low-elevation forests in my study area. Protected areas are also rarely large enough to contain large mammal predator-prey systems (Noss et al. 1996). Given these challenges, the approach of deriving a statistically based target moose population was likely the most appropriate (see Nielsen et al. 2007 and Patthey et al. 2008 for similar examples).

There is disagreement whether moose were rare or entirely absent from southern BC (Hatter 1950, Spalding 1990, Kay 1997) but it is clear that moose were far more abundant during the past decade than historically. The prediction of 303 (167 – 478) moose in a pristine landscape is similar to 204 moose estimated in 1984 (Bradley 1986; a decade after broad-scale logging began), but re-sightability in that study was low so the precision was poor (± 159, 95% CIs). Higher recruitment in the 1990s suggest that moose were not regulated by forage at that time but when numbers doubled by 2003, there appeared to be a density dependent reduction in recruitment to among the lowest recorded in BC. Furthermore, the 2003 wintering density (1.58/km^2) in this system was the highest recorded in BC, > 5 times higher than the mean reported in

Hatter's (1999) summary. The 2003 density estimate was also above what is considered "high density" habitat in Alaska (1.1/km^2; Gasaway et al. 1992, Keech et al. 2000). The central portion of my study area (Goldstream Valley) had a density of 4.8/km^2 (35% of the study area estimate), higher than the 50-yr peak value from the unexploited island system of Isle Royale National Park (4.5/km^2, though the mean density since 1959 in Isle Royale was < half this value; Vucetich and Peterson 2004). These recruitment and density comparisons suggest moose were near ecological carrying capacity in 2003.

An assumption of my temporal habitat comparisons is that resources selected by organisms reflect a positive fitness choice. Van Horne (1983) cautioned that this tenet was incorrect, but since then many studies have shown that resources selected by a range of vertebrates based on indices of animal density can have links to abundance (Wheatley et al. 2002, Bock and Jones 2004). Van Horne's (1983) concerns dealt with areas modified by humans that can create ecological traps because animals had not adapted to these novel habitats. Considering that moose evolved with early seral vegetation and associated predators, it appears this vegetation is not novel habitat for these ungulates. Therefore, the RSF I created probably reflects resource choice that relates to the fitness of the animals (Boyce and McDonald 1999, McLoughlin et al. 2006, 2007). It is likely that the selection patterns are robust to a range of ecological conditions including density and resource availability because my estimates of selection were consistent using a variety of techniques. These included a broad representation of moose using aerial census data, fewer moose but across time (and thus density) using radio-collar data, and match the outcome of a third study based on systematic snow track transects (Serrouya and D'Eon 2003).

Several factors may cause an underestimate of historical moose numbers including the habitat loss from flooding the Columbia River at Revelstoke in 1983. However, considering the current abundance of clearcuts and existing natural openings, habitat lost from flooding in 1983 amounts to only 1–2% of the current habitat area (Utzig and Holt 2008, R. Serrouya unpublished data). Dynamic factors associated with expanding moose populations could also affect the historic target. When organisms occupy a new region they sometimes exceed carrying capacity (Simard et al. 2008), then drop below this level leading to dampening oscillations towards an equilibrium (Caughley 1970). Although I provide evidence that moose were approaching carrying capacity, if the 2003 benchmark was below or above this level the pristine estimate would be affected correspondingly.

Processes associated with small populations were not considered in my estimate of historic moose carrying capacity because I assumed a direct relationship between habitat change and population change. For example, as some ungulate species decline, so do their average group size, making them more vulnerable to predation and contributing to a depensatory predation rate (McLellan et al. 2010). Moose group sizes have shown declining patterns in my study area (McLellan et al. 2010). In addition, given that moose habitat in the pristine landscape is more fragmented compared to the current landscape, other demographic factors associated with isolated and small subpopulations (Soulé 1986) could make moose viability more difficult under pristine conditions.

There is uncertainty when estimating the number of moose expected in a pristine environment, and consequently there will be further uncertainty when estimating the number of predators. Using Fuller et al.'s (2003) equation to predict wolf numbers from ungulate biomass, 303 (167 – 478) moose yields 9 wolves (6.5 – 12.1), or a density of 8.1/1000 km^2 (5.9 – 11.0/1000 km^2). This wolf density is similar but slightly higher than Bergerud and Elliot's (1986) target of 6.5/1000 km^2, which was based on the wolf density where caribou mortality equals recruitment. However, my target estimate is based on winter wolf distribution, so it is not directly comparable to Bergerud and Elliot's. When converted to a summer density, my target is roughly 1/3 the winter value (*c*. 2.7/km^2).

Now that a target population has been developed for the dominant ungulate, the next step is to test the outcome of reducing the number of these animals to determine if caribou survival and recruitment increases. This active adaptive management experiment (Walters and Holling 1990, Chee and Wintle 2010) is underway with an adjacent reference area where moose numbers are not being reduced. However, because some mountain caribou populations are in imminent danger of extinction (Serrouya and Wittmer 2010), moose and predator targets may need to be lower to further reduce extinction risk. If the smaller mountain caribou populations recover, then this approach and target will be useful for decision-making and adaptive evaluation until the early-seral habitat recovers. Furthermore, I suggest that the approach developed here can be applied across ecosystems including the boreal forest where woodland caribou are also declining (Festa-Bianchet et al. 2011), and to caribou-deer-cougar systems that are more prevalent in southern Canada and northwestern USA (Kinley and Apps 2001).

The effort required to recover mountain caribou in British Columbia highlights the importance of social values in making management decisions regarding predators and valued game species. In Alaska, elected officials have decided to use ongoing predator control to reduce wolf, grizzly and black bear populations so moose numbers will increase allowing hunters to kill more moose (Boertje et al. 2010). Whereas in British Columbia (adjacent to Alaska), moose populations are being greatly reduced so wolf control will only be needed for a short time period to encourage the recovery of an endangered ungulate. To allow recovery of caribou, a truly “ecosystem management” (Grumbine 1994) approach would be to manage moose and predators at historic levels until the habitat recovers completely. Complete habitat recovery may be unrealistic given the economic pressure to harvest forests, but recent recovery plans have set aside substantial old-growth reserves to prevent their conversion into young forests and additional forage for moose and deer, and plans include a strategy to recruit early seral stands to old forests (RHLPO 2005). Despite these protection measures, it is unlikely that a truly ecosystem-based recovery approach will be feasible, and continued management of moose to historic levels will be needed in perpetuity. However, the intensity of this management should be reduced with newly enacted protection of old forests. Furthermore, I suggest that liberalized sport hunting can be used to reduce moose populations (Chapter 6), despite abundant moose forage (and see Rempel et al.

1997). This approach appears more socially acceptable than predator control, at least in British Columbia (C. Ritchie, BC Ministry of Environment, Pers. Comm.).

The multi-trophic approach to caribou recovery in British Columbia is being recognized by independent researchers to be among the most comprehensive in North America (Hebblewhite et al. 2010, Festa-Bianchet et al. 2011). Habitat protection, without management of the predator-prey system, will be insufficient and will result in extinction of caribou subpopulations (Wittmer et al. 2010). These extinctions may lead to returning large areas of old-growth forest to short-term rotation forestry (Serrouya and Wittmer 2010). It is hoped that this multi-trophic level approach to conservation will be evaluated and adapted as the dynamics of the large mammals respond to the treatments described here.

LITERATURE CITED

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.

Arcese, P., and A.R.E Sinclair. 1997. The role of protected areas as ecological baselines. Journal of Wildlife Management **61**:587-602.

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

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Bock, C. E. and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment **2**:403-410.

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management **74**:917-928.

Boyce, M. S. and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution **14**:268-272.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281-300.

Bradley, R.M. 1986. Moose studies, Revelstoke Project. B.C. Hydro, Environmental Services Operation and Maintenance Division.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. 2nd edition. Springer, New York.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology **51:**53-72.

Chee Y.E. and B.A. Wintle. 2010. Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. Journal of Applied Ecology. doi: 10.1111/j.1365-2664.2010.01877.x

Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. Science **302**:1532.

Courtois, R., J. P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience **14**:491-498.

D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildlife Society Bulletin **30**:430-439.

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.

Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: Restoration ecology and conservation biology. Science **277**:515-522.

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.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Q. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management **155**:399-423.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161-191 *in* D. L. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

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

Grumbine, R.E. 1994. What is ecosystem management? Conservation Biology. **8**: 27-38.

Hatter, I. 1999. An evaluation of moose harvest management in central and northern British Columbia. Alces. **35:** 91-103.

Hatter, J. 1950. The moose of central British Columbia. Ph.D., State College of Washington.

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

Hebblewhite, M., C. White, and M. Musiani. 2010. Revisiting Extinction in National Parks: Mountain Caribou in Banff. Conservation Biology **24**:341-344.

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

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

Kay, C.E. 1997. Aboriginal overkill and the biogeography of moose in western North America. Alces. **33**: 141-164.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management **64**:450-462.

Kinley, T. A. and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin **29**:158-164.

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.

Loh, J., Randers, J., MacGillivray, A., Kapos, V., Jenkins, M., Groombridge, B. and N. Cox. 1998. Living Planet Report 1998. Gland, Switzerland: WWF.

McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. Ecology **91**:286-292.

McLellan, B.N., Serrouya, R., and K. Furk. 2008. Population census of caribou, the north Columbia Mountains. British Columbia Ministry of Forests and Range.

Revelstoke, British Columbia, Canada.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B-Biological Sciences **273**:1449-1454.

McLoughlin, P. D., J. M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. Van Moorter, S. Said, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology **88**:3192-3201.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. and W.P. Erickson 2002. Resource selection by animals. 2nd edition. Kluwer, Boston.

Margules, C. R. and R. L. Pressey. 2000. Systematic conservation planning. Nature **405**:243-253.

Meidinger, D.V., and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series 4. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology. **2:** 132-178.

Nielsen, S. E., E. M. Bayne, J. Schieck, J. Herbers, and S. Boutin. 2007. A new method to estimate species and biodiversity intactness using empirically derived reference conditions. Biological Conservation **137**:403-414.

Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. Journal of Applied Ecology **38**:1350-1361.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Orians, G., P. A. Cochran, J. W. Duffield, T. K. Fuller, R. J. Gutierrez, W. M. Henemann, F. C. James, P. Kereiva, S. R. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, Bears, and Their Prey in Alaska. National Academy Press, Washington.

Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1996. Foraging efficiency: Energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Zoology **74**:442-450.

Patthey, P., Wirthner, S., Signorell, N. and R. Altettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology. **45**: 1704–1711.

Poole, K. G. and K. Stuart-Smith. 2006. Winter habitat selection by female moose in western interior montane forests. Canadian Journal of Zoology. **84**:1823-1832.

Quayle, J. F., A. G. MacHutchon, and D. N. Jury. 2001. Modeling moose sightability in south-central British Columbia. Alces **37**:43-54.

R Development Core Team. 2006. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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

RHLPO. 2005. Revelstoke Higher Level Plan Order. [online]. Available from http://archive.ilmb.gov.bc.ca/slrp/lrmp/cranbrook/revelstoke/ files/plan_order.pdf [accessed 31 July 2010].

Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: Do they capture the full range of America's biological diversity? Ecological Applications **11**:999-1007.

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

Schwartz, C. C. and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs **113**:1-58.

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.

Seip, D. R. 2008. Mountain caribou interactions with wolves and moose in central British Columbia. Alces **44**:1-5.

Serrouya, R. and D'Eon, R. G. 2003. Moose habitat selection in relation to forest harvesting in a deep snow zone of British Columbia. Unpublished report prepared for the British Columbia Forest Investment Account and Downie Timber. http://www.for.gov.bc.ca/hfd/library/frbc2002/FRBC2002MR63.pdf

Serrouya, R. and H. U. Wittmer. 2010. Imminent Extinctions of Woodland Caribou from National Parks. Conservation Biology **24**:363-364.

Shackleton, D. 1999. Hoofed mammals of British Columbia. UBC Press, Vancouver.

Simard, M. A., S. D. Côté, R. B. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. Journal of Animal Ecology **77**:678-686.

Soulé, M. E. 1986. Conservation biology : the science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.

Spalding, D. J. 1990. The early history of moose (*Alces alces*): Distribution and relative abundance in British Columbia. Contributions of Natural Science No. 11. Royal B.C. Museum, Victoria, British Columbia.

Utzig, G.F. and R.F. Holt. 2008. Terrestrial productivity in the flooded terrestrial ecosystems of the Columbia Basin: impacts, mitigation and monitoring. Prepared for the Fish and Wildlife Compensation Program, Columbia Basin, Nelson, British Columbia, Canada.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. **47:** 893–901.

van Oort, H., Bird, C., Mowat, G., Gaynor, C. and DeGroot, L. 2010. Winter predator census results in the Kootenay-Columbia caribou recovery areas. Unpublished report prepared for the British Columbia Ministry of Environment.

Vucetich, J. A. and R. O. Peterson. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society of London Series B-Biological Sciences **271**:183-189.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Wheatley, M., K. W. Larsen, and S. Boutin. 2002. Does density reflect habitat quality for North American red squirrels during a spruce-cone failure? Journal of Mammalogy **83**:716-727.

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, G. S. Watts, and D. Hamilton. 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. R. E. Sinclair, and B. N. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

APPENDIX 3.1: DESCRIPTION OF METHODS USED TO ESTIMATE MOOSE ABUNDANCE FROM 1994 TO 2010

Aerial censuses in 2003 and 2007 (Serrouya and Poole, unpublished data) used a standard stratified-random block (SRB) design to estimate total moose abundance (Gasaway et al. 1986). The area was divided into 53 blocks averaging 19.7 km^2 (±0.91 SE) with 21 blocks surveyed each year. Pre-stratification flights were conducted using a fixed-wing aircraft to help minimize variance by placing each block into one of three strata (Gasaway et al. 1986). A sightability correction factor was applied to each group of moose observed by recording the oblique vegetation cover when moose were first seen. This correction factor was based on a regression of vegetation and detection rate of radio-marked moose, developed in southern British Columbia (Quayle et al. 2001). The correction factor ranged from 1.1 for moose in 0 – 20% oblique cover, to 41.8 for moose seen in > 80% cover.

In addition to these SRB censuses, aerial censuses were conducted in 2006 and 2010 but, due to limitations in resources, fewer blocks were surveyed (five). I used these surveys to track changes in demographic composition of moose (i.e. ratios of adult females to calves and to adult males). Beginning in 2003, I also conducted annual pellet counts along 17 transects distributed throughout the study area to monitor the relative change in moose abundance (Fig. A3.1). Specifically, I used circular 100 m^2 plots placed every 50 m along each transect with an average of 25.5 plots per transects. Pellets were recorded to species and cleared from the plots after each survey. The sampling design for pellet surveys was based on a pilot study that was used to determine the optimal sampling that minimizes the variance relative to sampling effort. I treated the transect as the sample unit and bootstrapped these to obtain variance estimates. I calculated the number of pellets divided by sampling effort (i.e. countable plots), because some plots were removed from the sample if they were subject to active or recent disturbance such as logging or flooding. Because pellet counts are suited to track relative change, I set the pellet transect data recorded in 2003 to the 2003 SRB population estimate, then present the annual change in moose abundance based on the relative change in pellets using 2003 as the benchmark starting value. I used the same approach for the partial aerial censuses done in 2006 and 2010, to determine if the relative change in moose seen mirrored the changes in pellet abundance. I present population estimates of moose as absolute numbers but when appropriate convert these values to winter densities (i.e., divided by 1050 km^2, the winter distribution of moose).

Prior to 2002, moose census data were available for the study area using the same survey block boundaries used after 2002 (J. Krebs, Fish and Wildlife Compensation Program, unpubl. data). These previous surveys, however, were not based on an SRB design to estimate abundance, but were intended to monitor relative change in abundance and composition. From the trend data (i.e. 2003 – 2010), I noted a high corroboration between the relative change in abundance of pellets, the SRB estimates, and moose seen in census blocks that were consistently sampled in 2003, 2006, 2007 and 2010 (see Figure 3.1). Therefore, I used the relative change in moose seen in the same survey blocks sampled in 2003, to those sampled in the 1994 and 1995, to estimate a population size for 1994 and 1995.

Comparisons of the same survey blocks covering 120 km^2 in a portion of the study area with the highest moose densities (Goldstream Valley) in 1994, 1995, and 2003, suggest an increasing population (130, 171, and 326, respectively; mean of 8.5 survey hrs in the 1990s, 9.5 hrs in 2003). In two survey blocks that were in the medium moose density strata, 19 moose were observed in 1994 but 54 were seen in the same area in 2003. Using this information, I estimated that there were 865 moose in 1995 (171/326 x 1650 = 865). In 1994, I estimated that there were 658 moose ([130+19]/[326+54] x 1650 = 658). These same survey blocks that were sampled in the 1990s and from 2003 onwards contained 35-50% of the moose estimated during the 2003 and 2007 SRB censuses, suggesting that monitoring these core habitat areas will best approximate substantial changes in the moose population.

LITERATURE CITED

Gasaway, W.C., DuBois, S.D., Reed, D.J., and Harbo, S.J. 1986. Estimating moose population parameters from aerial surveys. Biological Papers No. 22, University of Alaska – Fairbanks, Alaska, USA.

Quayle, J. F., MacHutchon, A. G. and Jury, D. N. 2001. Modeling moose sightability in south-central British Columbia. *Alces,* **37,** 43-54.

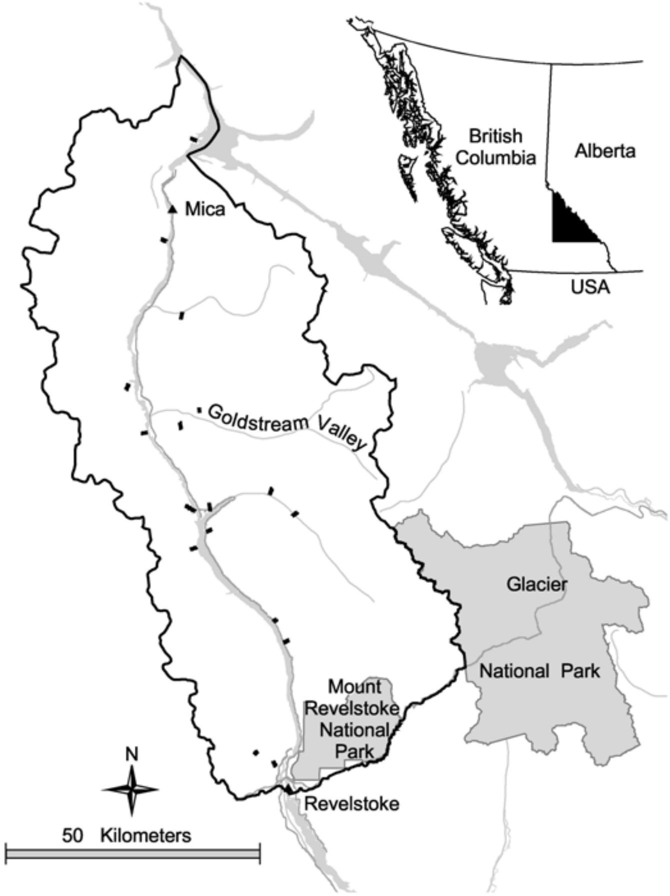


Figure A3.1. Map of study area showing locations of the 17 pellet transects (black lines) used to monitor relative abundance of moose.

APPENDIX 3.2: R CODE FOR GIS-RSF LINKED BOOTSTRAPPING TO ESTIMATE UNCERTAINTY OF THE ECOLOGICAL POPULATION TARGET

```
# GIS / RSF LINKED BOOTSTRAPPING CODE FOR UNCERTAINTY ESTIMATION IN A GIS
FRAMEWORK
# FOR DETAILS SEE: Serrouya, R., B.N. McLellan, S. Boutin, D.R., Seip, and S.E. Nielsen. 2011.
#Developing a population target for an overabundant ungulate for ecosystem restoration.
Journal of Applied Ecology.

#PART I, THE BOOSTRAPPED RSF
#clean up and libraries...
rm(list=ls(all=T))
library(MuMIn) # THIS LIBRARY IS FOR THE DREDGE COMMAND FOR MODEL AVERAGING ETC.
BUT SUBSET THE MODELS TO
#AVOID DATA DREDGING, SEE BELOW.

#sample sizes for initial data and boostrapping
#note: MAX_NUM matches the sorted excel file with column "USE" having the same number of
"ones"
# MAX_NUM IS THE SAMPLE SIZE OF THE "USE" DATA IN LOGISTIC REGRESSION (OR ANY
REGRESSION)
MAX_NUM = 337
#SAMPLES IS THE NUMBER OF BOOTSTRAP ITERATIONS
SAMPLES = 500
# NUM_ATTRIBUTES IS THE NUMBER OF INDEPENDENT VARIABLES
NUM_ATTRIBUTES = 6

#INPUT FILE NAME
FILE_NAME = "moocenfor_R.csv"
OUTPUT_FILE = "bootstrap_results.csv"

#bootstrap numbers...
M = matrix(nrow = SAMPLES, ncol = MAX_NUM)
for (i in 1:SAMPLES)
{
 x = sample(1:MAX_NUM, MAX_NUM, replace=T)
 M[i,] = x
}

#M is now a fully populated matrix with rows as each 'Bootstrap iteration'
#output the results of the bootstrapping numbers
#comment following line to prevent file output, THIS IS FOR ERROR CHECKS
#write.csv(data.frame(M), "M_samples.csv")

#from this point, data_file remains unaltered
data_file <- read.csv(FILE_NAME)
```

```
#loop through each row......note length(M[,1]) is equal to SAMPLES (bootstrap iterations)
#each row is a bootstrap run

#result data vector
result_data  = matrix(nrow = SAMPLES, ncol = NUM_ATTRIBUTES)
HEADERS <- NA
for (i in 1:length(M[,1]))
{
 #new copy of data_file to manipulate
 temp_data_file <- data_file

 #run through the sampled values:
 #length(M[i,]) is equal to MAX_NUM
 for (j in 1:length(M[i,]))
 {
  #replace the j-th row of temp_data_file with the M[i,j]-th row of data_file
  temp_data_file[j,] <- data_file[M[i,j],]
 }

 #output temporary moose file
 #comment following line to prevent file output, AGAIN USE FOR ERROR CHECKS
# write.csv(temp_data_file, paste("temp_moose_file_", i, ".csv"))
#temp_data_file=data_file
##########################
#execute inline calculations
# THIS IS THE MAIN MODEL CODE (example given, use (moose location) as a function of
covariates)
# USE are 1's or 0's
 determine <- glm( USE ~  HUMSER + Seral_dis + DEM25_M + AVY + RIP,
    data = temp_data_file,
    family = binomial(link = logit),
    #na.action=na.omit,
    weights = WEIGHT)
#WEIGHT is the sightability correction factor for moose censuses

# DREDGE MAKES A MODEL FAMILY FOR AIC COMPARISONS
# to avoid doing all possible subsets(i.e., data dredging), specify candidate models below, and
learn the logical operators, but
# they are fairly obvious.  Below are just examples

dd <- dredge(determine, subset =
(HUMSER & Seral_dis & DEM25_M & !AVY & !RIP) |
(HUMSER & Seral_dis & !DEM25_M & !AVY & !RIP)|
(HUMSER & Seral_dis & DEM25_M & AVY & !RIP) |
(!HUMSER & Seral_dis & DEM25_M & AVY & !RIP) |
(HUMSER & Seral_dis & DEM25_M & AVY & RIP) |
(HUMSER & Seral_dis & DEM25_M & AVY & RIP)
 )
```

```
 top.models.1 <- get.models(dd, subset = delta < 10)

#DOES MODEL AVERAGING AND UNCONDITIONAL S.E. CALCULATIONs
 model.avg(top.models.1) # get averaged coefficients

 models <- coef(model.avg(top.models.1))
 result_data[i,] = models
 HEADERS <- names(models)
}

#result_data
#make data frame

final <- data.frame(result_data)
names(final) <- HEADERS
#final ouput of bootstrapped parameter estimates
write.csv(final, OUTPUT_FILE)

#### PART II: THE GIS COMPONENT ############
#NEED TO MAX THE MEMORY, GIS VECTORS ARE HUGE
memory.limit(3999)
INPUT_FILE = "bootstrap_results.csv"
bootstrap_file <- read.csv(INPUT_FILE)

#IMPORTS GIS ascii FILES FROM ARCVIEW 3.3 AS VECTORS
DEM <- scan(file("dem25.asc", "r"), skip= 6)
fcbase <- scan(file("fcbase.asc", "r"), skip=6)
seral_dis <- scan(file("seral_dis.asc", "r"), skip= 6)
natse_dis <- scan(file("natse_dis.asc", "r"), skip= 6)

#DEM IS ELEVATION FOR EACH PIXEL, FCBASE MEANS FOREST COVER BASE LAYER, "DIS" MEANS
DISTANCE TO SERAL
# VEGETATION (NATSE=NATURAL SERAL, SERAL=ANY SERAL)

#THE AVALANCHE CHUTE LAYER
av = ifelse(fcbase == 4, 1, 0)

#THE RIPARIAN LAYER
rip = ifelse(fcbase == 5, 1, 0)

#THE HUMAN SERAL LAYER
humser =  ifelse(fcbase <= 2, 1, ifelse(fcbase > 10, 1, 0))

#THE HUMAN SERAL LAYER IN THE PRISTINE LANDSCAPE
humserpristine = 0

results = c()
```

```
for (i in 1:length(bootstrap_file$AVY))
{
#sums RSF of pristine landscape over all pixels divided by 2003 landscape
# DOES THE STANDARD LOGIT BACKTRANSFORMATION W(X) = EXP (SUM OF LINEAR
PREDICTOR)
# BUT ALSO DOES 1 - (PRISTINE LANDSCAPE RSF/2003 LANDSCAPE RSF) TO CALCULATE THE %
REDUCTION IN HABITAT
#QUALITY AT EACH BOOTSTRAP ITERATION AS PER EQ. 2 IN THE PAPER. "SUM" IS THERE TO
SUM ALL PIXELS IN THE LANDSCAPE
#The code loops through bootstrapped parameter estimates.
  z <- 1-sum(exp( humserpristine * bootstrap_file$HUMSER[i] +
   natse_dis * bootstrap_file$Seral_dis[i] +
   DEM * bootstrap_file$DEM25_M[i] +
   rip * bootstrap_file$RIP[i] +
   av * bootstrap_file$AVY[i]))/sum(exp( humser * bootstrap_file$HUMSER[i] +
   seral_dis * bootstrap_file$Seral_dis[i] +
   DEM * bootstrap_file$DEM25_M[i] +
   rip * bootstrap_file$RIP[i] +
   av * bootstrap_file$AVY[i]))
results = c(results, z)
}
results
write(results,"loopout.csv",ncolumns=length(bootstrap_file$AVY))
# THEN SORT THE CSV FILE AND USE PERCENTILE METHOD TO CALCULATE CIs.
```

CHAPTER 4

USING AN ECOLOGICAL TARGET TO MAKE QUANTITATIVE PREDICTIONS TO INFORM AN ECOSYSTEM EXPERIMENT

Understanding the population dynamics of large and vagile animals requires observational or experimental studies that cover broad areas. This generalization is particularly relevant for large carnivores because of the area needed to acquire prey that are often dispersed or migrate seasonally (Fryxell 1991, Hebblewhite et al. 2008). These broad scales constrain the ability of agencies and researchers to address important ecological questions because replicating or even implementing treatments comes with substantial logistical and social challenges (Walters and Holling 1990). Furthermore, when management actions are implemented, fixing mistakes that stemmed from uncertainty or unexpected processes can be costly, both economically and ecologically. Unexpected outcomes are prone to occur in complex ecosystems (Doak et al. 2008), and in some cases mistakes resulting from policy decisions are irreversible (Carpenter et al. 1999).

To reduce the chance of unexpected or negative outcomes, predictive models that reflect the ecological mechanisms that affect population change can be of great value to highlight risks and uncertainty. Ideally, these models should be developed before implementing management actions to understand the potential for unwanted outcomes. They can also be used to predict outcomes of alternative policy scenarios to help address management or conservation challenges. Using management to learn about the merit of alternative policy options has become a recurring theme in the natural resource literature (Gregory et al. 2006, Gunderson and Light 2006, Doak et al. 2008). In what has become a seminal piece of guidance, the “adaptive management” paper by Walters and Holling (1990) states that “the best policy choice for any year will be either to ignore uncertainty (passive adaptive) or to make a fairly dramatic and informative experimental disturbance; minor experiments are not favored because they erode average performance without significantly improving learning rates.”

Although Walters and Holling's essay focused on sustainable resource management, the principles also apply to endangered species recovery. In the case of woodland caribou there is general agreement that an unsustainable level of predation is the proximate cause of woodland caribou declines (Bergerud and Elliot 1986, Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005b, Latham et al. 2011, McLellan et al. 2012; but see Theberge and Walker 2011, Wasser et al. 2011). Yet, when it comes to understanding the ultimate factors that facilitate elevated predation rates, there is debate about the degree that habitat alteration due primarily from logging vs. global climate change has had on supporting the apparent competition mechanism (Wittmer et al. 2007, Dawe 2011). There is even greater uncertainty about which management options will contribute to the recovery of woodland caribou. Relative to the research effort placed on identifying causative factors of decline, few studies exist that have actively tested recovery options for endangered caribou populations (Steenweg 2011, Hebblewhite et al. in prep), and none have compared alternative approaches.

Given that woodland caribou are negatively affected by increases in primary prey, several recent theoretical (Weclaw and Hudson 2004) and empirical publications (James et al. 2004, Chapter 3) have suggested reducing primary prey as a means of indirectly reducing predation rates on caribou. This management strategy provides an alternative to predator control, which is now less appealing to the public (Orians et al. 1997). Furthermore, if predator control is implemented in the absence of other measures, it will have to be intensive and long-term, because predators will quickly recolonize areas where they have been removed (Bergerud and Elliot 1998, Hayes and Harestad 2000, Mosnier et al. 2008). Therefore, a reduction in primary prey is gaining appeal as a management strategy, but there are risks with this approach. In particular, it is likely that rapid and aggressive primary prey reduction may lead to predators consuming more caribou until predators respond numerically to the decline in primary prey. Models suggest that this risk is possible for rare species affected by apparent competition (Courchamp et al. 2003, Zhang et al. 2006), and empirical studies suggest that this risk is real (Norbury 2001, Wittmer et al. In press). The degree of risk may be affected by the time lag of the predators' numerical response, the relative abundance of primary prey to caribou, and the magnitude or rate of decline in primary prey. Each of these factors essentially changes the ratio of predators to caribou, which has been shown to affect predation rates in other predator-prey systems (Vucetich et al. 2011). Furthermore, gradually reducing the primary prey may mitigate or exacerbate the level of risk, but no information exists on this topic.

In this chapter, my goal was to use theoretical predator-prey equations to forecast the outcome of a variety of management options to help recover endangered mountain caribou populations. Such an approach may help to avoid costly mistakes that would be applied over very large areas. The scenarios I developed were focused on reducing primary prey to the management target identified in Chapter 3 (82 % less than 2003 levels), and to predict the response by caribou. However, I did not restrict management options to this approach, but explored additional options such as reducing predator levels concurrently, and varying the magnitude and rate that primary prey are reduced.

METHODS

The apparent competition mechanism was represented as a set of simultaneous ordinary differential equations (ODEs) for the population densities of two prey species and their common predator. The model was a mathematical representation of Rosenzweig and MacArthur's (1963) graphical predator-prey model, but with two important modifications (Eqn. 4.1 – 4.3). First, a second prey species was added to reflect the apparent competition scenario. The next modification was to make the predator's mortality density dependent. This modification was appropriate because for territorial predators, such as wolves or cougars, there may be an upper density that is set by social factors (Messier 1994, Hebblewhite 2013), independent of prey abundance. Furthermore, preliminary analyses showed that this modification helped to dampen the number and magnitude of oscillations during the transient phase of the model.

The model takes the following form:

$$\frac{dP_1}{dt} = r_1 \cdot P_1 \cdot \left(1 - \frac{P_1}{K_1}\right) - \frac{a \cdot P_1 \cdot C}{1 + a \cdot T_h \cdot (P_1 + P_2)} \qquad \text{eqn 4.1}$$

$$\frac{dP_2}{dt} = r_2 \cdot P_2 \cdot \left(1 - \frac{P_2}{K_2}\right) - \frac{a \cdot P_2 \cdot C}{1 + a \cdot T_h \cdot (P_1 + P_2)} \qquad \text{eqn 4.2}$$

$$\frac{dC}{dt} = C \cdot \left(\frac{b \cdot a \cdot (P_1 + P_2)}{1 + a \cdot T_h \cdot (P_1 + P_2)} - m \cdot C - h\right) \qquad \text{eqn 4.3}$$

where the P_i are the densities of the two prey species, the K_i are the corresponding carrying capacities, r_i the intrinsic growth rates, C is the predator density, a the predator foraging efficiency, T_h the handling time of prey, b the conversion factor of prey to predator density, m the natural mortality constant of the predator, and h is an additional mortality imposed to the predator from management. The prey equations are based on logistic growth minus consumption by the predator, represented as a Type II functional response. Because there were two prey species, I adjusted the functional response to include the handling time for both prey, similar to McLellan et al. (2010). The predator equation is based on what prey is consumed (i.e., the Type II functional response), with a conversion factor (b), minus a density dependent natural mortality rate ($m * C$), and a density independent mortality rate (h) caused by management. Hereafter, I treat P_1 as the primary prey that has higher growth and/or lower vulnerability to predation, and P_2 as the secondary prey, or the "victim" of apparent competition.

In the system of ODEs (eqns 4.1 – 4.3), the densities change in response to the current state of the system. However, predator populations in nature often exhibit time lags in their response to changes in prey populations (Mech 1977, Gasaway et al. 1983, Krebs et al. 2001). I modified Equation 4.3 so that the rate of change in predator density is a function of the prey densities T_d units of time earlier:

$$\frac{dC(t)}{dt} = C(t) \cdot \left(\frac{b \cdot a \cdot (P_1(t - T_d) + P_2(t - T_d))}{1 + a \cdot T_h \cdot (P_1(t - T_d) + P_2(t - T_d))} - m \cdot C - h\right) \qquad \text{eqn 4.4}$$

Model assumptions

All models make simplifying assumptions and this one makes many. Because it is a system of ODEs, events like reproduction and death occur continuously. Furthermore, I ignored seasonal differences that affect the spatial overlap among prey and predators, and did not account for any social organization of prey or predator. In other words, the predators and prey were freely moving independent particles. The assumptions about social organization are important when it comes to wolf – caribou systems. Wolves are social animals that usually hunt as a pack, but in summer that structure breaks down and varies substantially (Metz et al. 2011). Estimating a and T_h in summer would be impractical because the data do not exist in our system, and are only beginning to be estimated elsewhere (See Chapter 6 and Sand et al. 2005, Metz et al. 2012).

Explicitly incorporating all the above factors could greatly complicate the model. Therefore, I chose to parameterize the model for a simple system involving an asocial predator, cougar (*Puma concolor*), and white-tailed deer (*Odocoileus virginianus*) as the primary prey, with caribou as the secondary prey. Cougar – deer systems predominate to the south of my study area (i.e. south of the Trans-Canada Highway), and are most relevant at the southern limits of mountain caribou distribution (Kinley and Apps 2001). Therefore, the inference from the model's predictions could be applicable in those areas. Because deer and caribou are approximately the same size, I used the same T_h for both species, again allowing the model to remain simple. I assumed that the predator was equally efficient at capturing deer and caribou because there are limited data on this process; therefor a was the same for both prey (but see Haber 1977).

An equally important reason for choosing cougar and deer is that a natural case study exists where I could validate the model, at least qualitatively. In 1997 a severe weather event suddenly reduced deer populations by 70 – 80% in southeastern BC, and deer, cougar and caribou trend data exist to compare against the model's predictions (see Validation section).

Parameter values

The parameter values for the simulations were estimated using a combination of field data from Revelstoke (BC), information from the literature, and educated guesses. In the case of the latter, I varied these less-known parameters to determine how this uncertainty affected the result. Intrinsic growth rates (r_i) for deer and caribou were obtained from Heard (1990) and Hennemann (1983). Hennemann specified r for deer as 0.48, but also presents a relationship indicating that larger animals have lower intrinsic growth. The value 0.48 was for small animals (62 kg) that occupy productive habitats. At the limit of their range in a deep-snow ecosystem, this value would likely be lower, so I used 0.39. The difference between 0.39 and 0.48 yielded results that were only *c*. 4% different (and 0.39 was more conservative). The conversion factor of prey to predators, b, was estimated by dividing the average number of cougar offspring per adult per year by the number of deer eaten per year. Assuming predator satiation, T_h was estimated as the inverse of the number of deer eaten per year per cougar (~30; Bird et al. 2010, Knopff et al. 2010).

Fryxell et al. (2006) estimated a for lions (*Panthera leo*) by taking the product of their velocity, search buffer, and attack success, providing a value with the units km^2 / time. I took a similar approach using cougar data from Bird et al. (2010), which was collected in my study area. The mean distance covered per day was approximately 2.9 km, and I assumed a search buffer of 300 m and an attack success of 0.1. Thus, I set a = 32 km^2/yr. Yet, to deal with the uncertainty of a and to make the inference of the model applicable to predators beyond only cougars, I varied a from 22 to 46 km^2/yr. For simplicity, T_h and a were the same for both prey. The carrying capacity of caribou (K_1) was based on the number of caribou per area of old forest when caribou populations were stable to increasing, in the early 1990s (Wilson 2006). Deer carrying capacity (K_2) was based on expert opinion. There is much uncertainty in the estimates of the K_i, but more important than the absolute values is the ratio of K_1 to K_2. I varied the deer carrying capacity (K_1) and held the caribou carrying capacity (K_2) constant because the former was more closely linked to deer food production as a result of forest harvesting, and thus provided a link to management. In summary, unless specified otherwise, the baseline parameters used for the model were: r_1 = 0.39 yr^{-1}, r_2 = 0.25 yr^{-1}, T_h = 0.035 yr, K_1 = 1.0 individuals/km^2, K_2 = 0.4 individuals/km^2, m = 30 yr^{-1}, b = 0.032, a = 32 km^2/yr, h = 0, and T_d = 1 yr (unless specified). T_h, m, b, K_2 and the r_i were always held constant, but the other parameters were varied to incorporate uncertainty but more importantly to address the specific objectives of this chapter (see Scenarios and Simulations section).

Scenarios and simulations

Before modelling different scenarios, I wanted to ensure that the model correctly represented the process of apparent competition. This hypothesis predicts that prey species with lower intrinsic growth rates and/or a higher risk of death once encountered (i.e. foraging efficiency, *a*), would exist at lower equilibrium or be driven to extinction (Holt 1977). Although I held *a* constant for both species, caribou have lower intrinsic growth rates (*r*) relative to moose and deer (Shackleton 1999), likely because they are adapted to living in resource-poor environments. Therefore, having a higher growth rate (r) for P_1 relative to P_2 (i.e., $r_1 > r_2$) was sufficient to evaluate the model's ability to represent apparent competition.

After this evaluation, the model was used to answers five questions relating to the recovery of the rarer species, the secondary prey. Specifically, I wanted to know how the abundance of secondary prey was affected by:

1. the magnitude of the reduction of primary prey,
2. the relative carrying capacities (K) of primary and secondary prey,
3. time lags of the predator's numerical response (T_d),
4. management of the predator (*h*), and
5. a gradual reduction of the primary prey (i.e. through hunting), as opposed to a sudden decline (i.e. a stochastic weather event).

To answer questions 1– 4, I reduced the primary prey abundance in one instantaneous time step. First, I had to ensure that all populations were at equilibrium, and I did this by running the model for 1000 years, which I called t_1, and was always sufficient to achieve a steady state for the parameter space I used. Then, I reduced the primary prey abundance instantaneously by a specified percentage (0 – 90%). This range included the 82% reduction (95% CI: 71 – 90%) suggested in the previous chapter. This reduced value became a new initial condition for the primary prey, but the other two species retained the values from the time step before the primary prey reduction. After this perturbation, the system eventually goes back to its equilibrium. However, I focused on the transient dynamic of the model and recorded the first minimum value of the secondary prey P_2^{min} following the reduction of the primary prey. I then considered the percent change of the secondary prey from its equilibrium value P_2^* as $100*(P_2^{min} - P_2^*) / P_2^*$, which was the primary response metric for all analyses.

To answer the 5th question, I repeated the above process but with one modification. To evaluate the effect of gradually reducing the primary prey, I subtracted a constant G from Equation 4.2, that was non-zero only for n time steps between t_1 and t_1+n. For a given n, I chose the magnitude of G, such that the density of P_1 at time $t_1 + n$ was at a certain proportion of the pre-reduction (equilibrium) density. In other words, G is the hunting rate necessary to achieve the management target after exactly n years. This two-point boundary value problem with an unknown parameter was solved using the shooting method (Heath 2002). The model was implemented in R 2.15 (R Core Team 2012), and the PBSddesolve package (Schnute et al. 2008) was used to solve the differential equations (complete R code for the model is available upon request).

Following this perturbation, all simulations had an oscillation where prey and predators increased in abundance beyond their equilibrium values before returning to the equilibrium (see Results). I did not consider the portion of the transient phase beyond the decline of all three species because there is little reason to believe that temperate systems are equilibrium-based and will always return to prior values following a perturbation. I address this topic further in the Discussion.

RESULTS

The model reflected the basic prediction of predator-mediated apparent competition because as the carrying capacity of the primary prey increased, so did the equilibrium density of the predator, and the equilibrium density of the secondary prey declined (Fig. 4.1).

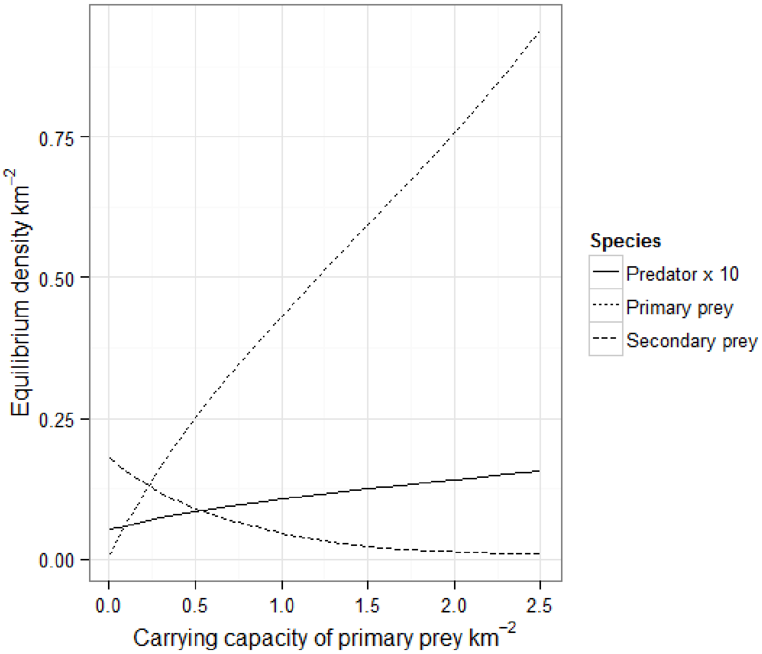


Figure 4.1. Equilibrium densities of all three species as a function of the carrying capacity of the primary prey. All other parameters were held constant.

Time series representations of the model with a crash of the primary prey resulted in an initial decline of the secondary prey and the predator, followed by an oscillation of all three species back to their equilibrium values (Fig. 4.2). The oscillation lasted about one phase. In this example, an 82 % crash of the primary prey combined with a 2-year lag of the predator response resulted in a 17.9 % reduction of the secondary prey (Fig. 4.2).

The magnitude of reduction of the secondary prey increased with an increasing carrying capacity of the primary prey (Fig. 4.3), an increasing time lag of the predator’s numerical response (Fig. 4.4), but was inversely related to the predator's mortality rate (Fig. 4.5). In all cases, as the magnitude of the (instantaneous) decline of the primary prey increased, so did the magnitude of decline of the secondary prey (Fig. 4.3 – 4.5). The most severe reductions occurred when the primary prey's carrying capacity approached 2.5/km^2 or if the time lag of the predator exceeded two years, and in these cases the reductions ranged from 20 – 30% (Figs. 4.3 and 4.4). Predators with lower foraging efficiency for a given prey species had less of an impact on the decline of the secondary prey (Fig. 4.6), but the effect appeared unimodal because at very high efficiency values, the effect on the secondary prey appeared to stabilize or decrease slightly.

Increasing the time to reduce primary prey to the management target reduced the magnitude of decline of the secondary prey (Fig. 4.7 and 4.8). The magnitude of decline of secondary prey was lessened by the greatest rate if the primary prey decline was spread out over 5 to 10 years, and if the predator's numerical response lagged the prey's abundance (Fig. 4.8).

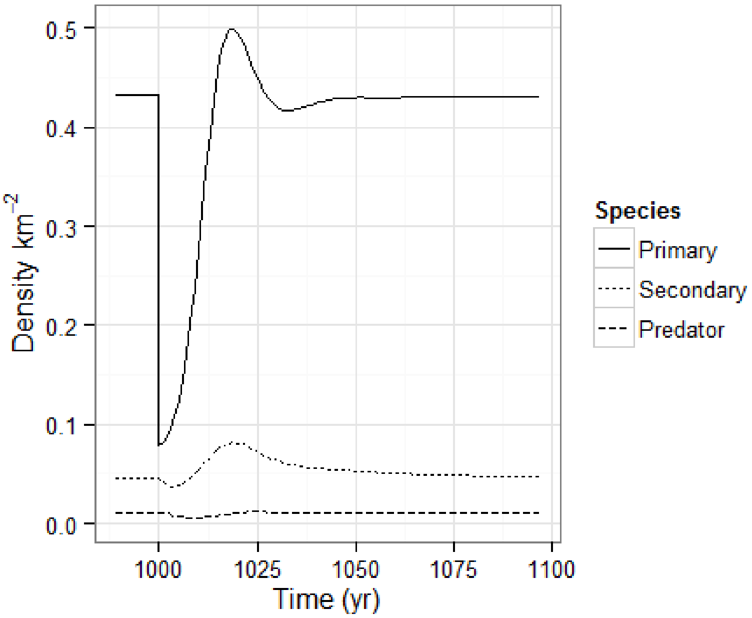


Figure 4.2. A time series of the model simulation with an instantaneous 82% crash of the primary prey. The change in the secondary prey's density from its equilibrium value represents a drop of 17.9%. In this case the predator's numerical lag was 2 years.

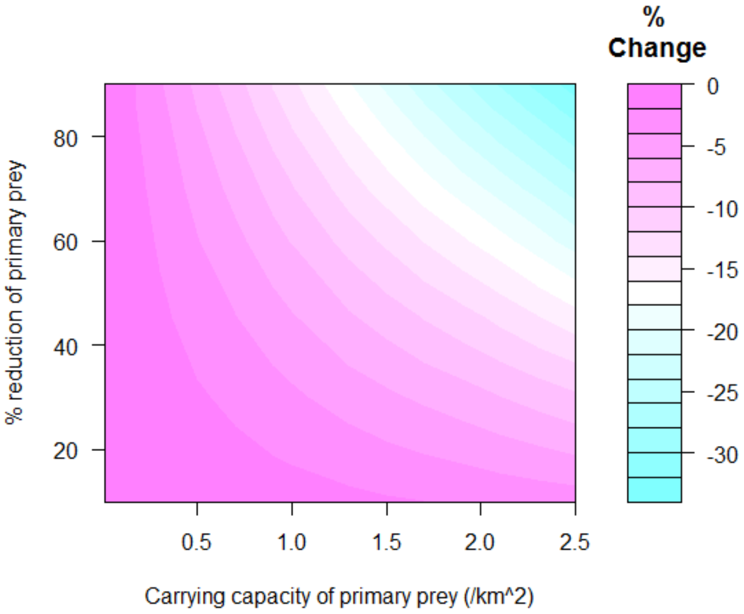


Figure 4.3. Change in density of the secondary prey (as a percent of the equilibrium value), as a function of the primary prey's reduction (%) and the carrying capacity of the primary prey.

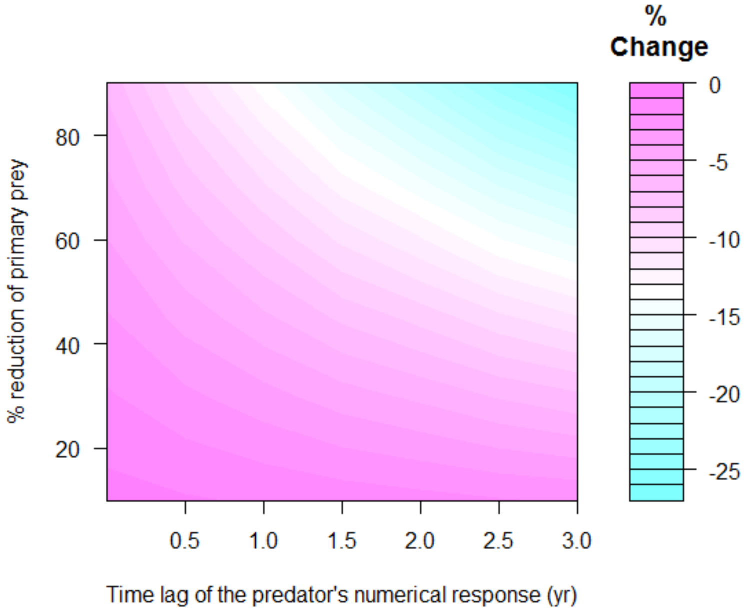


Figure 4.4. Change in density of the secondary prey (as a percent of the equilibrium value), as a function of the primary prey's reduction (%) and the time lag of the predator's numerical response.

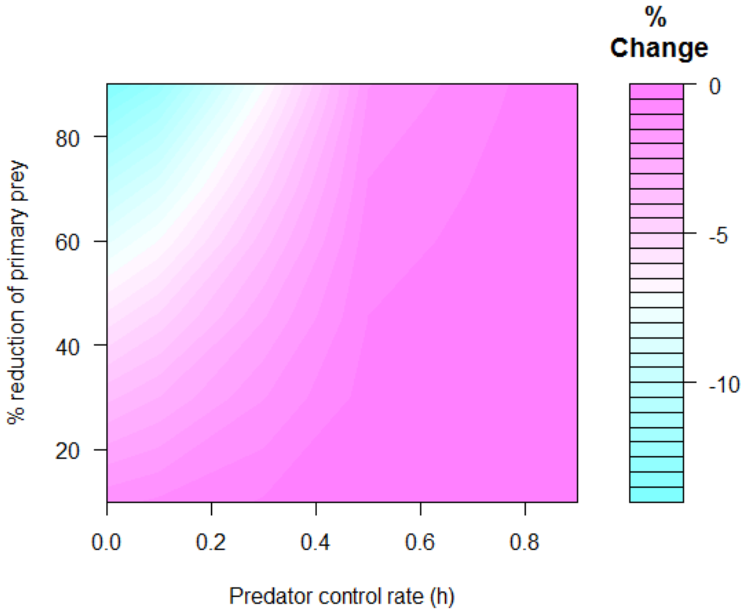


Figure 4.5. Change in density of the secondary prey (as a percent of the equilibrium value), as a function of the primary prey's reduction (%) and the rate of predator control, *h*.

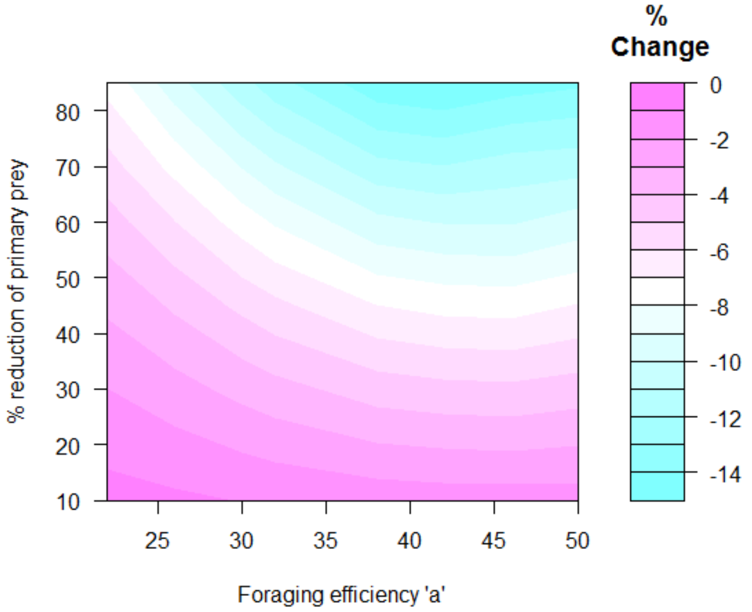


Figure 4.6. Change in density of the secondary prey (as a percent of the equilibrium value), as a function of the primary prey's reduction (%) and the foraging efficiency (*a*) of the predator.

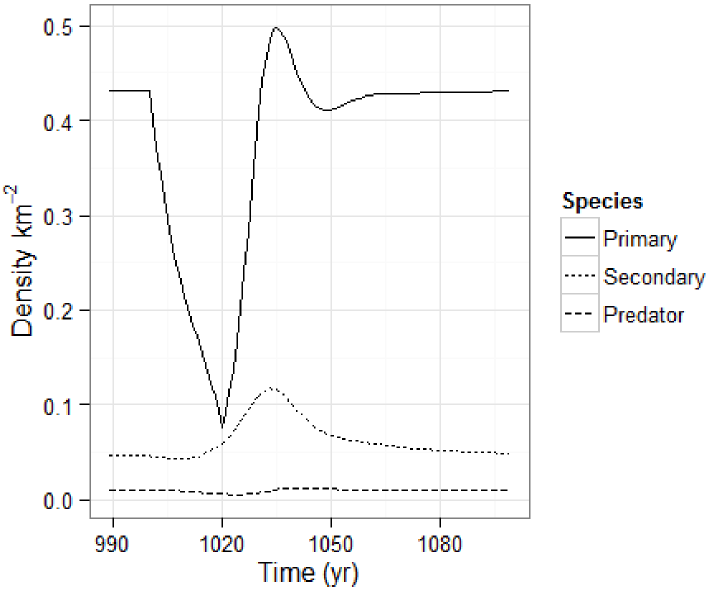


Figure 4.7. An illustration of a gradual reduction of the primary prey by 82%, spread out over 20 years. The change to the secondary prey in this case is –6.8%, compared to –17.9% from Fig. 4.2 where the primary prey decline was instantaneous.

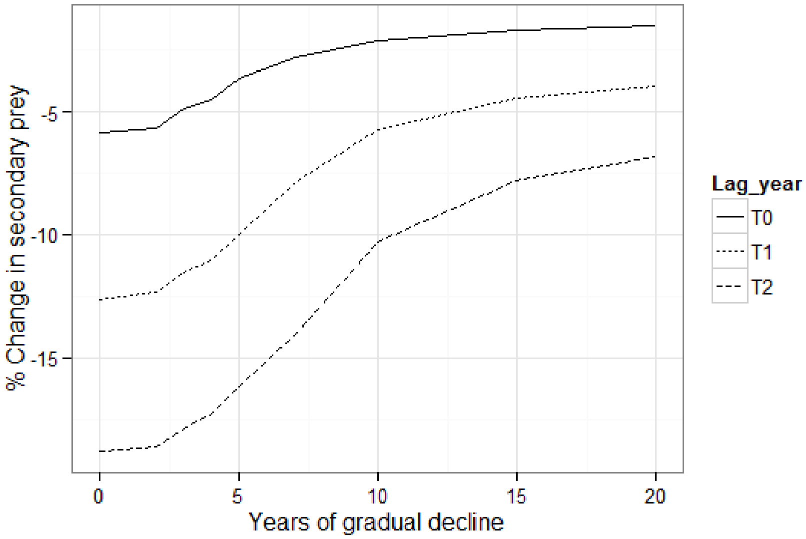


Figure 4.8. The percent change in secondary prey as a function of how spread out the decline is for the primary prey. Results are stratified by an immediate numerical response of the predator ($T_d = 0$), along with a lag of 1 and 2 years ($T_d = 1$ and $T_d = 2$).

A qualitative validation of the model

I compared the model's predictions to a case where deer populations declined suddenly following an extreme snow event in 1997 (Fig. 4.9). Deer and cougar trend data were based on catch-per-unit-effort harvest (CPUE) indices. For deer, the index was the percent of hunters successfully killing a deer, based on hunter survey data. Two independent indices of cougar abundance were used, one based on compulsory reporting of hunted animals, and the second was non-hunting kills from conservation officers. These abundance indices are known to have biases (Walters 2003, Peacock and Garshelis 2006) and should be validated. However, the biases most often occur when humans expand the area being exploited, so a higher CPUE can reflect increased kills but not an increasing animal population (Peacock and Garshelis 2006). In my case I was focussing on population decline, so there is less likelihood that a bias would occur in these cases. The two independent cougar indices matched with a correlation of $r_{pearson}$ = 0.85, suggesting reliability of the trend. Other metrics of ungulate harvests have been validated in my region, particularly for moose (Chapter 4 and 6). Caribou population estimates were based on censuses updated from Wittmer et al. (2005), and see details in Chapter 6.

Following the deep snow event during the 1997 winter, the deer CPUE during the next fall's hunting season (fall 1997) was substantially reduced (Fig. 4.9), suggesting a much reduced deer population. Cougar populations began to decline 1 – 2 years thereafter. In 1998 there was a peak of cougars killed by conservation officers, likely reflecting hungry cougars searching more broadly and having more human conflicts near settled areas. From 1997 to 2002, the caribou populations in the Revelstoke area declined by approximately 40%. From the time radio collaring began in 1992, to 1997, 129.1 caribou-years of telemetry data were collected. During this period, one collared caribou was killed by a cougar – in 1996 when the cougar population was near its peak. In the two years following the deer crash, based on 65.3 collar-years of data, three collared caribou were killed by cougars.

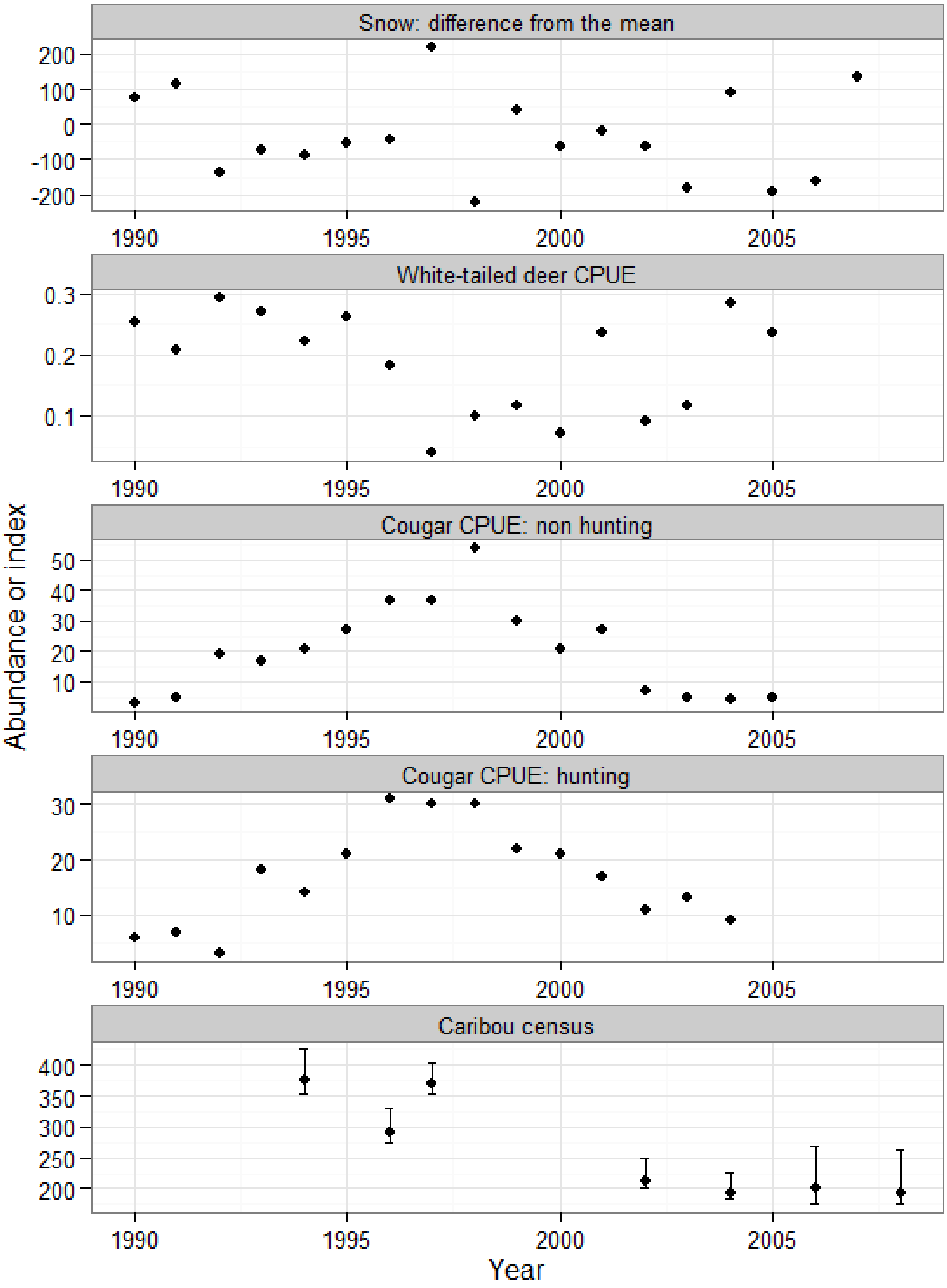


Figure 4.9. The abundance of abiotic and biotic components in the ecosystem. Snow fall (cm) represents the difference from the mean value (mean = 396 cm, n = 100 yr), in the City of Revelstoke, BC. Deer represents catch per unit effort harvest data for three management units within and adjacent to the study area, two independent measures of cougar abundance (hunter kills and conservation officer kills, r = 0.85) for the Kootenay

region, and caribou abundance from winter censuses for subpopulations in the Revelstoke area (Wittmer et al. 2005a). 1997 was an extreme snowfall year that appeared to initiate some major changes in the ecosystem.

DISCUSSION

My objective was to use theoretical predator-prey equations to answer five questions to determine how to reduce apparent competition for an endangered species, with a specific focus on reducing primary prey. The scenerios I developed represented some of the key factors linked to the process of apparent competion affecting woodland caribou throughout North America (Seip 1992, Schaefer 2003, Courtois et al. 2007, Wittmer et al. 2007, Latham et al. 2011). By varying the carrying capacity of the primary prey, I was representing either climate change or forest harvesting, both of which influence the abundance and distribution of moose and deer (Rempel et al. 1997, Dawe 2011). Increasing the predator's mortality rate reflects the option of conducting predator control. Finally, a sudden reduction in primary prey could represent a stochastic weather event, as was shown in the validation case study, whereas gradually reducing the primary prey was more likely to reflect an intentional management action.

Reducing primary prey to counteract apparent competition is increasingly suggested as a strategy to recover a secondary prey species that is at risk of extinction (Courchamp et al. 2003, James et al. 2004, Weclaw and Hudson 2004, Steenweg 2011, Wittmer et al. in press). But my analysis highlights important risks that may not have been anticipated when this recovery option was suggested. My results predict higher losses to the secondary prey when there are more primary prey, and a greater instantaneous reduction of those primary prey. In biological terms, the more deer in the system, the more predators can be sustained and switch to caribou if deer are reduced. However, the model suggests that the magnitude of the caribou loss can be reduced if predators are removed following periods of sudden collapses in primary prey. This approach has also been proposed by Norbury (2001) for conserving native skinks (*Oligosoma* spp.) in New Zealand following sudden declines in rabbit (*Oryctolagus cuniculus*) abundance, because of the predators shared by the two prey. Short-term predator control may be even more effective when we consider that time lags of the predator's response to a lower deer density greatly increased the modelled predation rate on caribou. Predator time lags of 1 – 2 yr, or longer, have been observed in many terrestrial systems (Krebs et al. 2001, Mech 1977).

Two other modeling exercises involving predator-mediated apparent competition (Courchamp et al. 2003, Zhang et al. 2006) suggested caution in reducing primary prey in the absence of predator reductions, and my simulations matched their predictions. The novel questions I addressed dealt with the time lag of the predator's numerical response, and whether spreading out the prey's decline over a number of years would benefit or harm caribou. Predictably, increasing the predator's time lag had a strong influence on the amount that caribou were reduced. Gradually reducing the primary prey provided some benefit, though it was most pronounced if the reduction was spread out over 5 – 10 years. Gains were modest if spread out over <5 years, which is a typical management window for most harvest agencies. Of the 18 mountain caribou subpopulations, only one exceeds 500 in number, and most are less than 100. With these small numbers, any loss increases extinction risk (Shaffer 1981). Therefore, a concurrent predator reduction would be of greater value than relying solely on primary prey reduction, even if the prey reduction is spread out over a number of years. This is an important result for management agencies that are considering a broad-scale manipulation of the predator-prey system to try and recover endangered caribou or other species at risk from apparent competition (DeCesare et al. 2010).

In Chapter 3, I suggested that moose numbers could be reduced by 82% to approximate an ecological population target. The species involved in this chapter were different, with parameters based on deer and cougar because they were more likely to meet the model's assumptions, parameter estimates were more readily obtained, and a natural, sudden, and severe deer reduction existed to help validate the model. Changing the carrying capacity of the primary prey and the predator's attack rate makes the model and its predictions applicable to a variety of species, possibly including moose and wolves. Once more information is gained on the attack rate of wolves, particularly in summer where such data are rare (see Chapter 6, and Metz et al. 2012), this model could be revisited. Nonetheless, the qualitative predictions of the model are relevant, particularly in the southern third of mountain caribou distribution. These predictions suggest that a substantial reduction in primary prey (> 80%) could produce a loss of seconday prey by 10 to 30%, depending upon the primary prey's carrying capacity, the predator's time lag and its efficiency at consuming a given prey.

My qualitative attempt at validation suggests that the model underestimates the magnitude of reduction for the secondary prey. For an 80 to 85% reduction in primary prey, the model predicts a 12 to 19 % reduction in caribou, depending if I assume a 1 or 2 year lag of the predator's numerical response. In comparison, the caribou population in my study area declined by >40% following the collapse of deer populations over a similar time period. Mountain caribou are affected by more than just deer-cougar dynamics, because they are also consumed by bears and wolves (Wittmer et al. 2005a). These mortality sources are likely cumulative because mountain caribou are far below their forage-based carrying capacity, when density dependent changes in vital rates are unlikely to occur (Fowler 1981, Wittmer et al. 2005b). Moose populations doubled from 1994 – 2003 (Chapter 3), likely resulting in increased wolf abundance during the time period that coincided with the deer collapse and subsequent cougar decline. These important ecosystem dynamics were not captured with the simple model used here. Allee effects have also been documented with these same mountain caribou populations (Wittmer et al. 2005b), and this mechanism was not included in the ODEs, again leading to an underestimate of impacts. Finally, I used the same predator foraging efficiency for both deer and caribou, though there are indications that caribou are more vulnerable than other cervids once encountered by a predator (Haber 1977). The simulations suggest that a higher foraging efficiency on a given species would increase its losses following the perturbation. A combination of these factors probably explains why the model underestimated the magnitude of decline in real caribou populations.

Two improvements to the model could be made to add realism. First, by ignoring the spatial separation that occurs between caribou and predators for about

25% of the year (Stotyn 2008, Bird et al. 2010, Appendix 6.2), the model likely overestimates impacts to caribou from reducing the primary prey. A spatial component could be added to estimate how much spatial separation would buffer the impact to caribou. On the other hand, by assigning the same predator attack success for both primary and secondary prey, impacts to the secondary prey (caribou) were likely underestimated. The relative benefit to caribou of spatially separating from predators, compared to the caribou's increased vulnerability to predation, could be clarified with sensitivity analyses. These modifications would help refine predictions, but would not change the qualitative conclusions derived from the model.

A key assumption of this work is that the density-independent reduction of the primary prey occurs when all species are at coexistence equilibrium. However, caribou, other ungulates and their shared predators may not be at equilibrium when the primary prey reduction occurs. Due to changes in climate and habitat, all densities are subject to continuous change (Andrewartha and Birch 1954, Chesson and Case 1986). Consequently, the sudden or gradual reduction of primary prey might be superimposed on a changing density, which makes it more difficult to attribute impacts of the deer reduction to caribou. Future work could be to develop techniques for quantifying indirect effects of perturbations to systems that are changing concurrently.

My approach may be criticised because I focussed only on the declining portion of the transient phase, not the subsequent oscillation including population increase with the eventual return to equilibrium. In reality, the management intent would be to maintain P_1 at the reduced level and not let it recover to the previous equilibrium. I did not specifically simulate this because the result would be as predicted in Figure 4.1 – an improvement for caribou. However, any return to equilibrium is predicated on the concept of 'balanced' equilibrium systems, which ecologists have questioned repeatedly since Charles Elton first pointed out this simplistic view in the 1930s (Andrewartha and Birch 1954, Connell and Sousa 1983, Chesson and Case 1986, Connell et al. 1997). If systems are dominated by changing environments with frequent destabilizing events, then focussing on the initial transient phase becomes increasingly appropriate. This contemporary view of community ecology has become particularly relevant in a world where the magnitude and frequency of environmental stochasticity is expected to increase (Easterling et al. 2000). Even if increases in stochastic events fail to materialize, there is growing recognition that stochastic pulses can play a key role in shaping community structure (Holt 2008).

Ultimately, reducing primary prey is expected to increase caribou abundance, as Figure 4.1 illustrates. This conclusion essentially ignores any transient dynamics and is an oversimplification. Reduced population sizes generated during the transient phase are subject to stochastic processes and Allee effects. An extension of the model that accounts for both of these factors could be used to quantify the change in extinction risk that occurs during the transient phase.

LITERATURE CITED

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. The University of Chicago Press, Chicago.

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

Bird, C., R. Clarke, D. Lewis, and R. Serrouya. 2010. Cougar ecology, predation, and caribou in the Columbia Mountains of British Columbia. Fish and Wildlife Compensation Program – Columbia Basin, Nelson, British Columbia.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications **9**:751-771.

Chesson, P. L., and T. J. Case. 1986. Overview, nonequilibrium community theories: chance, variability, history, and coexistence. Pages 229-239 *in* J. Diamond and T. J. Case, editors. Community Ecology. Harper & Row, New York.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs **67**:461-488.

Connell, J. H. and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist **121**:789-824.

Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. Science **302**:1532.

Courtois, R., J. P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience **14**:491-498.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada. University of Alberta, Edmonton.

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.

Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology **89**:952-961.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science **289**:2068-2074.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology **62**:602-610.

Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. American Naturalist **138**:478-498.

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

Gregory, R., D. Ohlson, and J. Arvai. 2006. Deconstructing adaptive management: Criteria for applications to environmental management. Ecological Applications **16**:2411-2425.

Gunderson, L. and S. S. Light. 2006. Adaptive management and adaptive governance in the Everglades ecosystem. Policy Sciences **39**:323-334.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. University of British Columbia, Vancouver.

Heath, M.T. 2002. Scientific computing. An introductory survey. McGraw-Hill, Boston, Mass.

Hebblewhite, M. 2013. Consequences of ratio-dependent predation by wolves for elk population dynamics. Population ecology **In press**.

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.

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

Holt, R. D. 2008. Theoretical perspectives on resource pulses. Ecology **89**:671-681.

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

Kinley, T. A. and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin **29**:158-164.

Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. Journal of Wildlife Management **74**:1435-1447.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001. Ecosystem dynamics of the boreal forest: The Kluane Project. Oxford University Press, New York.

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.

McLellan, M., R. Serrouya, B. McLellan, K. Furk, D. Heard, and H. Wittmer. 2012. Implications of body condition on the unsustainable predation rates of endangered mountain caribou. Oecologia **169**:853-860.

Mech, L. D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. Journal of Mammalogy **58**:559-574.

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

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**:553-563.

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.

Mosnier, A., D. Boisjoly, R. Courtois, and J. P. Ouellet. 2008. Extensive predator space use can limit the efficacy of a control program. Journal of Wildlife Management **72**:483-491.

Norbury, G. 2001. Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced rabbits. Journal of Applied Ecology **38**:1350-1361.

Peacock, E. and D. L. Garshelis. 2006. Comment on "On the regulation of populations of mammals, birds, fish, and insects'' IV. Science **313:**45.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

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

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

Rosenzweig, M. L. and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist **97**:209-223.

Sand, H., B. Zimmermann, P. Wabakken, H. Andrèn, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin **33**:914-925.

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

Schnute, J. T., A. Couture-Beil, and R. Haigh. 2008. A User’s Guide to the R Package “PBSddesolve” Version 1.05 – August 20, 2008.

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.

Shackleton, D. 1999. Hoofed mammals of British Columbia. UBC Press and the Royal Bristish Columbia Museum.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. Bioscience **31**:131-134.

Steenweg, R. 2011. Interactions of wolves, mountain caribou, and an increased moose-hunting quota - primary-prey management as an approach to caribou recovery. University of Northern British Columbia, Prince George, British Columbia.

Theberge, J. and G. Walker. 2011. Managing for caribou and ecological integrity: reply to Serrouya and Wittmer 2010. Conservation Biology **25**:858-859.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology **80**:1236-1245.

Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Canadian Journal of Fisheries and Aquatic Sciences **60**:1433-1436.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Wasser, S. K., J. L. Keim, M. L. Taper, and S. R. Lele. 2011. The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands. Frontiers in Ecology and the Environment **9**:546-551.

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

Wittmer, H. U., L. M. Elbroch, and A. J. Marshall. In press. Good intentions gone wrong: did conservation management threaten endangered huemul deer in the future Patagonia National Park. Oryx.

Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, G. S. Watts, and D. Hamilton. 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. N. McLellan, R. Serrouya, and C. D. 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. R. E. Sinclair, and B. N. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

Zhang, J., M. Fan, and Y. Kuang. 2006. Rabbits killing birds revisited. Mathematical Biosciences **203**:100-123.

CHAPTER 5

TESTING PREDATOR-PREY THEORY USING BROAD-SCALE MANIPULATIONS AND INDEPENDENT VALIDATION

A primary goal in ecology is to identify principles that are general enough to transcend ecosystems, but useful enough to make predictions within specific study areas (Levins 1966, Krebs 2009). This undertaking is particularly challenging in field ecology because complex and often unpredictable relationships can obscure our basic understanding of how natural systems operate (Strong 1986, Doak et al. 2008). Yet, if ecological relationships can be applied across systems, even when parameterized with independent data, then this approach constitutes one of the strongest means of validating whether the theory is an accurate portrayal of the observed patterns.

Predation is a fundamental ecological interaction and its effects are continually debated in the literature (Schmitz et al. 2000, Shurin et al. 2002), even within a specific study system (Post and Stenseth 1998). The impacts of predation have reportedly ranged from compensatory (Errington 1946, Vucetich et al. 2005), to limiting (Gasaway et al. 1983), to regulating prey populations (dependent on prey densities; Messier 1991, 1994). These distinctions have important implications for the structure of ecological communities. If predation is completely compensatory, then it does not have an effect on the equilibrium abundance of prey, whereas equilibrium prey density is reduced if predation is limiting (Sinclair and Pech 1996). Finally, if predation is regulating, it is possible that multiple equilibria can be established (Messier 1994), and predation becomes a key mechanism promoting the coexistence of predators and prey due to the feedback between the two trophic levels.

For vagile and large-bodied animals, the most relevant scale to investigate factors limiting population growth is at the ecosystem level, and in recent decades ecologists have been urged to use management experiments to achieve this goal (Walters and Holling 1990, Doak et al. 2008). Several ambitious management experiments have been attempted to quantify the effect of predation on large-mammal communities (Hayes et al. 2003, Hurley et al. 2011). Although there are notable exceptions (Hurley et al. 2011), predator removal experiments often result in increased recruitment or abundance of prey, particularly when predation is a substantial component of prey mortality (Bergerud and Elliot 1986, Hayes et al. 2003, Krebs 2011). However, although predator removal experiments reveal the degree that predation is compensatory or additive, they do not address whether it is regulating (Boutin 1992). An alternative experiment that is only recently receiving attention involves manipulating prey numbers to evaluate the role of predation. This experiment is important for two reasons: 1) By varying the abundance of prey, its per-capita predation rate (PCPR) can be estimated across a range of prey densities. This approach will help resolve whether predation is density independent, dependent, depensatory (i.e. inversely density dependent), or compensatory; and 2) A number of species are endangered because of predator-mediated apparent competition between prey (DeCesare et al. 2010), and it remains unknown whether reducing the overabundant prey will help reduce predation on the rare and declining prey (Serrouya et al. 2011, Steenweg 2011, Wittmer et al. 2013).

In my system, I made use of a broad-scale experiment to evaluate the impact of wolf (*Canis lupus*) predation on moose (*Alces alces*) by reducing moose density using sport hunting across a 6,500 km^2 area. The treatment was to increase the number of moose hunted by a factor of 10 for three years, with an associated reference area where moose harvests were comparatively stable. Because the moose population continued to decline substantially after the hunting treatment was reduced, it became clear that factors other than hunting were influencing moose population dynamics. What was unclear was the relative importance of these factors. Therefore, my objective was to contrast a set of hypotheses, expressed as mathematical models, to explain the continued decline in moose following the cessation of high human harvest. I tested four hypotheses as to the role of wolf predation in the system: it was completely compensatory, density dependent, density independent, or depensatory (i.e. PCPR increased as moose densities declined; Fig. 5.1). The last hypothesis is of particular interest because its prediction was modeled by Messier (1994) as a unimodal predation rate, but has received little field validation (but see Hossie and Murray 2010). For each of these models I took a reductionist approach by decomposing the PCPR into functional and numerical responses, because it was these fundamental relationships that were used to generate the PCPR curves (see Fig. 5.1). My fifth hypothesis was that hunting was not a factor in the decline, but the decline was driven solely by predation, so to be conservative I modeled the most severe form of predation, where it was depensatory.

The strength of my approach was that I compared alternative hypotheses using functional and numerical response models that were parameterized with independent empirical data (i.e. data collected outside my study system) from meta-analyses with spatial replication (Messier 1994, Fuller et al. 2003). If these independent equations could reliably predict moose population dynamics in this experimental system, then not only would their generality be supported, but so would the theoretical relationships that are used to predict the magnitude of predation. This type of independent validation rarely occurs in field ecology (Vucetich et al. 2011), particularly for large mammal systems.

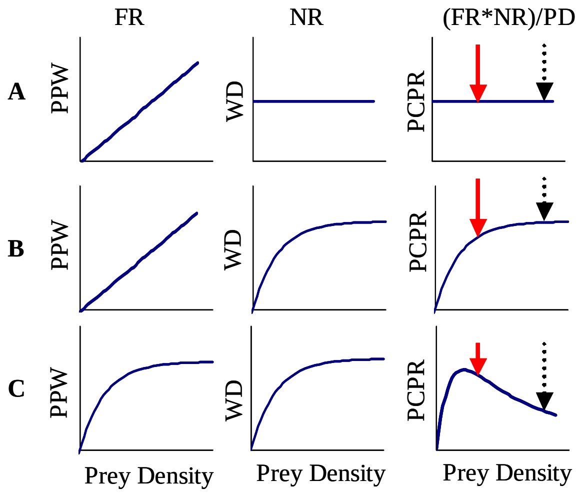


Figure 5.1. Predation-related hypotheses of the moose decline based on different per capita predation rates (PCPR), generated from varying the form of the functional (FR) and numerical response (NR). PPW is prey consumed per wolf and WD is wolf density. See text for details. A) a Type I FR and Type 0 NR yields a density independent PCPR; B) a Type I FR and Type II NR yields a density dependent PCPR; C) a Type II FR and Type II NR can transition from a depensatory PCPR to a density dependent PCPR. For scenario B, this can also be achieved by reversing the forms of the FR and NR (i.e. a Type II FR and

Type I NR). Dotted arrow and red arrow respectively indicate the hypothetical moose population at the beginning and latter part of the moose reduction.

In addition to the basic relationships presented above, many other factors can affect predator-prey dynamics including time lags of the predator's numerical response (Gasaway et al. 1983), alternative functional response relationships (e.g., ratio dependent; Jost et al. 2005), body condition mediated by winter severity (Hurley et al. 2011) or summer nutrition (Brown 2011). Including all these possible combinations would result in many candidate models to apply to a single study system with the possible criticism of data dredging (Burnham and Anderson 2002). Therefore, I restricted the initial analyses to the five hypotheses presented above, but then conducted post hoc, heuristic analyses to incorporate time lags and alternative functional responses. I also include wolf functional and numerical response data from my study system (Chapter 6) to determine if local information improved the outcomes predicted by the independent data of Messier (1994) and Fuller et al. (2003). Finally, I discuss my results in the context of other systems that have been subjected to increased human exploitation, but where there was little consideration of how changes to the per capita predation rate may have contributed to population decline.

STUDY AREA AND METHODS

The study occurred in a 9400 km^2 area along three parallel mountain ranges oriented N-S in the interior of British Columbia, Canada: the Selkirk, Monashee, and Cariboo mountains. The treatment area was 6500 km^2, and was bounded by the Selkirk and Monashee mountains (which are part of the Columbia Mountains). The reference area was 2900 km^2, was between the Monashee and Cariboo mountains (Fig. 5.2), and had similar ecosystem characteristics (precipitation, temperature, forest composition; Meidinger and Pojar 1991). These areas range from 500 m asl in valley bottoms to mountain peaks reaching 3500 m. The climate is wet, with >200 cm of annual precipitation, most of which falls as snow. Forests are highly productive and consist primarily of western red cedar (*Thuja plicata*) and hemlock (*Tsuga heterophylla*) trees at low elevations, and subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea engelmannii*) at higher elevations (> 1300 – 1500 m asl). Regenerating cut blocks include willow (*Salix* spp.), cottonwood (*Populus balsimifera*), red-osier dogwood (*Cornus stolonifera*), huckleberry (*Vaccinium membranaceum*), falsebox (*Paxistima myrsinities*), thimbleberry (*Rubus parviflorus*), and Indian hellebore (*Veratrum viride*).

Large mammals consist of wolves, black and grizzly bears (*Ursus americanus* and *U. arctos*), and moose. Cougars (*Felis concolor*), mule and white-tailed deer (*Odocoileus hemionus* and *O. virginianus*), mountain goats (*Oreamnos americanus*), and woodland caribou (*Rangifer tarandus*) also occur but are uncommon. Moose densities in 2003 were 1.58/km^2 in the treatment area. In 2007 moose were surveyed in both the treatment and reference area and density estimates were the same, at 0.96/km^2 (Serrouya and Poole 2007).

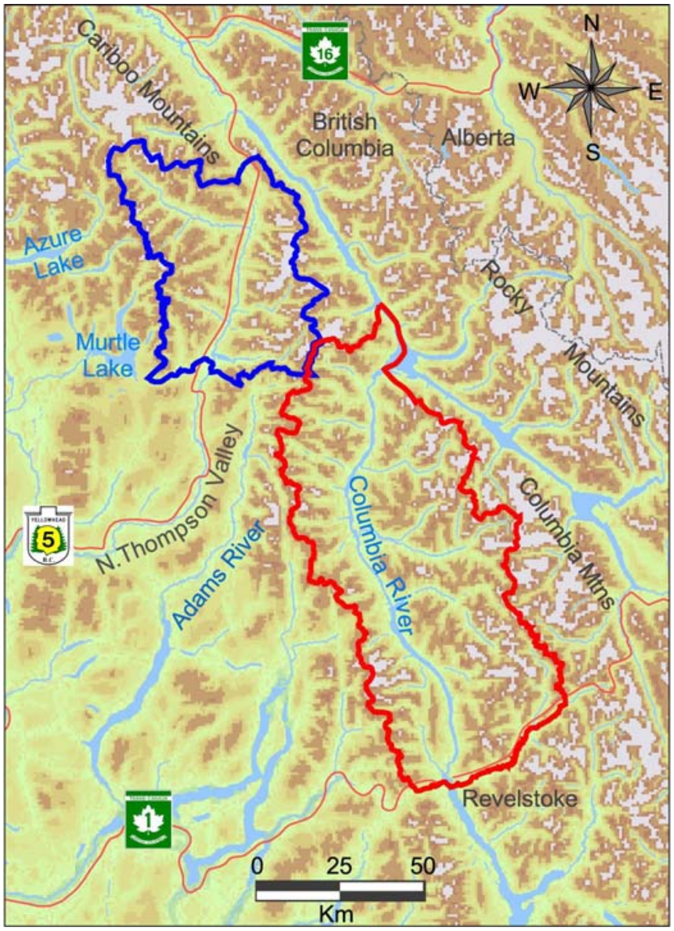


Figure 5.2. Study area, with the moose reduction treatment area outlined in red and the reference area in blue.

Moose reduction and hypothesis testing

The moose reduction began in the treatment area with a 10-fold increase in hunter harvest from 2003 to 2005, followed by a much reduced harvest level (Table 5.1). During the decade preceding the increased harvest, the moose population doubled (Serrouya et al. 2011, Chapter 3), and harvest was light (<4%, males only). No major change to moose hunting allocations occurred in the reference area (Table 5.1), and wolf harvest was not manipulated in either area during the study. Moose abundance was estimated in the treatment area based on aerial censuses and annual transects where pellets were counted and cleared each spring in 100-m^2 plots (details in Chapter 3 and Serrouya et al. 2011). In the reference area, only one moose population estimate was done (Serrouya and Poole 2007), so I relied on catch per unit effort (CPUE) data to compare population change between reference and treatment areas. CPUE is fraught with biases (Walters 2003, Peacock and Garshelis 2006) that are rarely evaluated, but I had the ability to independently assess the reliability of the CPUE. This evaluation was done by correlating moose population estimates in the treatment area with CPUE data for that same area, and the correlation was r = 0.91 (Appendix 5.1). The comparison of moose trend between the treatment and reference areas served to determine whether the moose decline in the treatment area was initiated by hunting, or broad-scale climatic factors that are known to affect large-mammal predator-prey systems (Post and Stenseth 1998, Vucetich et al. 2005, Murray et al. 2006, Brown 2011).

Table 5.1. Harvest levels of moose in the treatment and reference areas. The moose reduction treatment began in 2003.

Year	Treatment	Reference
2000	18	9
2001	19	8
2002	13	10
2003	164	11
2004	250	19
2005	128	17
2006	46	16
2007	29	8
2008	27	10
2009	49	13
2010	27	11

My approach was to use difference equations to represent competing hypotheses to explain the magnitude and causes of the moose population decline (Table 5.2). The equations included variables with both known (i.e., estimated) and unknown values. Estimates included the annual moose population size, ratios of adult females, calves and adult males, hunting mortality and natural, but non-predation mortality (i.e., accidents or poor condition; Table 5.2). Condition-related mortality included malnutrition, potential disease or old age. The difference equations were programmed in MS Excel and can be used as a tool by managers to potentially predict short-term moose population dynamics with certain key inputs obtained from the field, including recent harvest estimates and calf:cow ratios.

Table 5.2. Model structure for each hypothesis used to explain the decline of moose.

Hypothesis[1]			Births	Calf deaths	Condition deaths	Hunting deaths	Wolf predation deaths[2]
Hunting caused the decline, no predation	$N_{t+1}=$	N_t	$+ N_b$	$- N_{dn}$	$- N_{dc}$	$- N_{dh}$	
Hunting, and Predation is DI (Fig. 1a)	$N_{t+1}=$	N_t	$+ N_b$	$- N_{dn}$	$- N_{dc}$	$- N_{dh}$	$- aNC_0$
Hunting, and Predation is DD (Fig. 1b)	$N_{t+1}=$	N_t	$+ N_b$	$- N_{dn}$	$- N_{dc}$	$- N_{dh}$	$- aNC_2$
Hunting, and Predation is DD and DEP (Fig. 1c)	$N_{t+1}=$	N_t	$+ N_b$	$- N_{dn}$	$- N_{dc}$	$- N_{dh}$	$-aNC_2/(1+aNT_h)$
Predation is DD and DEP, but no hunting	$N_{t+1}=$	N_t	$+ N_b$	$- N_{dn}$	$- N_{dc}$		$- aNC_2/(1+aNT_h)$

[1] DD is density dependent, DI is density independent, and DEP is depensatory

[2] *a* is the attack rate for the Type I or II functional response, *Th* is the handling time from the Type II functional response, N is moose abundance, C_0 is wolf abundance that does not change with moose abundance, C_2 is wolf abundance that changes asymptotically with moose abundance (equation from Messier 1994).

Recruitment and sex/age composition were estimated from aerial censuses, and births were estimated by multiplying the pregnancy rate (89.7 %) by the number of adult females. The number of adult females was obtained from composition data based on aerial surveys, and ranged from 47 to 57 % of the population. Calf recruitment (CR, ratio of 8-month-old calves to adult females) was found to be density dependent based on data from Serrouya et al. (2011) and was represented by $CR = -0.21 \times \ln(MA) + 1.75$, where MA is moose abundance. I calculated the number of calf deaths by subtracting the number of 8-month-old recruits (based on the CR equation above) from the number of births (Table 5.2). These calf deaths were likely caused by a variety of factors (bears, wolves, nutrition) that were not estimated separately, but were simply treated as calf deaths. Hunting deaths were estimated by the BC government using annual harvest questionnaires and compulsory reporting from guides and resident hunters (BC Government data files; values are in Table 5.1).

Condition-related mortality was estimated based on radio-collar assisted mortality investigations and analysed using the Heisey-Fuller approach (Heisey and Fuller 1985). Condition-related deaths may have been caused by poor nutrition, disease or old age but were grouped to estimate natural (but non-predation) mortality. To help reduce possible biases associated with differential mortality risk throughout the year, I chose 12 risk periods corresponding to each calendar month. Annual survival rates were calculated from the product of the 12 monthly rates. Monthly survival rates were calculated by exponentiating the daily survival partitioned within each month, by the number of days within that month. Daily survival was calculated as 1 – (no. deaths) / (∑ monitoring days in the corresponding month). Annual survival rates were used to determine whether survival and recruitment values could corroborate the observed population decline, but annual survival was not required in the difference equations (Table 5.2). Uncertainty was calculated using 1000 bootstrap replicates using Pop Tools (Hood 2010) in Excel using the individual animal as the sample unit.

The unknown value in the difference equations was predation deaths due to wolves, and the magnitude of predation was treated as competing hypotheses based on the forms in Fig. 5.1, with the equations detailed in Table 5.2. I used an approach based on first principles by varying the type of the FR and NR to obtain the predation rates, using existing equations from the literature. The per capita predation rate was calculated as PCPR = (FR × NR)/ Prey density (Holling 1959b, Messier 1994). Predation was density independent if there was a Type I FR and a Type 0 NR (Fig 5.1a, Table 5.2). The wolf abundance was set at 33.2 for the Type 0 NR, based on 1650 moose and the equation from Fuller et al. (2003). Predation was density dependent if there was a Type I NR with a Type II FR, or if there was a Type II FR with a Type I NR (Fig. 5.1b). Predation was depensatory if both the FR and NR were Type II, but transitioned to density dependent at lower prey densities (Fig. 5.1c; Messier 1994). Parameters for the Type I and II NRs were obtained from Fuller et al. 2003, and Messier 1994, respectively.

Parameters for *a* and *Th* (the attack rate and handling time, respectively; Holling 1959a) for the functional response were estimated based on Messier (1994) (See Appendix 5.2 for details).

I also tested the hypothesis that predation was compensatory by completely removing wolf predation from the model. Because wolf diets in the treatment area consist mainly of moose (Stotyn 2008, Chapter 6b), removing this source of mortality from the model implies that wolf predation was compensatory. Similarly, I removed hunting from the model to test whether this factor was compensatory. This approach allowed me to compare the relative influence of predation vs. hunting to explain the magnitude of the moose population decline. In summary, five alternative hypotheses with associated predictions were compared, four involving predation of various forms, and the fifth included only hunting (Table 5.2).

Heuristic models

In addition to the primary hypotheses outlined above, I considered the following modifications: time lags of the wolf numerical response, a ratio-dependent functional response, a function accounting for compensatory predation that was density dependent (i.e. stronger at higher moose abundance, rather than dichotomously compensatory or not, Appendix 5.3), and derivation of parameters from my study system as opposed to the literature (Appendix 5.2). I included a 1-year time lag of the wolf numerical response by setting the wolf population as a function of the previous years' moose abundance, and predicted that this would increase the predation rate because moose were declining. The ratio-dependent functional response was calculated as kill rate = (*a* MA) / (P + *a* MA *Th*), where P is the predator abundance (Abrams and Ginzburg 2000).

To determine if local data improved the general predictions from the broader research (Messier 1994, Fuller et al. 2003), I included FR and NR response data from the treatment area. I obtained a new functional response curve by estimating parameters for *a* and *Th*, using Messier's data but supplemented with 11 winter kill rate estimates from five wolf packs during the moose decline in the treatment area (see Appendix 5.2

for parameter estimation). I also estimated *a* and *Th* using the local data only, though fitting a disc equation curve to 11 data points may be suspect. In any case, I assessed the influence of including local data in two different ways, once by adding them to the Messier data, and once by treating the local data on their own. I also used empirical wolf abundance estimates from my system (Chapter 6a) that were available from 2007 – 2012 instead of the independent predictions from Messier's (1994) Type II NR and Fuller et al. (2003) Type I NR, again to determine if local data improved predictions. I assessed each hypothesis using predicted vs. observed plots of population trajectory, using three criteria: slope and intercept closest to 1 and 0 respectively (i.e., perfect fit or accuracy), and by comparing the residual sums of squares (RSS) among models. This approach was preferable to the AIC metric because I was dealing with independent validation, whereas AIC makes use only of RSS, and does not account for model accuracy (i.e. slope and intercept).

RESULTS

Based on the CPUE data, moose declined in the treatment area 4.6 times more than in the reference area (Fig. 5.3), and the decline was highly significant in the treatment area but non-significant in the reference area (slopes were –6.27 [–8.10 to –4.60] compared to –1.35 [–3.58 to 1.11], for the treatment and reference areas, respectively). In the treatment area, radio-collar data indicated that annual adult moose survival was 0.815 (0.723 – 0.886, 95% CI). This estimate was based on 89.6 moose-years of monitoring 54 moose (39 F, 15 M). For just adult females, the survival rate was 0.828 (0.713 – 0.925). For larger cervids, this survival rate, coupled with observed calf:cow ratios that ranged between 22 and 35%, is suggestive of a declining population (DeCesare et al. 2012) and corroborates the trend observed in the treatment area. Seventeen moose deaths were recorded (11 F, 6 M), with six (35.3%; 3 F, 3 M) caused by hunting, five from predation (29.4%; 4 F, 1 M), four were from unknown causes (23.5% 3 F, 1 M), one from an MVA (5.9%; 1 M) and one from poor body condition (5.8 %; 1 F). Unknown deaths were not caused by vehicle collisions, but were likely caused by either predation, poor nutrition, or natural accidents. To be conservative and not overemphasize the top-down effects of predation or hunting, I assigned one unknown cause, that may have been an accident, as a natural (non-predation) death. Thus, the annual death rate from condition/accidents was 0.024 (0 – 0.066) and was treated as a density independent rate in the difference equations (Table 5.2).

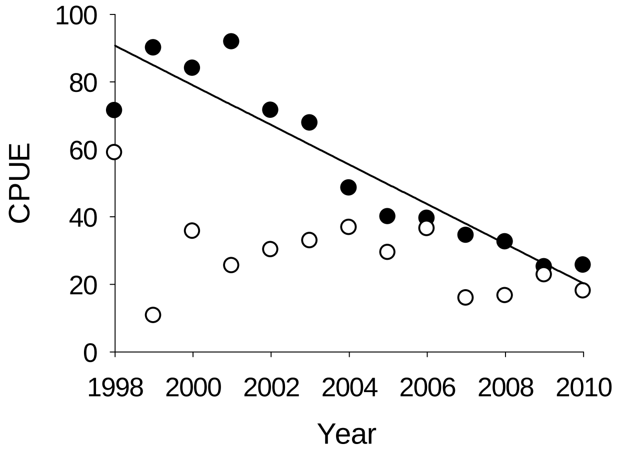


Figure 5.3. Catch per unit effort (CPUE; % hunter success) of moose harvest in the treatment (solid circles) and reference (open circles) area. The slope of the treatment area is –6.27 (–8.10 to –4.60), but non-significant for the reference (–1.35, –3.58 to 1.11). CIs were obtained from bootstrapping years (n=1000). CPUE data were validated with empirical abundance data from the treatment area (Appendix 5.1).

Hypotheses explaining the moose decline

Models that excluded either hunting or predation failed to predict the magnitude of the observed moose decline. However, models that included predation (without hunting) produced a much more realistic population decline compared to the effect of hunting without predation (Fig. 5.4). Including hunting, without any effects of predation (i.e. compensatory predation), produced the least plausible explanation because it predicted an increasing moose population (Fig. 5.4). Of the models that included predation, those using a Type II NR and FR provided the best explanation of the decline, indicating that the predation rate was depensatory (Fig. 5.1c) for the initial phase of the decline (from 2003 – 2006). Evidence supporting the depensatory hypothesis was strongest because its goodness-of-fit plot included a slope closest to 1, intercept closest to 0, and lowest deviation from predicted values (lowest RSS; Fig. 5.5a). Models that included predation, but without a depensatory component did not predict the same magnitude of the moose decline (Fig. 5.4, Fig. 5.5a). These models overestimated the moose population by at least 70%, based on abundance values in 2011 (Fig. 5.4).

The heuristic models including variations such as predator time lags, a ratio-dependent functional response or local data produced two improvements over the basic models (Fig. 5.5a vs. 5.5b). The model with depensatory predation that was supplemented with a function that accounted for density dependent compensatory predation mortality (i.e. compensation that was strongest at high moose densities; Appendix 5.3) produced an accurate prediction of the moose decline. Relative to all other models, this model had the lowest RSS (147656) and a slope closer to 1 (Fig. 5.5a, b). The model with only the local FR and NR data from the treatment area produced a similar slope (1.32), but it was less precise (RSS = 317016). The models that included local FR and NR data to supplement Messier's Type II FR (Table 5.3b) did not produce any improvement over the models with only Messier' data (Fig. 5.3a). Considering all 15 models, those that had a depensatory predation component (i.e., Type II NR and Type II FR) had slopes closer to 1 and a lower RSS. Models with time lags or the ratio-dependent functional response were not well supported (Fig. 5.3b).

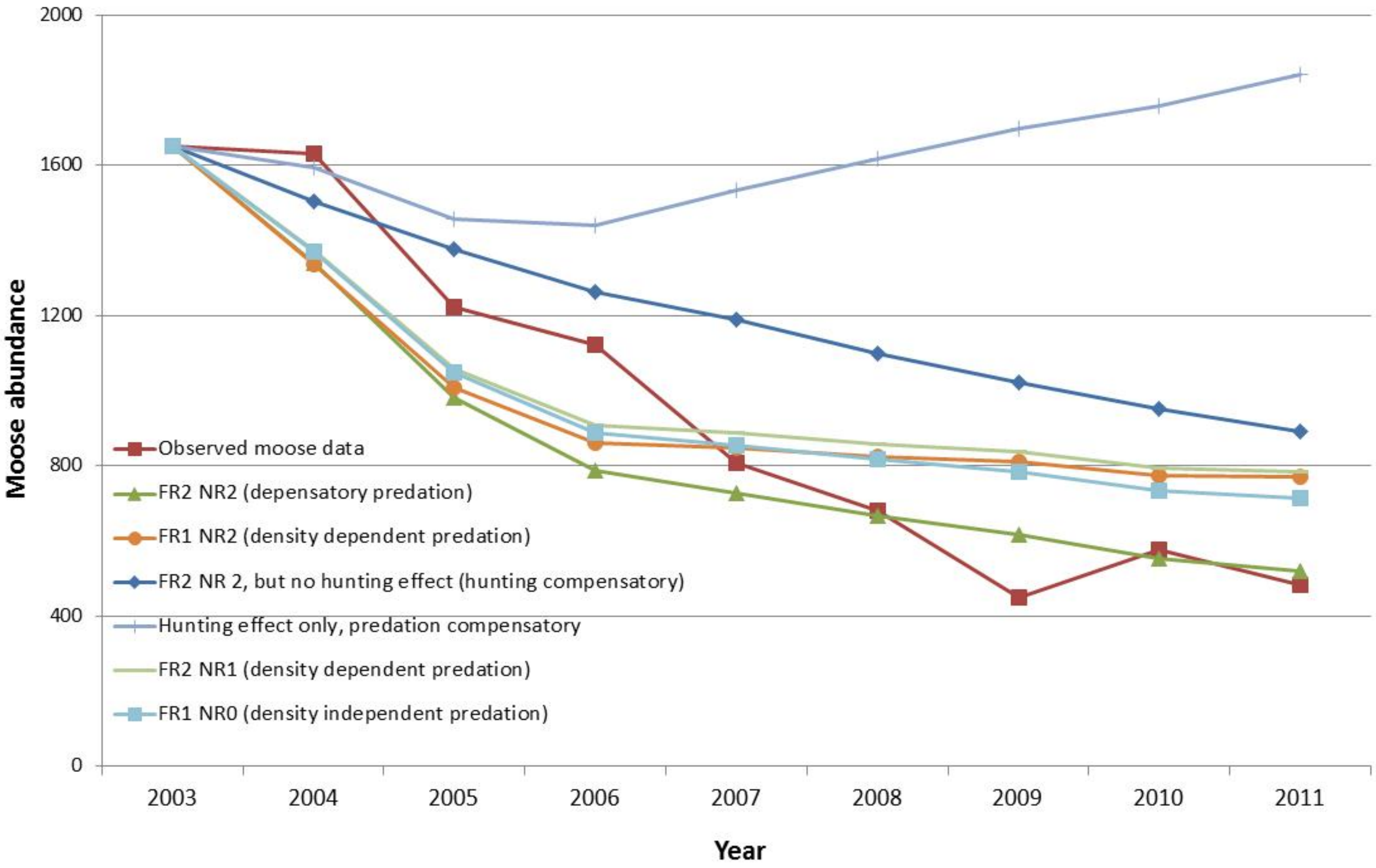
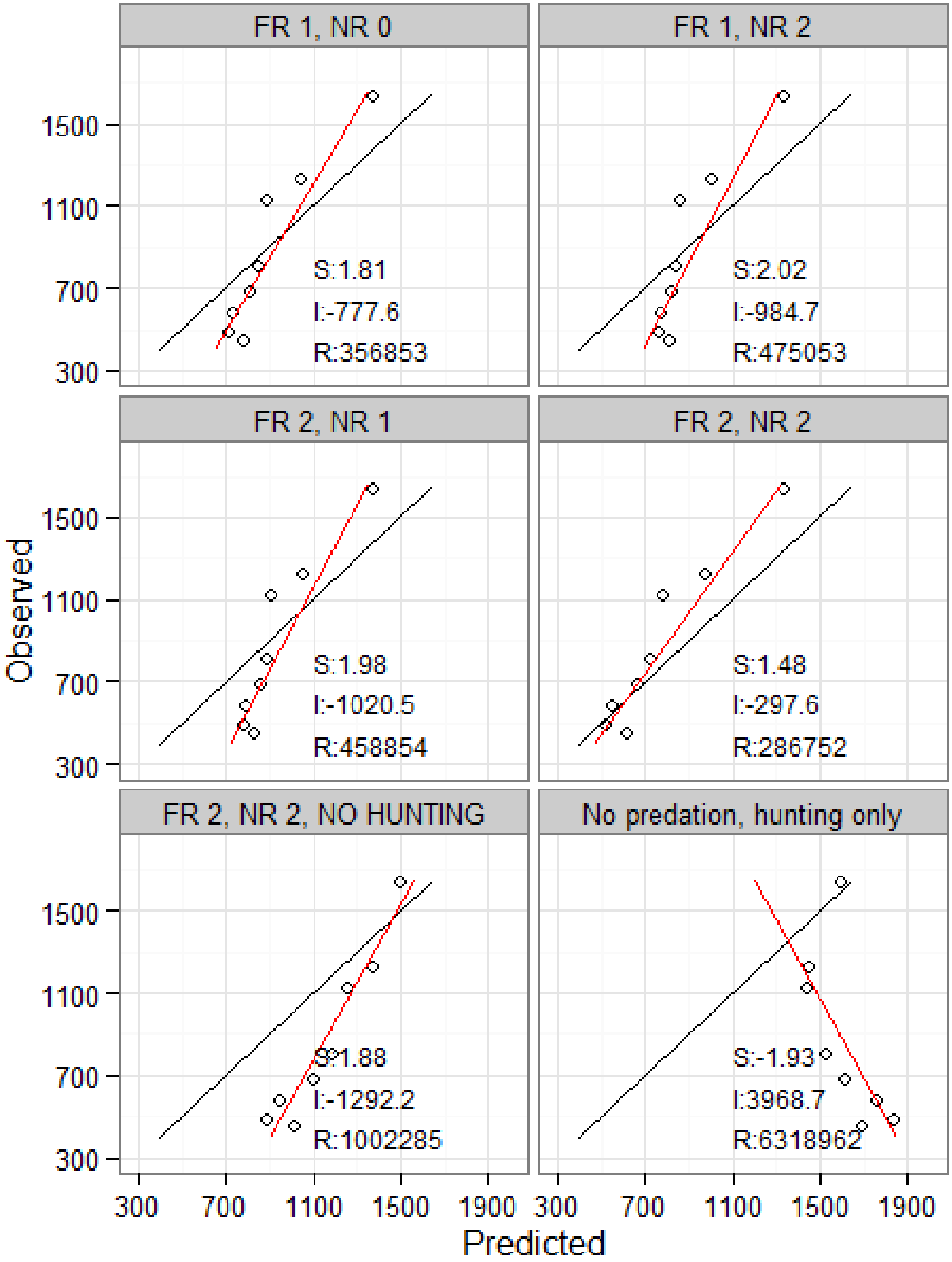


Figure 5.4. Comparison of model predictions to observed moose abundance. Hypotheses are: hunting caused the decline (thus predation was compensatory), predation caused the decline (FR2 NR2) and no effect of hunting, or hunting and predation but predation was 1) depensatory (FR 2, NR 2); or 2) density independent (FR1 NR0); or 3) Density dependent (FR 1 NR 2 or FR2 NR 1).

A)


FR 1, NR 0
S:1.81
I:-777.6
R:356853
FR 1, NR 2
S:2.02
I:-984.7
R:475053
FR 2, NR 1
S:1.98
I:-1020.5
R:458854
FR 2, NR 2
S:1.48
I:-297.6
R:286752
FR 2, NR 2, NO HUNTING
S:1.88
I:-1292.2
R:1002285
No predation, hunting only
S:-1.93
I:3968.7
R:6318962
Observed
1500
1100
700
300
Predicted
300
700
1100
1500
1900

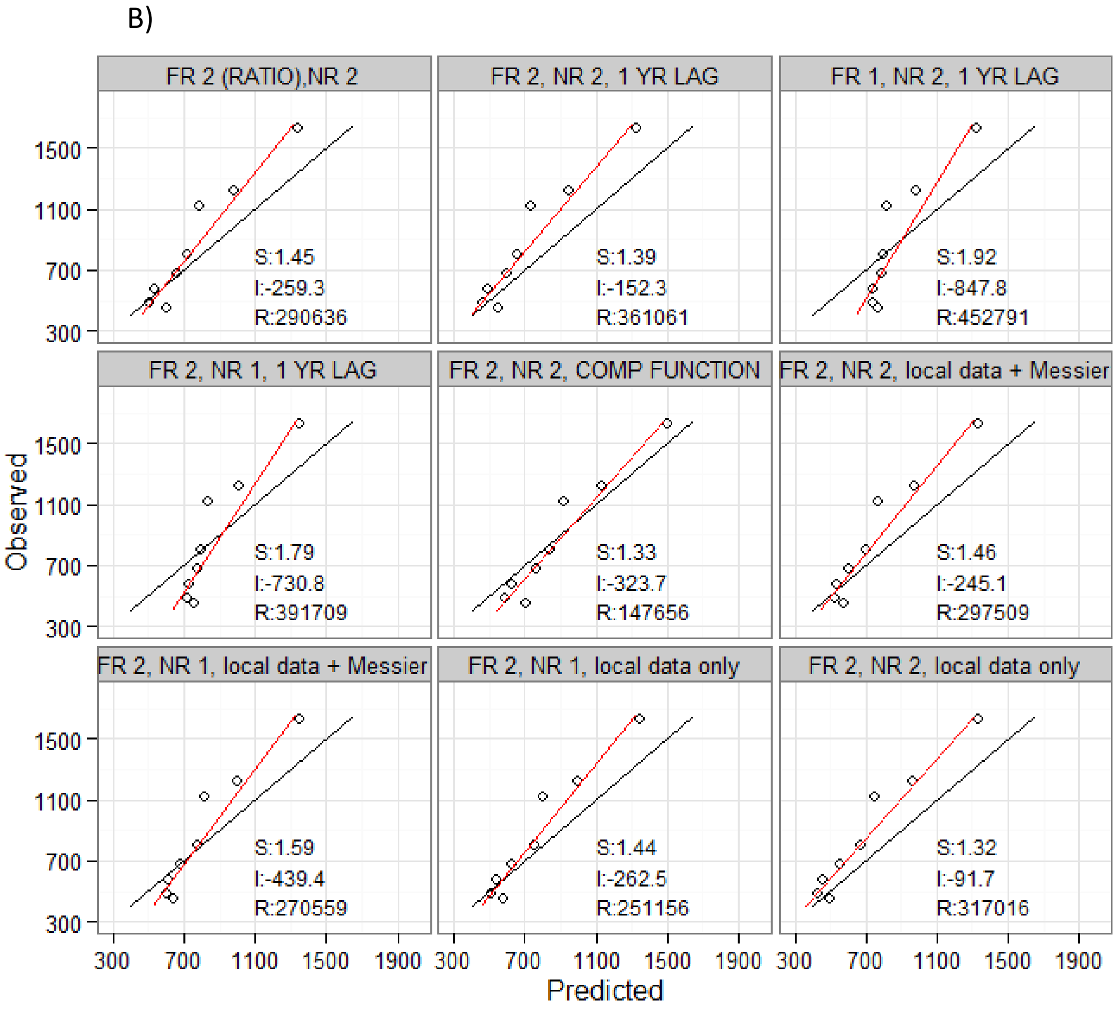


Figure 5.5. Observed vs. predicted validation plots for competing hypotheses used to explain the moose population decline in the treatment area. Panel A shows the initial hypotheses, with FR and NR parameters from outside the study system (i.e. Messier 1994 and Fuller et al. 2003). Panel B shows the heuristic models: COMP FUNCTION = compensatory predation function, RATIO = a ratio-dependent functional response, 1 yr lag = a 1-yr lag of the predator's numerical response to moose abundance. FR = function response, and NR = numerical response, with numbers indicating the Type. S, I and R represent the slope, intercept, and residual sums of squares (RSS), respectively of the goodness of fit (GOF). Models are more accurate with a slope closer to 1 and 0 intercept, and more precise with a lower RSS. Red line is the GOF plot, and black line is the idealized 1:1 plot.

DISCUSSION

My approach was to use predator-prey theory, parameterized with functional and numerical response data from elsewhere, to determine which hypotheses could be used to predict population dynamics at a local scale (Hilborn and Mangel 1997). Although no equation was perfect, it was notable how well some independent relationships predicted population dynamics within the study system. Furthermore, the spatial reference area allowed me to establish that the moose decline observed in the treatment area was not caused by broad-scale climatic processes, but was initiated by the hunting treatment.

Models that included a depensatory predation rate were best able to predict the decline of moose in the treatment area. This finding is consistent with the hypothesis proposed by Messier (1994) who suggested that the combination of Type II functional and numerical responses would produce a unimodal predation rate (Holling 1959b) with a depensatory phase (Fig. 5.1c). Although Messier's functional and numerical responses were parameterized from meta-analyses, the resulting predation rate he modelled has not been specifically evaluated, yet has been suggested as a primary mechanism of moose-wolf dynamics by researchers in both Europe (Jedrzejewski et al. 2002) and North America (Gasaway et al. 1992). The underlying mechanism for a depensatory predation rate is that at high moose density, wolves are satiated by the limitation imposed by handling time. Also at high moose density, wolf numbers are constrained, possibly due to social factors associated with territoriality or strife among packs. Then, as moose are reduced, a similar number of wolves consume a similar number of moose (on a per wolf basis), but out of a smaller moose population, thereby increasing the per capita predation rate on moose. This pattern holds until the inflection point on either the Type II FR or NR is achieved, at which point the predation rate is relaxed.

An unexpected outcome of this work was that supplementing independent predictions with local data (FR and NR of wolves) failed to improve model predictions, despite enormous cost and effort to collect these data. The local data, without the inclusion of data from the literature, helped to refine the accuracy of the predictions, but did so less precisely. These results may be viewed as a failing but also an opportunity: if approximate and short-term predictions are all that are required, then the task of managers is greatly simplified. Using basic parameters that are often collected by management agencies (age and sex ratios and harvest statistics of prey), short-term moose dynamics can be predicted in the absence of local wolf behavioural and numeric data, which are far more difficult to collect. If environmental changes occur that facilitate disease or condition-related mortalities (Murray et al. 2006), then the models' predictions would not hold. Periodic radio-collaring of moose to estimate mortality causes can help safeguard against this risk.

My results are not in agreement with some other large mammal predator-prey systems. Following the reintroduction of wolves in the Yellowstone ecosystem, wolf predation was found to be primarily compensatory when the magnitude of an elk (*Cervus elaphus*) decline was similar to our moose decline (Vucetich et al. 2005). Vucetich outlines several plausible reasons for why predation may have been additive vs. compensatory, yet I suggest an additional explanation that in Yellowstone, wolf predation was a relatively minor component of elk mortality (< 9% but most often <5%, as an annual PCPR; Vucetich et al. 2011), whereas in my system wolves may be a greater source of adult moose mortality (15 to 19% PCPR). These differences highlight the need to focus on major limiting factors when attempting to generalize predator-prey dynamics among ecosystems (Sinclair 1989, Krebs 2009).

The models may be criticised for failing to explicitly incorporate nutritional and climate-related factors that are known to influence population dynamics of large herbivores (Post and Stenseth 1998, Vucetich et al. 2005, Murray et al. 2006, Brown 2011). Yet, several lines of evidence suggest that nutrition and climate were not primary factors of the moose decline, including few mortalities caused by body condition, the adjacent reference area did not show a population decline in the absence of an increased harvest, and the treatment population was initially more abundant but reduced with hunter harvest.

The results from this study have important implications for any organism that is preyed upon but that also has, or will be, subject to increased human exploitation. If sustained harvest models fail to account or at least assess the potential for depensatory predation, then yields may be excessive. The outcome would be a negative feedback loop of increased per capita predation and harvest that would be difficult to reverse even with a substantial reduction in harvest. North Atlantic cod (*Gadus morhua*) stocks were driven to historic lows because of overharvest, but predation by seals continued, which did not decline proportionately in abundance during or after the cod collapse. This would theoretically result in a depensatory predation rate that would accelerate the decline and even inhibit recovery, and evidence of this phenomenon is emerging (Fu et al. 2001, Frank et al. 2005, Trzcinski et al. 2006). To my knowledge, harvesting models do not explicitly account for increasing per capita predation rates and I suggest this would be an important avenue for future work, particularly for systems that are subject to increased harvest by humans or perturbations from other factors.

In the last decade there have been several attempts, across taxonomic groups, to reduce overabundant prey where rare prey are being driven to extinction by predator-mediated apparent competition (Courchamp et al. 2003, Serrouya et al. 2011, Steenweg 2011, Wittmer et al. 2013, Wittmer et al. In press). Yet, if depensatory predation is not accounted for while reducing the overabundant prey, these populations may decline faster than anticipated and exacerbate switching of predators to the rare prey. The outcome may be to unintentionally increase extinction risk to the rare prey. Given these risks, the most prudent action may be to concurrently reduce overabundant prey and predators, and keep prey at low numbers to reduce the need for long-term predator management (Serrouya et al. 2011, Chapter 4).

LITERATURE CITED

Abrams, P. A. and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? Trends in Ecology & Evolution **15**:337-341.

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

Boutin, S. 1992. Predation and moose population dynamics - a critique. Journal of Wildlife Management **56**:116-127.

Brown, G. S. 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. Journal of Animal Ecology **80**:1288-1298.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. 2nd edition. Springer, New York.

Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. Science **302**:1532.

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.

DeCesare, N. J., M. Hebblewhite, M. Bradley, K. G. Smith, D. Hervieux, and L. Neufeld. 2012. Estimating ungulate recruitment and growth rates using age ratios. Journal of Wildlife Management **76**:144-153.

Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology **89**:952-961.

Errington, P. L. 1946. Predation and vertebrate populations. Quarterly Review of Biology **21**:144-177.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science **308**:1621-1623.

Fu, C. H., R. Mohn, and L. P. Fanning. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences **58**:1613-1623.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161-191 *in* D. L. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

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

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

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

Heisey, D. M. and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management **49**:668-674.

Hilborn, R. and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, NJ.

Holling, C. S. 1959a. Some characteristics of simple types of predation and parasitism. Canadian Entomologist **91**:385-398.

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

Hood, G. M. 2010. PopTools version 3.2.5.

Hossie, T. J. and D. L. Murray. 2010. You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. Oecologia **163**:395-404.

Hurley, M. A., J. W. Unsworth, P. Zager, M. Hebblewhite, E. O. Garton, D. M. Montgomery, J. R. Skalski, and C. L. Maycock. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs **178**:1-33.

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

Jost, C., G. Devulder, J. A. Vucetich, R. O. Peterson, and R. Arditi. 2005. The wolves of Isle Royale display scale-invariant satiation and ratio-dependent predation on moose. Journal of Animal Ecology **74**:809-816.

Krebs, C. J. 2009. Ecology: the experimental analysis of distribution and abundance. 6th edition. Benjamin Cummings, San Francisco, Calif. ; London.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B-Biological Sciences **278**:481-489.

Levins, R. 1966. The strategy of model building in population biology. American Scientist **54**:421-431.

Meidinger, D. V. and J. Pojar, editors. 1991. Ecosystems of British Columbia. British Columbia Ministry of Forests, Victoria, British Columbia.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology **60**:377-393.

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

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs **166**:1-29.

Peacock, E. and D. L. Garshelis. 2006. Comment on "On the regulation of populations of mammals, birds, fish, and insects'' IV. Science **313:**45.

Post, E. and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology **67**:537-543.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist **155**:141-153.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785-791.

Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 2011. Developing a population target for an overabundant ungulate for ecosystem restoration. Journal of Applied Ecology **48**:935-942.

Serrouya, R. and K. 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. Unpublished report.

Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197-241 *in* J. M. Cherrett, editor. Ecological Concepts. Blackwell, Oxford.

Sinclair, A. R. E. and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos **75**:164-173.

Steenweg, R. 2011. Interactions of wolves, mountain caribou, and an increased moose-hunting quota - primary-prey management as an approach to caribou recovery. University of Northern British Columbia, Prince George, British Columbia.

Stotyn, S. 2008. Ecological interactions of mountain caribou, wolves and moose in the north Columbia Mountains, British Columbia. University of Alberta, Edmonton.

Strong, D. R. 1986. Density-vague population change. Trends in Ecology & Evolution **1**:39-42.

Trzcinski, M. K., R. Mohn, and W. D. Bowen. 2006. Continued decline of an Atlantic cod population: How important is gray seal predation? Ecological Applications **16**:2276-2292.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology **80**:1236-1245.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos **111**:259-270.

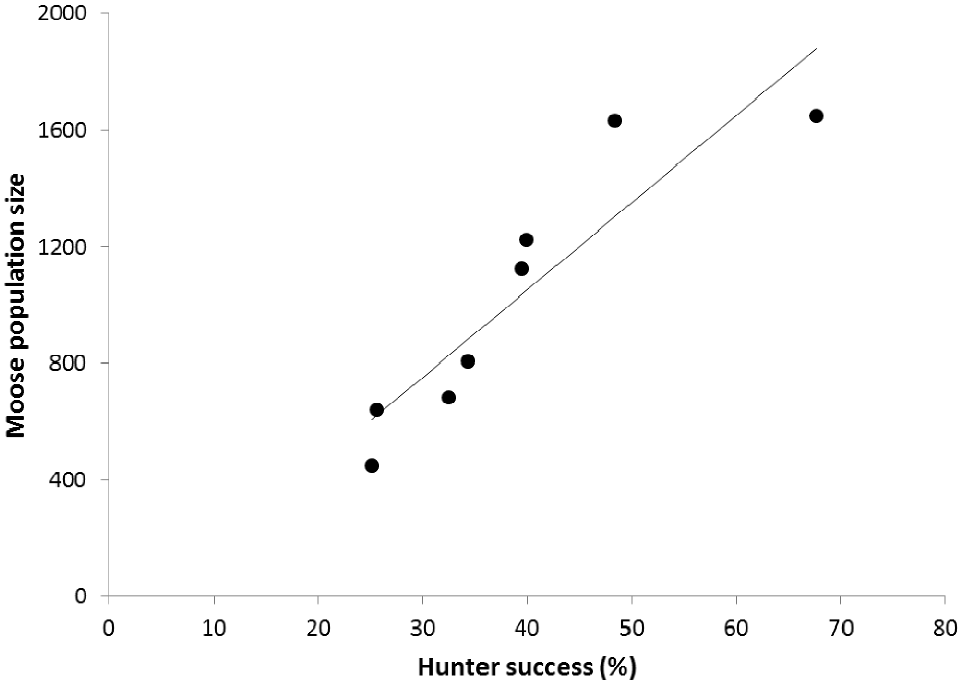
Walters, C. 2003. Folly and fantasy in the analysis of spatial catch rate data. Canadian Journal of Fisheries and Aquatic Sciences **60**:1433-1436.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Wittmer, H. U., L. M. Elbroch, and A. J. Marshall. In press. Good intentions gone wrong: did conservation management threaten endangered huemul deer in the future Patagonia National Park. Oryx.

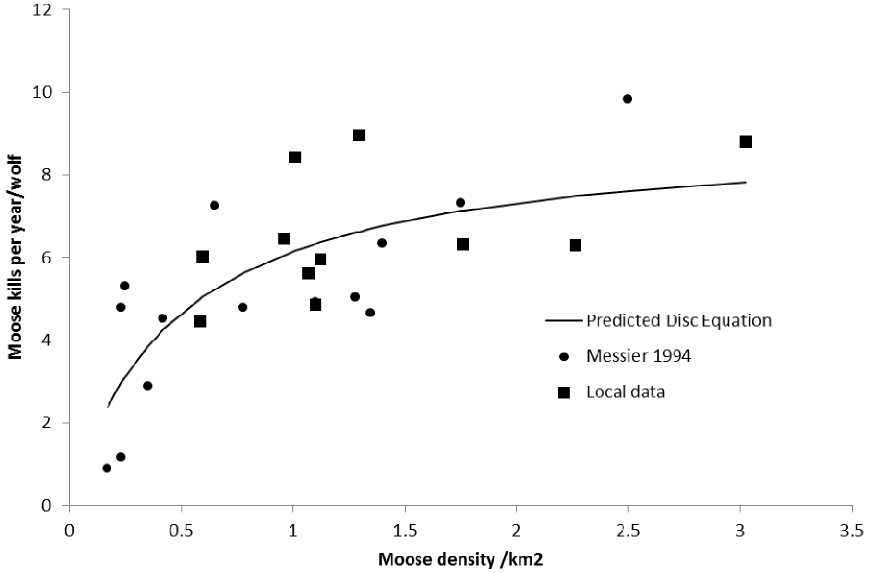
Wittmer, H. U., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation strategies for species affected by apparent competition. Conservation Biology.

APPENDIX 5.1. LINKING MOOSE ABUNDANCE TO CATCH PER UNIT EFFORT DATA.



In the treatment area, the correlation between hunter success and census population size is 0.91. These data were collected annually in the treatment area from 2003 – 2010. The moose population estimate was based on methods outlined in Chapter 3, and % hunter success was estimated from hunter questionnaires (BC Ministry of Environment data files).

APPENDIX 5.2. ESTIMATE OF THE RATE OF DISCOVERY (A) AND HANDLING TIME (TH) FROM HOLLING'S DISC EQUATION



Solver in MS Excel was used to estimate two parameters, *a* and *Th*, based on Holling's disc equation. For parameter estimation, moose density was multiplied by 1100 to represent the actual abundance of moose in the study system, so that a and *Th* were directly usable in the difference equations. *a* and *Th* were estimated with and without the "local data" to be used in the different model scenarios (see Methods). Using Messier's data, *a* = 0.0166 and *Th* = 0.112. Using Messier's plus the local data: *a* =0.0175, *Th* = 0.111. Using only the local data, *a* = 0.0416 and *Th* = 0.135, but *a* is highly non-significant as would be expected with few data and none near the low range. The solid line predicts the Disc equation kill rate for Messier (1994) plus the local data collected in the treatment area. For the Type I FR models, *Th* was set to 0 (by definition), thus *a* was estimated to be 0.0041. Note that the data here differ from Chapter 6 because these are based on kill frequency whereas in Chapter 6 an approximate biomass correction was used.

Messier presented his winter kill rates as moose killed / wolf / 100 d, but scaled this to an annual rate by multiplying by 3.65, then by 0.71 based on an approximation that summer kill rates are lower. I did the same here, so the *a* and *Th* parameters are scaled to an annual rate. It is noteworthy that Vucetich et al. (2011) used the same 0.71 value to calculate annual PCPRs, and suggested that it represented a suitable approximation for wolves in Banff and Yellowstone National Parks.

APPENDIX 5.3: DENSITY DEPENDENT COMPENSATORY PREDATION FUNCTION

In the main analysis predation was either completely compensatory, or completely additive (Table 5.2). Yet, even though per capita predation rates can take various forms (density dependent or independent), animals lost to predation can have a lower impact on the population growth rate at higher prey densities, because animals lost to predation may be nutritionally mediated (Mech 2007). In other words, a proportion of predation may be more compensatory and higher prey density, rather than completely compensatory or not. Vucetich et al. (2005) appeared to show that wolf predation on elk was completely compensatory, but it is likely that such an effect is density dependent. To account for this possibility, I used the following equation:

$$PC = 1.88*MA / (1 - 1.88 * MA * 19.5)$$

where PC is the proportion of mortality that is compensatory, and MA is moose abundance. The value 1 was subtracted from PC, and the resultant was multiplied by the number of deaths due to predation (Table 5.2) to obtain the adjusted predation number, which was then considered additive. Parameters in the above equation were estimated using Solver in Excel. For the range of moose abundance observed in the treatment area from 2003 – 2011, the PC would vary from approximately 0.01 at 400 moose, to 0.08 at 1650 moose.

Literature cited:

Mech, L. D. 2007. Femur-marrow fat of white-tailed deer fawns killed by wolves. Journal of Wildlife Management **71**:920-923.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos **111**:259-270.

CHAPTER 6

EXPERIMENTAL MOOSE REDUCTION TO COUNTERACT PREDATOR-MEDIATED APPARENT COMPETITION WITH ENDANGERED CARIBOU

When species colonize new areas, the consequences for native organisms can be profound, sometimes with positive (Gleditsch and Carlo 2011) but often with negative impacts caused by competition or predation. An exotic predator can have dramatic effects on native prey (Smith and Quin 1996), particularly on islands where prey have evolved few anti-predator strategies (Sinclair et al. 1998). Similarly, extreme forms of interference competition can have pronounced and obvious impacts, such as the invasion of the Eurasian zebra mussel (*Dreissena polymorpha*) into North America where it now dominates available substrate and smothers native bivalves (Ricciardi et al. 1998). In both cases, the ecological interactions can be severe but straightforward to document. Interactions involving indirect processes can be much more difficult to confirm because they are not well explained by simply tracking the abundance of individuals. One such process is apparent competition (Holt 1977), which can occur when a novel prey species occupies a new area, stimulating an increase in the abundance of one or more predator species. The novel prey need not be an introduced exotic, but may be expanding its range either because of natural or anthropogenic factors (Dawe 2011). A secondary, but native prey may then become victim of apparent competition, usually because it is less fecund or less able to escape predation than the novel prey. The secondary prey can be driven to extinction because there is little or no feedback to predator numbers, given that predators are sustained by the more abundant novel prey (Holt 1977, Latham et al. 2011). Identifying this mechanism can be difficult because the cause of the secondary prey's decline could be confused with other indirect interactions such as exploitative competition.

Woodland caribou (*Rangifer tarandus caribou*) represent a classic case of apparent competition, especially the endangered ecotype of mountain caribou that inhabit the interior rain forests of British Columbia and Idaho. Increases in moose (*Alces*

alces) and deer (*Odocoileus* spp.) are the primary factors leading to the unsustainable predation rates facing caribou. Recovery options for mountain caribou can be summarized into three interrelated approaches (Seip 2008). The first is to reduce or eliminate forest harvesting in caribou range because this activity increases forage for moose and deer. Forest harvesting also reduces the abundance of arboreal lichens that are the primary food for mountain caribou during winter. However, the option of reducing forest harvesting, on its own, will not prevent the imminent extinction of many caribou subpopulations (Wittmer et al. 2010) because it will take decades for natural succession to reduce forage for moose and deer. The second option is to directly reduce predator numbers. In numerous systems this approach has been shown to increase caribou vital rates and population trend (Bergerud and Elliot 1998, Seip 1992, Hayes et al. 2003). Predator reduction, however, must be continuous because if the treatment is stopped, predator numbers recover, as long as their primary prey are still abundant (Ballard et al. 1987, Hayes et al. 2003). Predator control is also much less acceptable to the public than it was in the past (Orians et al. 1997, but see Boertje et al. 2010). The third option involves reducing the primary prey that supports predator populations, under the premise that this action will indirectly reduce predator numbers.

In 2003, the Wildlife Branch of the BC Government increased moose hunting permits across a 6500 km^2 area, primarily to increase recreational opportunities for hunters but also to reduce browsing damage to regenerating cedar (*Thuja plicata*) plantations (D'Eon et al. 2003). At this point I began working with government managers and researchers to turn this new policy into an experiment where we could learn about recovery options for mountain caribou. My goal was to implement some basic principles of adaptive management, including linking managers and researchers to identify key treatments and relevant response metrics, consider the appropriate spatial scales to apply the treatment, predict outcomes using computer simulations, and to coordinate research across jurisdictions and agencies. One of the contrasts I measured was a spatial reference area, where a moose reduction was not initiated. Measuring experimental responses in spatial reference areas are often neglected in broad-scale manipulations (Boutin 1992), but help to distinguish between active vs. passive adaptive management (Walters and Holling 1990).

The broad hypothesis I tested was whether reducing moose, the wolves' (*Canis lupus*) primary prey, to an ecological target (Chapter 3) would reduce predator populations and thus positively affect caribou population growth. Although there is intuitive support for this hypothesis, the life-history traits of the main species involved could invalidate this approach as a recovery tool. If predator numbers lag behind the moose reduction (Mech 1977), then the ratio of wolves to prey would increase, which could be detrimental to caribou because they would become a higher proportion of prey available. There is increasing evidence that higher predator to prey ratios translate to higher per capita predation rates (Vucetich et al. 2011). From a behavioural perspective, if wolf foraging follows a "disc-equation" functional response (Holling 1959b, Messier 1994), the prediction would be that as prey are reduced, wolves will spend more time searching and less time handling their primary prey. More searching time could increase encounter rates with caribou, leading to an increased predation rate. Thus, not only do numerical aspects such as predator to prey ratios influence prey vulnerability, but so do behavioural changes that can alter foraging patterns, and both must be considered to properly understand the implications of complex and indirect trophic interactions.

I divided this chapter into two sections; the first addresses the numerical response of moose, wolves, and caribou to increased moose hunting permits. The second section focuses on changes in wolf behaviour as a result of the treatment, by addressing their functional response based on kill rates, movement rates, their habitat overlap with caribou, and changes in wolf diet based on scat analyses.

CHAPTER 6A

THE NUMERICAL RESPONSE OF WOLVES AND CARIBOU TO AN EXPERIMENTAL MOOSE REDUCTION

Because ecosystems are complex, it is important to understand if management actions designed to recover threatened species are actually working. Evaluating the success of these actions usually involves monitoring a population-level response. At times, however, it may also be important to ensure the linkage between actions and responses do fit the mechanistic hypotheses. Ideally, both the ecological processes and abundance can be measured, but in this chapter I focus on the numerical outcome of the treatment, and in the subsequent chapter (6b) I describe some of the behavioural mechanisms underlying why the system responded as it did.

Recent recovery actions across the range of mountain caribou have included protecting > 2 million hectares of old-growth forest from logging, closing areas to snowmobiling, and using “best management” practices for commercial backcountry recreation. These actions occurred incrementally to existing protected areas such as Wells Gray Provincial Park and Mount Revelstoke and Glacier National Parks. Yet, because these management actions do not deal with proximate limiting factors, a population response from caribou has not been observed nor should it be expected (Serrouya and Wittmer 2010). Viability analyses suggest that under current conditions, without any additional habitat degradation, many mountain caribou populations are on a trajectory to extinction (Wittmer et al. 2010). Clearly this means that manipulating the abundance of large mammals is needed, and that such actions should be implemented across the broad spatial scales (Carpenter et al. 1995) that large mammal predator-prey systems are known to encompass (Hayes et al. 2003, Mosnier et al. 2008).

I was able to take advantage of a major change in policy that had the potential to affect the population trend of moose, the dominant ungulate in the system. I evaluated the hypothesis of whether reducing moose to an ecological target (Chapter 3) would reduce predator populations and thus positively affect caribou population growth. Within this broad hypothesis, there were three specific hypotheses, each contingent on the previous one: 1) sport hunting could be used to reduce moose to an ecological target; 2) wolves in the Columbia ecosystem were primarily limited by moose abundance; and 3) mountain caribou were partially limited by wolf predation.

The ability to use sport hunting to reduce ungulate populations is important because hunter access and the fecundity rate of the prey species make some cervid populations resilient to increased hunting (Brown et al. 2000, Lebel et al. 2012, Simard et al. 2013). To properly test this hypothesis, I had to establish whether any observed change in moose abundance was caused by the change in policy, or a broader ecological process such as climate or ecosystem change that can also influence ungulate population dynamics (Post and Stenseth 1998). A spatial reference area where moose permits were not increased helped to resolve these potential confounds.

The hypothesis that wolves were primarily limited by moose predicts that reducing moose will reduce wolf abundance. Descriptive studies from within the study area suggested that wolf diets were dominated by moose (Stotyn 2008), and across a variety of ecosystems there is a broad relationship linking ungulate biomass to wolf abundance (Fuller et al. 2003). However, wolf populations lag, sometimes by many years, in response to a decline in their primary prey (Mech 1977, Gasaway et al. 1983). In addition, wolf populations may not track the availability of moose biomass, but instead respond to the abundance of vulnerable (old) moose (Peterson et al. 1998). These factors may result in an equivocal relationship between wolf abundance and the moose reduction treatment, particularly at a local scale.

My final hypothesis was that mountain caribou were limited in part by wolf predation (Wittmer et al. 2005a), and therefore my prediction was that reducing wolf numbers would at least reduce the rate of caribou decline compared to before the treatment and to the spatial reference area. This hypothesis has received support across many woodland caribou subpopulations, either through manipulation (Seip 1992, Hayes et al. 2003) or mensurative experiments (Seip 1992, Rettie and Messier 1998, McLoughlin et al. 2003, Wittmer et al. 2005b, Latham et al. 2011). I also predicted that caribou recruitment would increase following the treatment, recognizing that caribou calves might be killed by bears or meso-predators to a greater extent than wolves (Adams et al. 1995, Gustine et al. 2006). Again, these predictions were dependant on the previous hypothesis, where a reduction in wolves could be achieved by reducing moose.

In addition to evaluating support for the above hypotheses, a secondary objective of this chapter was to compare the results of this study to a similar experiment occurring in central British Columbia (the “Parsnip Study”; Steenweg 2011, Heard 2012), where moose were also reduced across a broad area to try and recover endangered mountain caribou. Although the Parsnip Study paralleled my objectives and had some similar response metrics, it was not treated analytically as a replicate to this study. Nonetheless, it deserves mention here because of similarities to this study, and it is another attempt to reduce predators by reducing their primary prey.

STUDY AREA

The study area was located within two major mountain ranges in the interior of British Columbia, the Columbia and Cariboo Mountains. The treatment area was 6500 km^2 whereas the reference was 11500 km^2, and they were separated by the Monashee Mountains, a sub-range of the Columbias with a maximum elevation of 3274 m. Both areas were rugged and remote. Half of the treatment area was on the west side of Lake Revelstoke and accessible only by boat (Fig. 6.1), with very little human presence. In the reference area there was a major highway and railway, whereas in the treatment area there was one dead-end highway with relatively little traffic. Warm summers and cool, wet winters with excessive snowfall (> 20 m) are typical in the central portion of these ranges at mid elevations (1800 m a.s.l.) where caribou spend most of the winter. In valley bottoms (400 – 500 m) snowfall averages 396 cm (n = 100 yr, SD = 120), which is where most other ungulates and their predators spend the winter. As the snow melts in summer, moose and deer, along with wolves, bears (*Ursus* spp.), and cougars (*Puma concolor*), spread out in the mountains. As a rough index of moose to deer abundance, sampling from 17 pellet transects cleared and measured each spring from 2003 to 2011 (Chapter 3) recorded 969 moose and 61 deer pellet groups.

Below approximately 1300 m, western red cedar and western hemlock (*Tsuga heterophylla*) are the typical climax tree species, whereas above this elevation the forest transitions to Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Forest age classes are typically bi-modal, with either old (> 250 yr) or young (< 40 yr) regenerating stands following harvesting, and relatively little (<15 %) mid-seral vegetation. Natural shrub openings occur in avalanche paths, marshes, and at higher elevation as the forest transitions to alpine areas.

The caribou subpopulations in the treatment area included Columbia North, Columbia South, and Frisby-Queest. The latter two each numbered less than 50 caribou when the moose reduction treatment began, but Columbia North numbered *c*.150 when the treatment began (McLellan et al. 2006). In the reference area, caribou subpopulations were Wells Gray (South) and Groundhog. Although Wittmer et al. (2005a) considered Wells Gray North and South to be one subpopulation, more recent analyses revealed limited demographic exchange between these areas (van Oort et al. 2011, Serrouya et al. 2012, Chapter 2), so the comparison was limited to the Wells Gray South portion (Fig. 6.1) of the larger Wells Gray subpopulation.

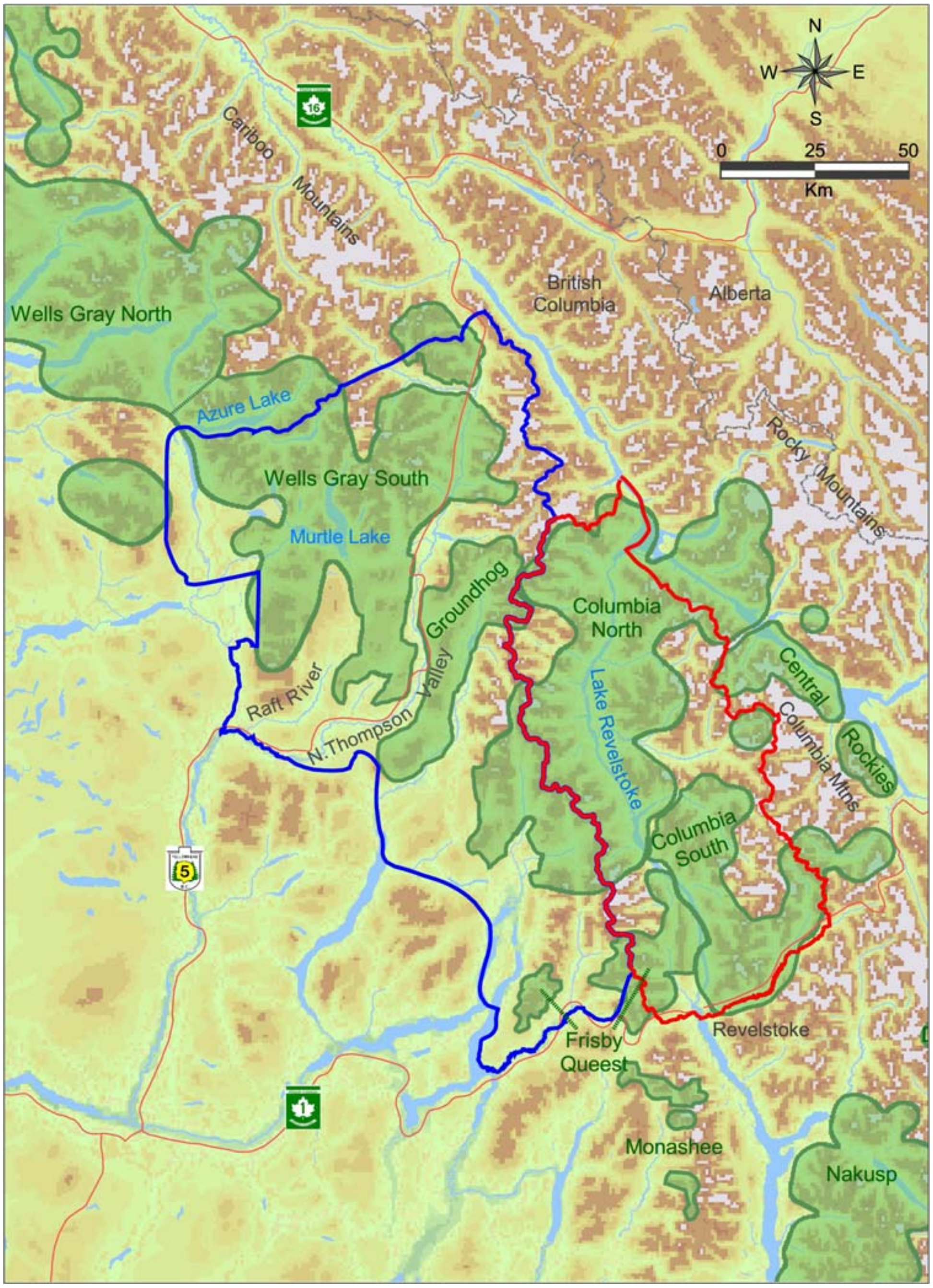


Figure 6.1. Map of treatment (red) vs. reference areas (blue). Caribou subpopulations are shaded green.

METHODS

To estimate population size, trend, recruitment, survival, mortality causes and dispersal rates, animals were captured and fitted with VHF or GPS radio collars. Caribou and moose were captured by aerial net-gunning, whereas wolves were captured using leg-hold traps and net-gunning. Net-gunning was conducted in winter when snow cover facilitated tracking and minimized the risk of injury to animals, whereas leg-hold traps were used in summer for some wolf captures. Captures adhered to BC Provincial Government and University of Alberta animal care protocols (permit # VI08-49757, and 690905, 2004-09D, 2005-19D).

Animals were monitored every two to four weeks from fixed-wing aircraft. If an animal was not found during a monitoring session, the pilot (D. Mair, Silvertip Aviation) scanned for these animals while *en route* to other projects centered 150 to 300 km away in BC and Alberta, flying at a high altitude (> 2500 m) to maximize collar detection. If the animal was still missing we searched a 50 – 100 km buffer around the study area using a meandering flight path.

Study design and response metrics

The design was based on an ecosystem-level perturbation intended to reduce moose populations in one area (treatment) and compare the results to the reference area where no attempt was made to reduce the moose population. In the treatment area, a substantial increase in the number of moose hunting permits began in 2003 (Table 5.1), but no major change in policy occurred in the reference area. The reference area was larger than in Chapter 5 because the relevant scale in this case was bounded by the wolf ranges, and the caribou subpopulations that were measured as a response.

In the treatment and reference area I estimated moose population trend, wolf survival and dispersal, and caribou abundance, trend, and recruitment. In the treatment area alone, I also estimated wolf abundance, trend, and recruitment, and moose survival (Table 6.1). Caribou monitoring began in 1992 (summarized in Wittmer et al. 2005a), so I was able to compare population parameters before and after the moose reduction treatment began, and against the spatial reference area, conforming to a before-after control impact (BACI) design. Moose abundance and survival estimates began in 2003, but trend information based on hunter harvest data could be estimated in both areas prior to this date. Wolf survival and dispersal comparisons began in 2004, but abundance estimates began in 2007.

Table 6.1: Response metrics within the treatment and reference areas.

Metric	Treatment	Reference
Numerical Chapter 6A		
Wolf survival and dispersal	Y	Y
Wolf abundance	Y	N
Wolf trend	Y	N
Wolf recruitment	Y	N
Moose trend	Y	Y
Moose abundance	Y	Y
Moose survival	Y	N
Caribou abundance and trend	Y	Y
Caribou recruitment	Y	Y
Functional / Behavioural Chapter 6B.		
Functional response: wolf use in caribou habitat and movement rates	Y	Y
Functional response: wolf kill rates	Y	N
Diet: scat analyses	Y	N

Moose abundance, trend, and survival

Methods to estimate moose abundance and trend were described in Chapter 3 and Serrouya et al. (2011). Briefly, in the treatment area moose abundance was estimated using stratified random block aerial surveys (Gasaway 1986) and trend was monitored using annual pellet transects (Serrouya et al. 2011). Catch per unit effort hunting data were calibrated against these values (Chapter 5) and compared to CPUE data from the reference area. In the reference area, moose abundance was estimated in 2007 in the northern third of the area (see reference area in Chapter 5), and in the Raft River in 2009 (Klafki et al. 2009). These two point estimates were not used to estimate population trend, which was estimated using CPUE data.

Wolf abundance, trend, and vital rates

Wolf survival, dispersal, and cause-specific mortality rates were compared between the treatment and reference (Table 6.1). These rates were estimated using the Heisey-Fuller method (Heisey and Fuller 1985). To help reduce potential biases stemming from changing mortality risk throughout the year, I chose 12 risk periods corresponding to each calendar month. Annual survival rates were calculated from the product of the 12 monthly survival rates. Monthly survival rates were calculated by exponentiating the daily survival partitioned within each month, by the number of days in that month. Daily survival was calculated as 1 – no. deaths / ∑ of monitoring days in the corresponding month. With each animal treated as the sampling unit, I bootstrapped the distribution of animals 2000 times to obtain confidence intervals and p-values for survival, cause-specific mortality rates, and dispersal rates. P-values were based on matching each bootstrap iteration from the treatment and reference, counting the number of times the treatment values were greater, and converting this to a percentile. I also calculated an effective survival rate by considering a dispersed animal to be "dead" from the study system. Cause-specific mortality was separated into five categories: starvation, road kill, hunting and trapping (combined), predation, and unknown cause.

I defined dispersal as animals leaving the experimental unit (i.e. the treatment or reference area) by at least 50 km and not returning by the time the study ended – which was similar to the definition of dispersal used in the Parsnip study (Steenweg 2011). However, because the reference unit was substantially larger than the treatment unit, the opportunity for dispersal in the reference area could be negatively biased. Therefore, I also quantified a more conservative dispersal rate from the treatment unit, by simulating an 11.3 km buffer around the treatment unit, which made it as large as the reference unit. The end result was that in the treatment area wolves would have to disperse at least 61.3 km from the edge. This adjustment was likely overly conservative, because the treatment area was bounded by large mountains so if a wolf left this area it probably reflected an important decision to expend energy and search for resources in a different area where its primary prey were not declining rapidly. Dispersals included wolves that may have been lost from monitoring but were subsequently found outside the study area (*sensu* Steenweg 2011, Webb et al. 2011) either because they were harvested or were recaptured by another project. Potential dispersers were also estimated and included animals whose radio-signal was lost before the expected end of the collar's life span (Mills et al. 2008, Steenweg 2011). Annual dispersal rates were calculated independently from the other cause-specific rates because including dispersals would have caused a negative bias in the other cause-specific rates (see equations in Heisey and Fuller 1985), particularly since emigrants are normally right censored from analyses. One annual risk period was used to estimate the dispersal rates.

Wolf abundance and trend were estimated in two ways. From 2008 to 2012 each valley below 1200 m elevation in the treatment area was surveyed within a short time frame (2 – 4 days). Surveys began one or two days after a large snowfall, allowing fresh tracks to be detected and easily counted (van Oort et al. 2009a). Helicopters were used extensively, but ground work was also done simultaneously along Highway 23, and in the large drainages on the east side of Lake Revelstoke. Flight paths focussed on areas where tracks could be easily spotted such as forestry roads, cutblocks and wetlands. Ground transects were surveyed using snowmobiles or trucks along plowed and unplowed roads. An attempt was made to locate all wolves in the survey area by trailing each pack until the group size could be counted or at least estimated from tracks (van Oort et al. 2009a). The 2007 estimate was based on an integrated count from multiple data sources over the second half of the winter, including 7 track transects sampled 2 – 3 times, an aerial survey, ground observations, and GPS telemetry for 3 of the 6 packs to define pack boundaries. The aerial survey was not a complete census but focussed on counting members of the packs with collared animals and the 3 known packs without a collared member. This estimate was considered a minimum because only known packs with territorial animals were enumerated (van Oort et al. 2009a). Because wolves on the edge of the study area are more likely to move in and out across years, a buffer survey was also conducted each year. The buffer was variable, with the Red Rock Harbour surveyed each year, but Encampment creek was surveyed in 2008 and 2012. I report these values as well to help address uncertainty with regards to population closure.

When trailing wolves, a minimum estimate was always produced. These estimates were obtained from tracking evidence such as splitting of routes followed, or from visual observations of the pack. A "maximum" estimate was also recorded which provided an upper limit for each pack. The maximum count was more subjective than the minimum count. Each time we encountered a pack we checked for the presence of a collared wolf to estimate the proportion of wolves missed during our census. This method did not produce a sufficient sample to calculate a correction factor, but did provide an approximate detection rate for the survey method.

Wolf recruitment was estimated only in the treatment area in 2010 and 2011 and was contrasted between a high and a low moose density zone within the treatment area. Moose density was 2.2-fold higher in the high zone (0.43 vs. 0.20/km^2, summer density). The objective of this comparison was to determine if this difference in moose abundance was enough to observe a response in wolf recruitment (*sensu* Messier 1985a). To estimate recruitment, I placed remotely triggered cameras (Reconyx, Inc., Holmen, Wisconsin) within home ranges of wolves that were monitored using GPS collars. I focused on three wolf packs with existing or recent telemetry data, which allowed me to estimate the location of denning areas. I also placed cameras along known travel routes that were near den sites. Three to four cameras were placed within each territory, and were occasionally moved to help maximize detection of wolves. Commercial wolf urine and gland lure (Kootenay Brand Lures, Kimberly, BC) was placed near the cameras to slow wolf movements as they passed by the cameras. Cameras were checked approximately once per month and lures were refreshed during these checks. My metric of recruitment was the number of different pups recorded in the photographs, as a minimum estimate of the number of pups in the pack.

Caribou population trends, abundance, and recruitment

Caribou population and recruitment estimates were compared among treatment and reference areas, and before and after the moose reduction was initiated. Caribou censuses were conducted every two years on average, from March to early April when they were high in the mountains and their tracks in the open snowfields made them highly visible relative to other times of year and to most other mammals. Their sightability is positively correlated with snowpack depth ($r_s = 0.96$, $p = 0.002$; Flaa and McLellan 2000), with deeper snow enabling them to reach arboreal lichens in the tree canopy. When snow depth exceeds 300 cm at 1800 m a.s.l. (which occurs most winters), sightability is > 90%. In the 1990s, a large sample of individuals marked with radio collars allowed researchers to correct for missed animals and estimate precision using program NOREMARK (details in Wittmer et al. 2005a). However, in years when the radiomarked sample was low (i.e. after 2003), the number of caribou observed was used as the estimate. In these years, caribou were not counted unless the snow depth reached 300 cm.

Calves were classified as a percent of the population because it was difficult to obtain adult sex ratios without undue harassment. Ungulate recruitment has high intra-annual variability (Gaillard et al. 1998) so there is little reason to believe that serial autocorrelation is important, and I pooled recruitment data before and after the treatment, again reducing the need to correct for autocorrelation. Therefore, I used a linear mixed effects model (LME) to test whether recruitment changed after the treatment, by creating a dummy variable with two levels (before, after), and evaluated this effect separately in the treatment and reference area. Caribou subpopulation was specified as the random effect. Because some populations declined dramatically over the monitoring period, it may be appropriate to correct for population size when estimating recruitment, so that estimates from populations with very few numbers carry less weight. Therefore, I repeated the previous analysis but weighted the model by population size. Survival rates were not calculated for caribou because they have been summarized elsewhere (Wittmer et al. 2005a) and sample sizes of collared animals were too small to compare between treatments after the moose reduction began.

RESULTS

Moose abundance and trend

Following the increased moose harvest in the autumn of 2003 in the treatment area, the moose population declined by 71 % from 2003 to 2011 ($\lambda_{annual} = 0.86$; Fig. 6.2). The average density across the treatment area declined from 1.58/km^2 to 0.44/km^2. However, the actual decline likely began 1–2 years after the treatment was initiated (Fig. 6.2), so before-after analyses were centered on 2004. The reference area also demonstrated a declining moose trend, but the magnitude was much less than the treatment area. The CPUE data revealed that the slope of decline was more than five times greater in the treatment compared to the reference area (slopes were –6.88 [–9.02 to –4.68, 95% CI]) compared to –1.32 (–2.46 to –0.265; Appendix 6.1). Details and mechanisms of the moose population decline in the treatment area were presented in Chapter 5.

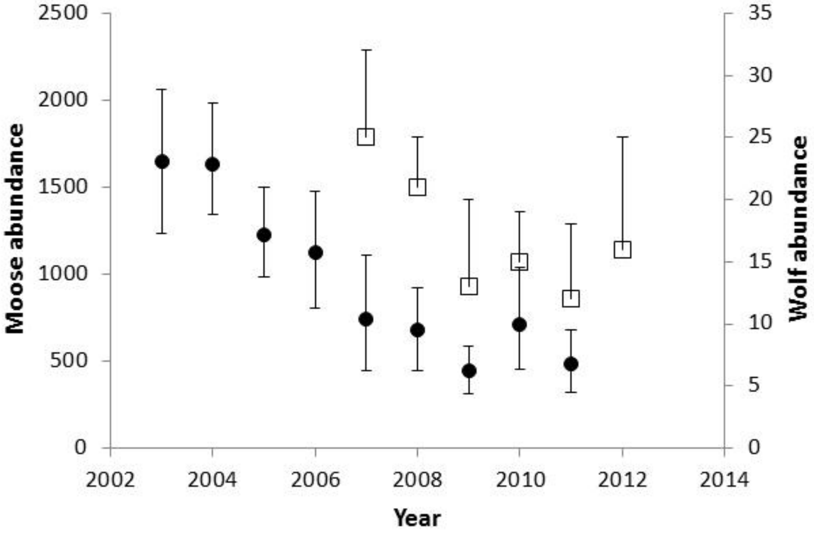


Figure 6.2. Moose (circles) and wolf (squares) abundance in the treatment area. Error bars for the moose estimates represent 90% CIs. The upper error bar for the wolf estimate show the maximum estimate, including a buffer around the treatment area. The square represents a minimum estimate. Data updated from van Oort et al. (2009a). Between 1994 and 2003 the moose population was estimated to have doubled (Serrouya et al. 2011).

Wolf dynamics

From 2004 – 2010, 63 different wolves were captured on 82 separate occasions. Five wolves were not located after capture and collar failure was suspected in each case (they were GPS collars) so these animals were not treated as dispersers and were excluded from analyses. Therefore, 58 wolves were available for survival and dispersal analyses, 34 wolves in the treatment area and 24 in the reference area, with the sex ratio evenly split in both areas. This sampling covered 32.4 monitoring years in the treatment, and 22.2 years in the reference area. There were 12 mortalities in the treatment area, but one of these died after dispersing and was not monitored during the intervening period so it was right censored. Another mortality was the result of a management removal so it was also right censored. Eight of 34 (23.5%) wolves dispersed from the treatment area, compared to 2 of 24 (8.3%) in the reference. If the larger buffer (61.3 km) is considered, then the number of confirmed dispersers from the treatment is reduced from 8 to 7. One additional wolf left the treatment area by crossing west over the Monashee mountains and its collar was shed on a remote logging road, but because it was only 10 km from the edge of the treatment area it was not counted as a disperser. However, this wolf was documented to be eating very little (see Pettipeace pack in Chapter 6b) based on kill rate estimates, and may have crossed these mountains in search of higher moose abundance and could be considered a disperser. If potential dispersers are included (those whose radio signals were lost unexpectedly), then 13 of 34 (38.2%) and 6 of 24 (25%) wolves dispersed from the treatment and reference areas, respectively. These dispersal values are presented as annual rates in Table 6.2.

In the reference area there were eight mortalities, two of which dispersed prior to dying (and were right censored for mortality estimation), and no other dispersals were recorded. Thus, in total, eight animals either dispersed or died from the reference area. Survival rates for the two areas were similar (0.726 [0.58 – 0.85] vs. 0.757 [0.56 – 0.92]; Table 6.2). In the treatment area, two wolves from separate packs starved and one was killed by other wolves. Two non-collared wolves from different packs were also found to have starved in the treatment area. One was a pup found at the den site of the collared female that had starved. The other was a subordinate male that starved weeks after its collared pack-mate starved. Human-caused mortality rates (roadkills, trapping and hunting) summed to 0.243 in the reference area but 0.129 in the treatment area (Table 6.2).

The 2007 integrated wolf population estimate was 32 as a minimum (van Oort et al. 2009a), but upon further re-examination this estimate may not have been a minimum because of the time elapsed between the aerial census and track transects. Based on timing of observations and the wolf GPS data, a minimum of 25 is more likely. In February and March, while censuses were occurring, the three GPS collared packs were never recorded crossing each other's boundaries. Over a 2-day period, the 3 largest packs (1 collared, 2 non-collared) were recorded in snow transects, confirming their separation. One pack was observed with 8 individuals while another was estimated through tracking to be 6, while a third was seen to be at least 5. It had been up to 7 earlier in the winter, but 5 was used as a minimum, though these visual observations were not synchronized. Two other collared packs were reliably counted as 2 each, and a third pack at the southern end of the treatment area was seen on 3 occasions as 2, 3, and 4, so the minimum 2 was used. Therefore, the minimum was estimated to be 25 (8, 6, 5, 2, 2, 2). This estimate does not include non-territorial wolves, which all subsequent estimates do. When the 2007 census is included, there is a decline in wolf abundance, but if this year is excluded, then there is less evidence of a decline. The most certain result indicating a decline in wolf numbers is that the maximum counts from 2009 to 2011 were less than the minimum count from 2007 and 2008. The 2012 estimate suggests an increase. From 2008 – 2012, all collared animals (n = 7) were recorded during the censuses.

Wolf recruitment was higher in the high moose density zone in both 2010 and 2011 (Table 6.3). Sample sizes were small however (one pack in the high and two packs in the low zone), so no statistics were performed. In 2011, photos from the end of September suggested that the eight pups seen in July for the pack in the high density zone were reduced to four pups. Similarly, the pups seen from the Bigmouth and Red Rock packs earlier in the summer were absent from photos in September that included adult wolves.

Table 6.2: Annual survival, mortality, and dispersal rates (95% CIs) for wolves in the treatment and reference areas. Effective survival considers animals that dispersed to have "died" from the area. P-values were calculated based on a bootstrap comparison of the difference between the two areas.

Parameter	Treatment	N	Reference	N	P-value
Survival	0.726 (0.58 – 0.85)	34	0.757 (0.56 – 0.92)	24	0.62
Road kill	0.024 (0 – 0.07)	1	0.082 (0 – 0.21)	2	0.78
Hunt / Trap	0.105 (0.02 – 0.21)	4	0.162 (0.04 – 0.33)	4	0.74
Starvation	0.063 (0 – 0.17)	2	0	0	NA
Predation	0.028 (0 – 0.09)	1	0	0	NA
Unknown	0.053 (0 – 0.13)	2	0	0	NA
Dispersal	0.221 (0.09 – 0.39)	8	0.087 (0 – 0.22)	2	0.08
Dispersal (max)[a]	0.333 (0.19 – 0.50)	13	0.239 (0.08 – 0.43)	6	0.20
Survival (effective)	0.513 (0.38 – 0.63)	34	0.586 (0.37 – 0.77)	24	0.73

[a] Maximum (max) dispersal considers any animal that disappeared while being monitored to be a potential dispersal.

Table 6.3. Maximum number of different pups estimated in the treatment area during the summer months using remote cameras in three different wolf territories within two zones of moose density. Moose density was approximately 0.43/km^2 in the High zone (H) and 0.20/km^2 in the Low zone (L) (summer density estimates).

Pack	Zone	Pups 2010	Pups 2011	No. cameras Sites	Trap nights	Photos with wolves
Gothics	H	3	8	7	727	208
Bigmouth	L	1[b]	2	6	583	49
Red rock	L	0	1[a]	7	706	158

[a] This pup was not recorded in the camera traps but was observed alone while deploying a camera trap along a logging road.

[b] This pup was found dead at the den site with its collared mother, which also appeared to starve.

Caribou abundance and recruitment

The two smaller caribou populations in the treatment area (Columbia South and Frisby-Queest) continued to decline after the treatment was initiated (Fig. 6.3). The rate of decline increased for Columbia South, yet was consistent for Frisby-Queest (λ = 0.92 – 0.94). The largest subpopulation in the treatment area, Columbia North, increased following the moose reduction (Fig. 6.3), though that increase was primarily because of the 2013 estimate, with 32 additional animals found compared to the 2011 estimate. In the reference area, the smaller subpopulation (Groundhog) continued to decline, and the Wells Gray South subpopulation initially appeared to stabilize but a marked reduction was observed in 2013 (Fig. 6.3).

There was no indication that caribou recruitment improved as a result of the treatment (LME β_{before} = 0.029, SE = 0.03, p = 0.34, n = 27, 3 groups; Fig. 6.4a). The predicted value of recruitment was 14.6% (before) vs. 12.4% (after), and if the analysis was weighted by population size then the values changed little, to 13.0 and 15.8%, respectively. Recruitment improved in the reference area after the treatment began (LME β_{before} = –0.052, SE = 0.02, p = 0.04, n = 19, 2 groups; 14.0% (before) vs. 19.0 (after); Fig. 6.4b), but when population size was accounted for the difference was negligible (15.4% to 16.7%), likely because the high recruitment value (33%; Fig. 6.4b) from Groundhog in 2011 was discounted due to its much reduced population size (n = 9; Fig. 6.3).

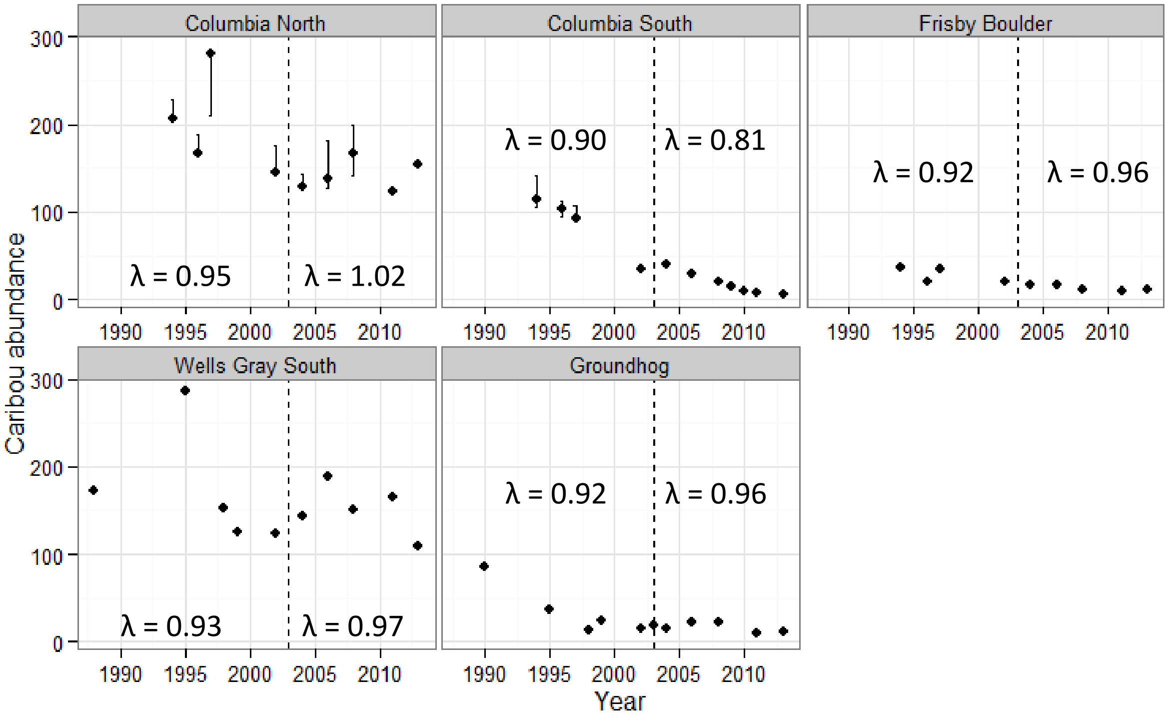


Figure 6.3. Caribou population estimates for five subpopulations, three in the treatment area (top row) and two in the reference area (bottom row). The dashed vertical line represents the beginning of the moose reduction treatment in 2003. Lambda values to

the left of the dashed line represent the years 1994 to 2004 whereas those to the right of the line represent the years 2004 to 2013. Data updated from Wittmer et al. (2005a).

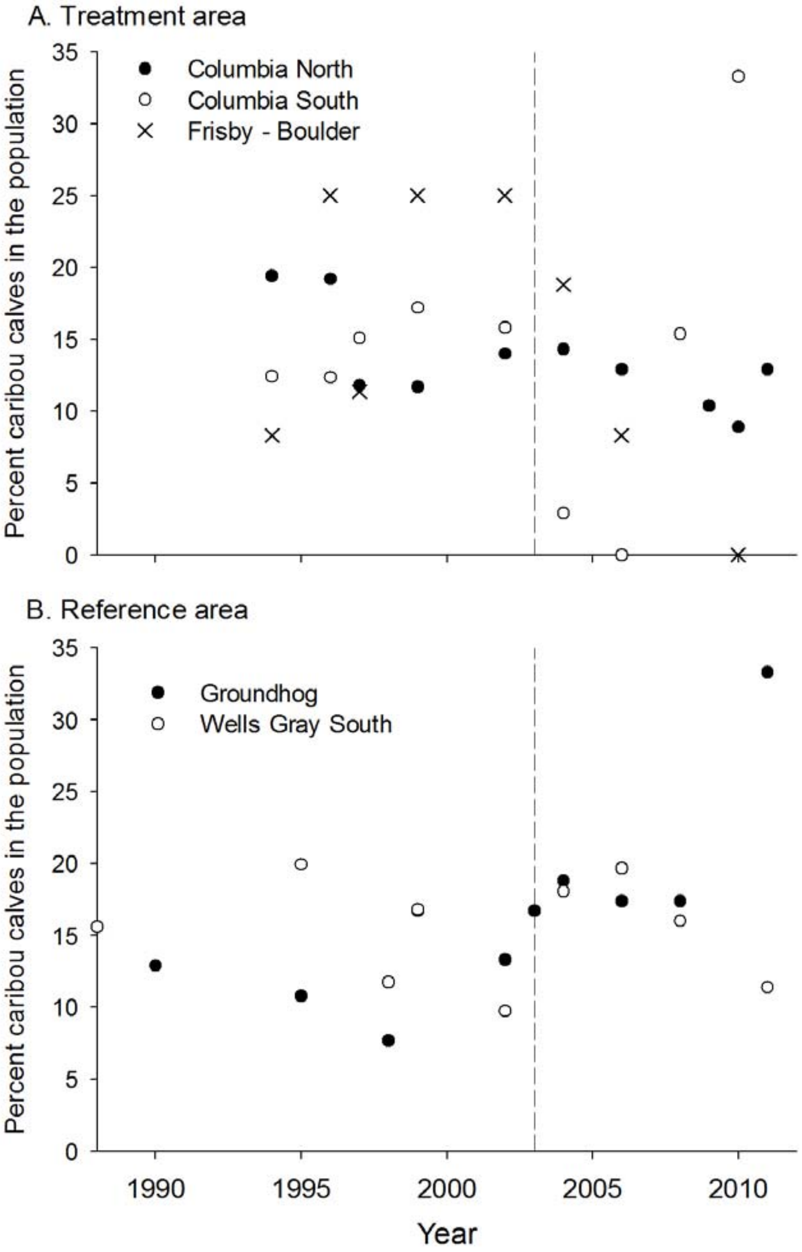


Figure 6.4. Caribou recruitment (% calves) within the treatment (A) and reference areas (B). The vertical line represents when the moose reduction began in the treatment area. Symbols represent separate subpopulations.

DISCUSSION

The primary hypothesis tested was that reducing moose abundance to an ecological target would reduce the caribou's rate of decline. Within this hypothesis was a series of nested hypotheses and predictions that also required testing. The first hypothesis was confirmed: moose were reduced using sport hunting, and two lines of evidence support this conclusion. First, the population declined at a rate that was 5-fold greater than in a spatial reference area where hunting permits were not increased. Second, by using predator-prey theory, I contrasted the effects of hunting compared to predation and found that both factors contributed to the decline, with hunting initiating the depensatory predation rate observed in the treatment area (Chapter 5). It may seem intuitive that increasing hunting pressure on a large herbivore would reduce its abundance, particularly with more females harvested. However, other North American cervids have been difficult to control using sport hunting (Brown et al. 2000, McDonald et al. 2007, Simard et al. 2013) because of poor access, urban refuges (Polfus and Krausman 2012), or high fecundity and immigration rates. Despite the remote nature of much of the treatment zone with only boat access for ~40% of the area, moose were successfully reduced using sport hunting. In one of the few other experimental attempts to reduce overabundant ungulates, Simard et al. (2013) found that white-tailed deer were not successfully reduced in replicated 20-km^2 treatments on a predator-free island, possibly because of compensatory vital rates or immigration from surrounding areas. Moose are less fecund than white-tailed deer, which may explain the discrepancy between the two systems. Furthermore, my treatment area was much (300 ×) larger, with less chance of immigration because of the closure imposed by rugged mountain ranges.

The second hypothesis was that wolves were primarily limited by moose abundance, with the prediction that reducing moose would reduce wolf numbers. Ostensibly, this hypothesis appears trivial because of established relationships between ungulate biomass and wolf abundance (Fuller et al. 2003), but others have proposed complimentary explanations related to the age or vulnerability of moose (Peterson et al.

1998), or social constraints within wolf packs that limit wolf abundance regardless of food availability (Messier 1994, Hebblewhite 2013). Nevertheless, the explicit goal of controlling wolves by reducing their primary prey has only recently been field tested (Steenweg 2011). In my case, this hypothesis was also supported, because wolf numbers declined following the moose reduction. The lack of wolf census data prior to 2007 may weaken this conclusion, as would the absence of trend data from the reference area. Nonetheless, I identified several mechanisms to explain the reduction in wolf abundance that support this conclusion. First, the dispersal rate was greater in the treatment area than the reference area, resulting in a relatively low effective survival rate. At 0.51, the effective survival rate is lower than the minimum level (0.64) estimated by Fuller et al. (2003) that is required to maintain a stable wolf population. These results mirror those from the Parsnip study, which found dispersal to be the primary wolf vital rate affected by the moose reduction treatment (Steenweg 2011). The dispersal rate in the treatment area was also greater than what was estimated by Webb et al. (2011), who reported an emigration rate of 0.13 in an adjacent population in Alberta. Second, I found evidence of reduced wolf recruitment in areas with lower moose densities (0.2/km^2). Messier (1985a) also found that at moose densities of < 0.2/km^2, wolves had difficulty recruiting pups. Third, wolf starvation occurred in the treatment area for animals that were documented to be eating very little (Chapter 6b). Finally, the diet analyses also supported the hypothesis that wolves were primarily supported by moose (Chapter 6b).

Although trappers removed wolves in the area, including a hired trapper who removed two wolves in the principal survey area in 2008, the overall trapping and hunting rate (0.11) is low compared to adjacent study populations. In Alberta, Webb et al. (2011) estimated that a harvest rate of 0.34 had little effect on population trend. Few wolves are trapped or hunted in the study area because the amount of snowfall confounds trap sets and thick cover obscures visibility for hunting. Therefore, changes in wolf abundance can likely be attributed to bottom-up processes and not intensive human harvest.

The prediction that reduced wolf numbers would reduce the rate of caribou decline relative to spatial and temporal contrasts was not consistently supported. Three smaller caribou populations continued to decline, regardless of the treatment. A number of well-documented mechanisms can negatively affect small populations including environmental stochasticity and Allee effects (Allee 1931) resulting from predation, and both of these processes have negatively affected woodland caribou (Hebblewhite et al. 2010, McLellan et al. 2010).

For the two largest subpopulations (Columbia North and Wells Gray), a modest increase was observed in the treatment area but a sharp decline in the reference area. The 2013 population estimate was the main datum accounting for this pattern, with an increase of 32 over 2011 values in the treatment but a decline of 52 in the reference area. Clearly sampling variation can affect these interpretations, but I consider the increase of 32 for Columbia North to be an actual increase, based on higher recruitment observed during the 2013 census. Also, the 2013 value was a minimum estimate that was greater than the upper confidence interval of previous estimates (i.e., 2002). Additional monitoring will be required to determine if these patterns hold.

It is tempting to conclude that the experiment failed because caribou population growth was not more immediate and pronounced in the treatment area. Several factors would render this conclusion premature. First, a clear measure of success was that moose numbers were reduced using a standard change in hunting regulations, addressing a more ultimate cause of the apparent competition problem, rather than focussing efforts solely on wolf control. Second, because moose were not reduced to the target suggested in Chapter 3 (~303 moose), or even to the lower range of the predicted target (lower 95% CI: 167 moose; Chapter 3), the caribou response may not have been as strong as anticipated. As the experiment progressed, the BC Government made a social decision to manage the moose population at 500, terming this a “social target.” Evidence beyond the statistical analysis in Chapter 3 suggests that prior to the 1940s, moose were at even lower densities and may have been absent from the Revelstoke area, based on a survey of local residents conducted in the 1980s (Rick

Bonnar pers. comm.). Detailed reviews from other areas in central and southern BC (Spalding 1990, Kay 1997, Santomauro et al. 2012) support this speculation. The precautionary principle (Doak et al. 2008) would suggest reducing moose even lower than 303 (biological target) or 500 (social target) to hold wolves at lower numbers. Third, existing wolf densities range between 10 and 22 /1000 km^2, still far above Bergerud's target of 6.5/1000 km^2. Converted to summer densities (3.6 – 7.6/1000 km^2), wolf numbers approach Bergerud's target, but these figures would not include animals recruited during the summer into autumn. Finally, the theoretical predictions from Chapter 4 suggested an approximate 10-year transient phase before the system would be expected to equilibrate to the lower moose and wolf abundances, suggesting a delay before a clear caribou response could be observed.

Wolves are highly mobile and fecund, so if their primary prey remain abundant during a period of wolf control, ingress occurs rapidly (Ballard et al. 1987, Hayes et al. 2003, Mosnier et al. 2008). Therefore, researchers have estimated that at least an 80 % annual reduction in wolf abundance is required to elicit a response in ungulate population growth (Hayes et al. 2003). However, if wolf control were to be implemented in my system, it would likely have to be less intensive and continuous relative to other areas where their primary prey species was not concurrently reduced (e.g. Yukon: Hayes et al. 2003; Quebec: Mosnier et al. 2008; Alaska: Gasaway et al. 1992; British Columbia: Bergerud and Elliott 1998).

Spatial and temporal variation in predation intensity has a major influence on population dynamics (Creel and Winnie 2005). Predation on adult mountain caribou by wolves or cougars shifts from predominantly wolves in northern areas to cougars in southern areas (Wittmer et al. 2005a). Bears are the second highest source of mortality in each of the southern and northern half of caribou range, but with both areas combined, they are the primary source of mortality. Furthermore, bears are a major predator of woodland caribou calves where such studies exist (Adams et al. 1995). McLellan's (2011) meta-analysis across 23 grizzly bear populations revealed that densities in non-coastal areas were inversely related to ungulate abundance (meat in the diet) and more closely linked to vegetative food, mostly fruit production. Because the bears' primary prey is vegetative, I did not expect a numerical response of bears to the moose reduction treatment. Cougar abundance and diets were monitored intermittently in the treatment area (Bird et al. 2010) using GPS cluster analyses (Anderson and Lindzey 2003, Knopff et al. 2009), with moose comprising 5 – 43% of the individuals' diet, and the largest male cougar consumed the most moose (Bird et al. 2010). Four caribou were also consumed by a GPS-collared cougar in one season. However, detection of cougar predation on radio-collared caribou only began in the mid 1990s, following the peak and collapse of deer populations (Chapter 4). After this dynamic, cougar numbers declined and wolf predation on caribou increased (Stotyn 2008). These examples illustrate how conclusions drawn from landscape-level field experiments must consider how limiting factors change, often unpredictably, over space and time (Doak et al. 2008). Nonetheless, by combining what was observed in this and other case studies (Courchamp et al. 2003, Wittmer et al. 2013), some generalities are being supported. In the context of apparent competition, high but especially fluctuating populations of primary prey can enhance extinction risk for rare prey (Chapter 4). Maintaining lower and thus more stable populations of primary prey is expected to reduce predator switching and help maintain predators at low numbers.

In addition to this study I am aware of three other experimental attempts to reduce apparent competition by reducing primary prey: 1) the Parsnip Study, 2) a study where 25000 domestic sheep were reduced to 2000 to try and recover endangered huemul deer (*Hippocamelus bisulcus)* in Patagonia (Wittmer et al. 2013, Wittmer et al. In press), and, 3) the removal of feral pigs to recover the island fox (*Urocyon littoralis*) on the Channel Islands of California (Courchamp et al. 2003), although periodic predator removal of golden eagles (*Aquila chrysaetos*) also occurred in that case. In a fourth case, a serendipitous experiment occurred when extensive poaching of African buffalo (*Syncerus caffer*) was linked to reduced lion (*Panthera leo*) numbers, resulting in a pronounced increase of impala (*Aepyceros melampus*; Sinclair 1995). In the Parsnip study, results were similar to ours, with high wolf dispersal rates, and no evidence of improved caribou trend but no marked decline either. In the case of huemul, their decline was exacerbated as a result of increased predation by foxes (*Lycalopex culpaeus*) and pumas (*Puma concolor*), likely resulting from the abrupt decline in sheep abundance. These collective findings suggest there has been no consistent response to reducing primary prey as a recovery tool for species affected by apparent competition. Such a conclusion will complicate the decision-making process for management agencies, but given the important caveats mentioned above, the evidence suggests that this approach should not be dismissed as an option when used in concert with addressing other proximate and ultimate limiting factors.

Historical accounts (Spalding 2000, Seip 1992) and population reconstruction studies (McLellan 2010) suggest that mountain caribou were once at least an order of magnitude more abundant than they are today. During this period of caribou abundance, it is possible that the trophic interactions were reversed, where moose were the victim of apparent competition with wolf predation and harvest by First Nations (Kay 1997) keeping them at low numbers. Extensive wolf control using poison and bounties occurred from 1906 – 1962 throughout BC (McLellan 2010), and this along with climate and ecosystem change made it possible for moose to expand into southern BC. Whether the caribou-dominant or moose-dominant periods represent alternate stable states is unclear (Beisner et al. 2003), but it is becoming increasingly evident that returning to the caribou-dominated system will require exceeding the biological population targets proposed by Bergerud and Elliot (1986) and Serrouya et al. (2011). Random processes associated with small populations, Allee effects due to predation (McLellan et al. 2010, Armstrong and Wittmer 2011), and possibly states with alternate equilibria governed by density dependent (or depensatory) processes (Carpenter et al. 1999) will make it increasingly difficult to recover mountain caribou populations.

CHAPTER 6B

BEHAVIOURAL CHANGES OF WOLVES TO AN EXPERIMENTAL MOOSE REDUCTION IN A MULTI-PREY SYSTEM: IMPLICATIONS FOR THE ENDANGERED PREY

Much of predator-prey theory is based on Holling's disc equation, where the upper limit of a predator's consumption rate is set by handling time: the time it takes to capture, ingest, and digest prey. The rate at which this upper limit is reached is dictated by a second parameter: the instantaneous rate of discovery (Holling 1959a), or the amount of area covered by the predator per unit time combined with the probability of success per attack. Together, these parameters describe a specific functional response, with a pattern of monotonic increase to an asymptote that is equivalent to the inverse of the handling time. In a simple system with one prey and one predator species, as the prey become less abundant the basic prediction is that predators will spend a greater proportion of their time searching and less time consuming their prey.

These simple relationships also apply to systems with more than one prey species. In the case of apparent competition (Holt 1977), there is often a difference in abundance between primary and secondary prey. If the primary prey are reduced, predators will again spend more time searching, possibly increasing predation on secondary prey as the predators cover more area. The degree of risk will depend on many factors, but none greater than the numerical response of the predator, because if it is instantaneous, then the expected predation rate on the secondary prey will decline (McLellan et al. 2010). However, if there is a lag in the numerical response, or if predator searching behaviour changes, then the risk to the secondary prey is predicted to increase. Clearly, there are other factors that can influence the degree of risk among prey that share common predators, such as the amount of spatial overlap (that can change substantially among seasons; Stotyn 2008), the probability of dying once encountered (Hebblewhite et al. 2005) which may differ among prey species (Haber 1977), or different grouping behaviour among prey (McLellan et al. 2010). Nonetheless, these processes can still be viewed under the fundamental concept of a predator's response to differing resource availability.

The theoretical relationships just described also have applied implications for conservation. In the case of woodland caribou, elevated predation rates are causing their extinction as a result of increased apparent competition with abundant moose and deer (Seip 1992, Wittmer et al. 2005b, Latham et al. 2011). One recovery option for caribou is to reduce the abundance of moose and deer to indirectly reduce predator numbers. This option is recently being attempted in several jurisdictions (Courchamp et al. 2003, Steenweg 2011) as an alternative to direct predator control because the latter has become less acceptable to the public (Orians et al. 1997); also, predator control is only a proximate solution. What remains untested is how predator behaviour will be affected by a reduction of their primary prey, and whether this approach to recovery will increase or decrease the mortality risk to mountain caribou.

Recently, the concept of the functional response has expanded beyond the classic definition of a foraging rate (Solomon 1949) to include patterns of habitat use and selection that may change in relation to available resources (Matthiopoulos et al. 2011). This broader definition has practical utility because it is much easier to collect information using remotely sensed data sampled intensively with GPS collars, than to collect information on animal predation events in the field. With this technology we can make similar predictions relevant to predator-prey theory, in particular how movement rates and habitat use (McPhee et al. 2012) may change as the abundance of a predator's prey is manipulated. Similarly, the functional response can be evaluated using diet analyses, by examining how composition changes in relation to the changing availability of prey (Latham et al. 2011).

During winter, wolves in mountainous systems of western North America are restricted to valley bottoms where their primary prey, often moose, are most concentrated. In contrast, mountain caribou are relatively safe from predation during winter (Jan – April; Appendix 6.2) because they move high in the mountains where they use the 2 – 5 m snowpack as a platform to access arboreal lichens. In spring and summer as the snow melts and moose move upslope, the spatial separation between wolves and caribou is greatly reduced (Seip 1992, Stotyn 2008; Appendix 6.2). Furthermore, each summer, the density of moose declines as they spread out into the mountains, potentially having a major impact on the foraging rate of wolves over a relatively short time frame. These seasonal patterns have several implications for my work. First, summer is the relevant season to test concepts related to changing risk to caribou because it is when variation in wolf foraging patterns are most likely to occur, whereas focussing on the functional response in winter may have little bearing to how wolves respond to changing prey biomass (Hayes et al. 2000, Metz et al. 2012). Given that biomass intake is lower in summer at least in some areas (Peterson et al. 1984, Metz et al. 2012), this also suggests that wolves are closer to their minimum forage requirements in summer, and therefore more likely to make decisions that will alter their foraging behaviour during this season. Finally, it is in summer when caribou are subject to wolf predation, whereas in late winter such predation is virtually absent (Wittmer et al. 2005a).

In this chapter, I describe how wolf behaviour changed in relation to the moose reduction treatment. My primary hypothesis was that the experimental moose reduction would alter the functional response of wolves by increasing their time spent searching, thereby increasing predation risk to caribou. My definition of a functional response included the classic metric of per capita consumption rates, but I also used broader definitions that included wolf habitat use, movement rates, and diet based on scat analyses. I evaluated this hypothesis using four predictions, each in the context of an experimentally reduced moose population. First, I predicted that wolves would increase their use of caribou habitat during the snow-free months (i.e. excluding Jan – April) because wolves are expected to travel more in search of fewer prey. This is the season when the three species partially overlap and risk to caribou is higher (Appendix 6.2). This prediction does not necessarily imply that wolves are actively switching to caribou, but that as wolves cover more ground to locate their primary prey (moose), they will intersect more caribou habitat due to the interspersion between where moose and caribou are found. Second, I expected that wolf movement rates would increase as a result of increased search time (McPhee et al. 2012). In both of these cases I expected no change in wolf behaviour in a spatial reference area where moose numbers were comparatively stable. Third, I predicted that per capita wolf consumption rates of moose would be relatively invariant to the manipulated moose density in winter (Hayes et al. 2000), but during summer consumption rates would be reduced (Metz et al. 2012). Finally, I expected that wolf diets would change as a result of the moose reduction with less moose and more alternate species eaten, and that this shift would be strongest in summer when wolf consumption is likely most limited (Metz et al. 2012, Knamiller 2011) in mountainous systems.

My alternate hypothesis was that the wolf functional response is relatively invariant to prey density, and would be explained by high foraging efficiency, regardless of season. A high foraging efficiency (i.e. a high value for *a* in the disc equation) has been suggested in other large mammal predator-prey systems (Hayes and Harestad 2000, Nilsen et al. 2009). In this case, I would predict no change in the wolves' use of caribou habitat or movement rates as the moose population declined, and this pattern would be similar to the reference area where the moose population was stable. Furthermore, moose would dominate the wolf diet independent of moose density. Finally, the kill rate would be relatively stable across a range of prey density, both in summer and winter. The implication of the alternative hypothesis is that as primary prey are reduced, wolves will show little behavioural change in foraging patterns, but at some very low prey density they either disperse or starve. If this occurs rapidly, there would be little opportunity to record foraging behaviour during this transient phase, and similarly, little increase in predation risk to caribou for any extended period.

METHODS

Study design

My design consisted of using spatial and temporal comparisons to estimate how wolf behaviour changed in response to the experimental moose reduction, with response metrics summarized in Table 6.1. Diet analyses and kill rates were only available in the treatment area, but were recorded over time as the moose population was reduced. Wolf habitat use and movement rates were based on radio collar information that was collected in both the treatment and reference area during the period of moose reduction (Table 6.4). VHF locations were obtained 2 – 4 weeks apart, but daily sampling was attempted during intensive sampling periods. GPS locations were obtained every 1 to 3 hr during intensive periods and every 8 hr during the remainder of the year. Intensive sampling occurred when kill rates were being estimated in the field (see below). In this ecosystem, caribou undergo a bimodal annual elevational migration, living at high elevation in late winter (Jan – April), then low elevation in spring (May – June), high elevation in summer (June – Oct), and low elevation in early winter (Oct – Jan; Apps et al. 2001). My analyses were stratified according to these four biological seasons, with the exception of the scat analyses and kill rates, which were done based on summer and winter (including early and late winter) seasons. Additional descriptions of the study area were provided in Chapter 6a.

Table 6.4. Sampled wolf packs, time periods and the sampling area (Treatment [T] or Reference [R]) for the analysis of wolf habitat use and movement rates. N is the total number of individuals sampled per pack.

Pack	N	Area	2004	2005	2006	2007	2008	2009	2010	2011
Bigmouth	4	T				X	X	X	X	X
Downie	4	T	X	X	X			X		
Gothics	11	T	X	X	X	X	X	X	X	X
Pettipeace	2	T						X	X	
Red Rock	2	T				X		X	X	X
Adamants	1	T					X			
Avola_Mud	5	R		X	X	X	X	X		
Clearwater	1	R						X	X	
Moonbeam	3	R		X	X	X	X			
Raft	1	R						X		
Seymour	1	R						X		
Anstey	1	R			X	X				

The functional response based on wolf use of caribou habitat and movement rates

The first prediction involved determining whether wolves changed their use of caribou habitat, because wolves are expected to search more broadly when their primary prey become less abundant. To estimate the wolf use of caribou habitat, I extracted the caribou habitat quality value (i.e. resource selection function; RSF produced by Apps et al. 2001, 2007) for each wolf telemetry location. This was done for three seasons when caribou are exposed to wolf predation: spring, summer, and early winter (Apps et al. 2001, Wittmer et al. 2005a), with the date of each wolf location corresponding to the appropriate RSF value for each caribou season. The late winter (Jan – April) is when wolves and caribou are separated so there is almost no wolf predation during that season (Wittmer et al. 2005a). The caribou RSF ranged in value (p) from 0 to 1, and was the dependent variable for analysis, but I linearized these values using ln [p/(1-p)]. To predict the wolves' use of caribou habitat, I considered three covariates including the time since moose reduction began (TSR), the annual change in moose abundance (absolute value), and timing of spring. Timing of spring influences animal distribution, particularly in mountainous ecosystems where many animals are constrained by snow to the valley bottoms during winter, but occupy approximately three times the area (and thus 1/3 the density) as summer progresses. Therefore, this factor should be accounted for to understand if there is a shift in habitat use by wolves. I developed an index of spring snowmelt based on daily snow measurements taken from an automated snow pillow station at 1850 m elevation within the treatment area (BC River Forecast Centre 2012, station 2A06P). At this station snow accumulation usually peaks in early May and averaged 1322 mm (snow-water equivalent; range 883 – 2113 mm; n = 20 yr). I arbitrarily chose a threshold of 100 mm, and recorded the earliest date when this value was achieved each spring. The date at which this threshold occurred varied by 27 days (15 June – 12 July) during my study period (2003 – 2011), and this variation was not sensitive to alternate thresholds ranging from 50 to 500 mm, suggesting it was a robust index of when mountainous areas became snow free.

The annual change in moose abundance and TSR were included as predictors to directly assess whether the moose reduction treatment affected wolf use of caribou habitat. I also included a quadratic term for TSR to account for the possibility that the relationship increased then declined over time. I used model averaging techniques with seven *a priori* candidate models based on the three independent factors. These analyses were conducted using linear mixed effects in R 2.11, where the individual wolf nested within its wolf pack was specified as a random intercept and the independent factors were fixed. Model averaging was conducted using the MuMin package (Version 1.6; Bartoń 2011). Correlations among the fixed effects were also evaluated to eliminate highly correlated predictors (> 0.70). A likelihood ratio test was performed for each analysis to determine if the global model provided a significant improvement over the null model (with the same specified random effects). As a spatial contrast, the above analyses were also performed in the reference area where moose populations were not manipulated. The analysis of spring snowmelt was replicated using a snow pillow station (1E02P) within the reference area.

My second prediction was that at lower moose density, movement rates should increase as wolves spend a greater proportion of their time searching and less time handling (McPhee et al. 2012), consistent with what would be expected from the disc equation. I estimated movement as m/hr using Pythagoras' theorem to calculate the distance between sequential locations, divided by the hours between those locations, but eliminated data that spanned > 24 hrs between locations. Preliminary analyses suggested that movement rates (m/hr) may not be a relevant metric, but rather the proportion of long movements would be more appropriate to reflect search rates. Research in other large mammal systems suggests that animals move short distances when consuming prey, interspersed by long distances between suitable foraging patches (i.e. "searching")(Anderson and Lindzey 2003, McPhee et al. 2012), and that this measure was more sensitive to resource availability. A histogram revealed that 300 m/hr would be a suitable breakpoint to differentiate between common vs. "long" movements. Therefore, I used logistic regression to predict the proportion of long movements as a function of the moose reduction treatment. The independent factors were moose abundance, snowmelt, and season (spring, summer, early winter, with late winter as the reference category), recognizing that females with pups would be restricted to dens so that this metric may not be relevant in spring and mid-summer when wolves tend to be more localized, regardless of prey availability. Snowmelt was not included in the late-winter season models because its influence from the previous spring would not be relevant. I plotted predictions from these models using the languageR (Baayen 2007) package in R.

The functional response based on kill rates

The third prediction was that kill rates would be invariant to prey density in winter, but kill rates would be lower in summer (Metz et al. 2012) and most sensitive to changing prey abundance. In this chapter I use the term kill rate to mean a biomass adjusted kill or consumption rate. Unfortunately, I did not have summer kill rate data throughout the moose reduction period, but only from 2009 and 2010. Nonetheless, I was able to test kill rate as a function of prey density in winter across a 5-fold range of moose abundance, and contrast these values with the more recent summer sampling. This contrast allowed me to characterize whether kill rates were asymptotic (i.e. limited by handling time) at all times of the year, or whether they varied by season.

I estimated winter kill rates using a combination of snow tracking (Huggard 1993), aerial flights, and clusters of telemetry locations, but in summer relied exclusively on telemetry clusters. Kill rates based on snow tracking were estimated in 2004, before downloadable GPS collars were commonly used. In 2005, a combination of snow tracking and GPS cluster data were used to estimate the kill rate. The 2004 and 2005 data were provided by Stotyn (2008; unpublished data), and used Hebblewhite's (2003) ratio-estimator method to calculate the kill rate. Clusters of telemetry locations have been used to delineate wolf kill sites since at least 1985 (Messier 1985b), but the advent of GPS collars has greatly advanced this technique (Anderson and Lindzey 2003, Webb et al. 2008, Knopff et al. 2009, Metz et al. 2011). I used a time/space clustering program to identify kill sites (SaTScan; Kulldorff et al. 2005) and tried to investigate clusters that potentially included a kill, plus a sample of locations that were unlikely to include a kill (i.e. single and 2-point clusters). A minimum of six weeks of monitoring for each pack and season was the intended sampling period because Hebblewhite et al. (2003) estimated that at least 25% of the winter should be sampled to obtain precise estimates, though Knopff (2011) also included 28-day estimates of cougar kill rates, and I did so in two cases. In winter, collars were programmed to obtain a location every two or three hours, and every hour in summer. However, in some cases the sampling period extended beyond the 1 hr program schedule of the collar, into the three hour program, and one estimate was based only on 3 hr sampling (but see results). A potential kill in winter was defined as a meta-cluster having a minimum of 10 locations within a 400-m buffer around a single location in a 4-day period. A meta-cluster was a group of clusters that overlapped in a 4-day window. The value 10 was chosen because it was the minimum value where a moose kill was found, based on preliminary fieldwork where 54 meta-clusters were visited and 16 calf or adult moose kills were detected (mean number of locations where a moose kill was found = 17.6, median = 16.5, range = 10 – 26; van Oort et al. 2009b). In summer, a sample of 174 clusters that had 6 hrs or less of wolf use revealed that 1.1 % (N = 2; 1 beaver, 1 moose) of these contained a kill. Therefore, the target was to visit samples that had 6 or more hr of use, but we also sampled smaller clusters and single locations.

SaTScan parameters were set to identify clusters for locations that were ≤ 300 m apart from each other within a maximum of 4 days apart from successive locations, as suggested by Webb et al. (2008). Prior to 2010, a similar algorithm was programmed in MS Excel (van Oort et al. 2009b). Cluster centers as well as individual locations were loaded into hand-held GPS units with the majority of sites accessed from the ground, although nine days of helicopter time were used to locate the most remote clusters. We navigated to the cluster centre, then to each telemetry location. If the kill was still not found, then a buffer of at least 100 m from the outermost locations of the clusters was searched. The GPS track file was on and examined while searching to help field crews ensure that the area was well covered. For 10 % of kills included in the kill rate, we were unable to do field verification so I used equation 5 in Webb et al. (2008) to determine if the cluster was a large-mammal kill, and if so, considered this an adult moose kill (Webb pers. comm.).

Pack cohesion varies throughout the year (Peterson et al. 1984, Messier 1985b) but is lowest in summer (Metz et al. 2011). Metz et al. (2011) found that summer kill rates would be underestimated by 32% had cohesion not been accounted for. However, cohesion was weakest for larger packs (> 10), but nearly 100% for packs of five or less during winter. Similarly, Jedrzejewski et al. (2002) found that cohesion was greater for smaller packs in both summer and winter, and noted that packs of two were always hunting and feeding together. Packs in the treatment area were most often < 5 adults (four of 11 winter kill rate estimates were based on packs of > 5 [6, 6, 7, and 8]), and never exceeded four adults when summer kill rates were recorded. Four of seven summer kill rate estimates were obtained from packs of less than 3 adults. Therefore, although I did not conduct a formal cohesion analysis (Metz et al. 2011), the small packs in the treatment area would have minimized the biases identified by Metz et al. (2011). Nonetheless, I applied the 32% correction factor to summer kill rates for the seasonal kill rate comparison, in addition to conducting this analysis with the uncorrected values. For the reasons mentioned above, I consider 32% to be conservative.

I focussed summer sampling from July to September, though sampling for one pack began in early June. Sampling later in summer was done to avoid difficulties with sampling ungulate neonates, and to sample the period when ungulates would be at a lower density as a result of expanding their range into the mountains (Appendix 6.2). This would provide a strong contrast to the winter season, when primary prey densities were much more concentrated. Pack sizes were estimated during aerial telemetry flights and with bed counts, but in 2010 and 2011 I also deployed infra-red cameras (Reconyx Inc., Holmen, Wisconsin) to assist with pack enumeration in winter but especially summer when wolves are more difficult to spot. Cameras were placed near den sites or typical wolf travel routes. I accounted for pups in the summer pack size estimates using the biomass equivalent of pups to adults, which was one of the methods proposed by

Metz et al. (2011). Pack size is needed to correct consumption rates to a per wolf basis, but also to be included as a covariate because it has been found to be an important influence on per capita kill rate (Messier 1985b, Hayes et al. 2000). The summer pack structure in this area appeared to be unstable relative to others reported in the literature (but see Messier 1985a), likely because their primary prey were declining rapidly. Several of the smaller packs (Bigmouth, Pettipeace, and Red Rock) that lived in the lower moose density areas appeared to share or scavenge kills at the edge of their range, even attending kills at the same time. In certain cases for summer clusters, I deemed it appropriate to divide the kills between these wolves, rather than assign them completely to one pack or another. I recognize that this was subjective, but should not affect population-level comparisons among seasons. In certain cases I also assigned biomass to other scavenges, for example if it appeared that a wolf had been displaced by a bear, I reduced the biomass assigned to the wolf.

To compare summer vs. winter biomass, the kill rate was estimated as the number of moose equivalent kills/wolf/100 d. In the treatment area, moose make up the dominant prey of wolves in both biomass and frequency in summer and winter (Stotyn 2008); in summer, however, moose calves and alternate species comprise a greater proportion of wolf diets. Therefore, I converted prey to moose equivalent units, based on estimates from Knopff (2010, Table 4.2) for juvenile ungulates sampled from July to September and from December to March. Adult moose were considered 65% consumable (Hayes et al. 2000). I did not differentiate sexes between adult moose, to facilitate population dynamics modelling (Chapter 5). Beaver and porcupine were treated as 1/15th of a moose. This was based on the assumption that a < 20 kg mammal would be 90% consumed. Calf ungulate prey sampled in summer were converted to adult moose units assuming that they were 90% consumed. Although these conversions are simplifications, they were nonetheless suitable to test the predictions I outlined.

In addition to kill rates, prey density estimates are required to calculate the wolves' functional response. To estimate the moose density within each pack's territory, I calculated the proportion of wolf telemetry locations in pre-defined moose density strata based on the methods of Gasaway (1986; see details in Chapter 3). These proportions were multiplied by the estimated moose density in each strata, adjusted by each annual moose population estimate, to obtain a moose density estimate for each wolf pack for each season and year.

To determine how kill rate varied with prey density and season, I compared the level of support among four different functional response models, using both winter and summer data: Type 0 (kill rate does not vary with prey density), Type I (increases linearly with prey density, no handling time constraint), Type II (Disc equation, increases monotonically to the handling time limit), and a ratio-dependent Type II (increases monotonically but as function of the ratio of prey to predators). These were evaluated by specifying the mechanistic equations using non-linear mixed effects with package nlme in R 2.11, with wolf pack as the random effect. AIC was used to discriminate among competing models. Start values for optimizing parameters (*a*, *Th*) for the nlme package were estimated using the non-linear nls function in R (which ignores the effect of pack). Because there were limited data, I could not incorporate the effect of season into this non-linear mixed-effects analysis, so then considered season by repeating the previous analysis in summer and winter, to determine if prey density influenced kill rates in each season. Finally to contrast the relative importance of season, moose density, or pack size at explaining kill rate, I used linear mixed effects, again with pack as the random effect. In this case, because the effect of season was an explicit contrast, I repeated the analysis with and without the 32% correction factor for summer kill rates.

Changes in diet based on wolf scat analyses

My fourth prediction was that wolf diets would shift from moose to alternate prey as moose abundance was reduced, and that this effect would be strongest in summer when wolf foraging is most constrained, and hibernating prey became available. Wolf diets were estimated by collecting scats only in the treatment area. My design in this case provided two contrasts, spatial and temporal. The temporal contrast consisted of comparing wolf diets during the high phase of moose abundance (2004 – 2005; 1.1 – 1.5 moose/km^2, Fig. 6.2), to the lower phase (2008 – 2010; 0.4 – 0.6

moose/km^2). The spatial contrast was to compare summer diets from 2008 – 2010 from areas of high moose density (the Goldstream Valley 0.43/km^2; summer densities), to adjacent areas where moose densities were 2.2-fold lower (0.2/km^2 summer densities). The spatial contrast was done to further discern if diets were affected by differential abundance of their primary prey (Messier 1985a), and to determine if there was an association with the wolf recruitment estimates reported in Chapter 6a. The recruitment comparison (Chapter 6a) made use of the same spatial contrast (High vs. Low moose density) described here.

Scats were collected at wolf kill, den, and rendez-vous sites, but also while travelling along roads or trails throughout the study area, or while walking hundreds of kilometers off roads while doing systematic moose pellet sampling (Serrouya et al. 2011), hiking to wolf kill sites, or snow trailing ungulates and wolves as part of related research (Serrouya et al. 2007). Steenweg (2011) found that scats collected at den and rendez-vous sites differed significantly in composition from those collected along roads, and suggested that systematic transects would provide the most objective method of characterizing wolf diets. Using a combination of approaches likely minimized sample bias, but I also restricted the analyses to two scats per kill site to avoid over-representing those prey (usually moose) in the sample.

Some hair samples are difficult to distinguish, particularly among calf ungulates. Genetic tests were performed at Wildlife Genetics International to validate prey composition for ambiguous samples. Juvenile deer and caribou may be confused, but it is important to differentiate these two species. Genetic tests could not be performed on hair follicles, which are relatively rich in DNA, because they get digested in the wolf's stomach, but instead had to be done on hair shafts using mitochondrial DNA for species identification (David Paetkau, unpublished methods). To my knowledge this is one of the first attempts to use DNA to validate prey composition in studies of wolf scats.

Scats were autoclaved for 90 minutes at 120^o C to kill any *Echinococcus granulosus* and *E. multilocularis* eggs. Scats were then individually washed to separate fecal matter from hair, plant cellulose, bones, rocks, conifer needles and cones. These scats were then dried and frozen until microscopic analyses were conducted.

Microscope analysis

Scats were dissected completely to reveal different hair types, bone fragments, hoof or dew-claw remains and plant matter. Twenty hairs were randomly chosen from each scat and placed onto a slide with double-sided tape. A compound light microscope at 100 × magnification was used to examine the microstructure of each hair, including the basal configuration, length, diameter, colour-band patterns and medulla pattern (Kennedy and Carbyn 1981, Moore et al. 1974, Jones et al. 2009). Examining these hair characteristics at this power was often sufficient to identify some genera such as leporids, marmots, beavers, squirrels, and bears, and separate them from cervids (Kennedy and Carbyn 1981, Moore et al 1974, Jones et al. 2009). Once the probable genus was identified, a few intact hairs, preferably guard hairs, were selected from the scat and imprinted onto a slide. To identify cervid species, the imprint of the hair's cuticle scale pattern was examined at 400 × magnification, though white-tailed and mule deer could not be confidently differentiated. Juvenile cervids less than 5-months old could be differentiated from adults based on the medulla structure and guard hair diameter (Kennedy and Carbyn 1981, Jones et al. 2009). Photographs and measurements of the microscopic image of ambiguous hairs were sent to colleagues at the University of Alberta for a second opinion. Scat bags were labelled with a sample ID only, so that the person doing the scat analyses had no prior knowledge of location, time period or seasons associated with each sample.

I used G-tests (P. Hurd, unpublished R script) to compare the proportion of wolf diet items in wolf scats among temporal and spatial contrasts, but I also bootstrapped ($n = 1000$) each distribution using the scat as the sample unit to contrast differences among individual prey items. All analyses were performed in R 2.11.

RESULTS

The functional response based on use of caribou habitat and movement rates

For the three seasons of analysis, I collected 18,974 locations on 24 different wolves across six packs in the treatment area, whereas in the reference area I had 6,942 locations on 12 wolves also from six packs. These data were collected from 2004 to 2011 and from 2005 to 2010 for the treatment and reference areas, respectively (Table 6.4). Each pack included at least one wolf fitted with a GPS collar. There were fewer wolves included in this analysis compared to the survival estimates (Chapter 6a) because I eliminated animals that contained fewer than 10 locations, which were usually wolves fitted with VHF collars or those that died or dispersed from the study area.

In the treatment area wolves increased their use of caribou habitat as the moose reduction progressed, and this pattern occurred during the spring, summer, and early winter seasons. This effect diminished with time, as explained by the negative TSR^2 term (Tables 6.5 – 6.7). Snowmelt was also an influential factor because earlier springs were correlated with increased use of caribou habitat (Table 6.5 – 6.7). Predictably, the annual change in moose abundance was correlated with TSR, but this correlation varied from 0.24 for spring, to 0.50 for summer, and 0.10 in early winter, so I retained both TSR and change in moose abundance in the models. There was little discrimination between the effect of snow melt and the treatment factors (i.e. TSR or the change in moose abundance), based on similar AIC weights among those factors. Snowmelt was not consistently correlated with TSR (0.07, -0.28, 0.10, for spring, summer, and early winter, respectively), suggesting reasonable independence between these predictors. The effect of TSR on wolf use of caribou habitat was strongest for spring, and weakest for the summer season (Fig. 6.5). For all three seasons, the likelihood ratio test revealed that the global model was a significant improvement over the null model (Spring: L-ratio = 162.6, $p < 0.001$; summer: L-ratio = 64.0, $p < 0.001$; early winter: L-ratio = 75.6, $p < 0.001$).

In the reference area, wolf use of caribou habitat in spring was unaffected by TSR, the change in moose abundance in that area, or snow melt (all $p > 0.30$). During summer the change in moose abundance was highly correlated with TSR (0.99), so the former was excluded from the analysis. There was a positive effect of TSR on wolf use of caribou habitat for the global model, but the model-averaged parameter estimate slightly overlapped 0 (Table 6.8), and the L-ratio test suggested a marginal improvement over the null model (L-ratio = 8.4, $p < 0.04$). Furthermore, by predicting the coefficients for the summer season, it is apparent that the magnitude of this effect was small relative to any season in the treatment area (Fig 6.5). In early winter, the only significant factor was TSR but the coefficient was negative (Table 6.9), meaning that wolves used less caribou habitat over time in the reference area.

Wolf data from the treatment area began one year before and ended one year after the reference data (Table 6.4), so to investigate the possible effect of these extra years, I removed the data from 2004 and 2011 and repeated the analysis in the treatment area. The results changed somewhat, but the multi-model averaged coefficient for TSR during summer was still positive, though weaker ($\beta = 0.74$ compared to $\beta = 1.76$ for the full data set), and unconditional CIs overlapped 0 slightly (–0.072 to 1.56). The top model contained only TSR, was 1.9 AIC units higher than the next model, and its effect was highly significant ($\beta = 0.90$, $p < 0.001$). The spring and early winter results were similarly robust to excluding the 2004 and 2011 data but like the summer season, the strength of the relationship was less pronounced, as expected with a reduced sample size.

The analysis of wolf movement rates included more telemetry locations because the late winter season was included (26678 locations in the treatment and 10258 in the reference areas). Analyses with m/hr as the dependent were not revealing, with most analyses producing non-significant results. However, using long movements (>300 m/hr) as a binary response, the effect of season was significant in both the treatment and reference areas, with the most long movements occurring in summer (Appendix 6.3). Therefore, each season was analysed separately, and in the treatment area, results were mixed, with movements in spring unaffected by moose density (Table 6.10). However, in early winter, there were more long movements as moose declined, but in late winter and summer long movements were positively linked to moose density (Tables 6.11 – 6.13). However, the likelihood ratio test indicated that only the early winter and late-winter models were significant improvements over the null model. Yet, the magnitude of the effect was strongest in early winter, where the proportion of long movements was about 10 % when there were many moose, compared to 40 % when there were fewer moose (Fig. 6.6).

In the reference area snowmelt and the moose abundance index were correlated (>0.90) so I retained the moose index in the analysis. As with the treatment area, in spring movements were unaffected by moose density (p = 0.34). Summer movements were also not significant (p = 0.69), but in early and late winter, there were more long movements with fewer moose (Tables 6.14, 6.15), even though the moose population was more stable compared to the treatment area (Appendix 6.1).

Table 6.5. Averaged coefficients for parameters used to predict the wolf use of caribou habitat (i.e. a caribou RSF value linearized to ln[p/(1-p)]) for the **spring** season in the **treatment** area, 2004 - 2011. Linear mixed effects models were used with random effect as wolf (N=21) nested within pack (N=5). The effect of TSR and TSR^2 is represented in Fig. 6.5.

Parameter	Coefficient	Adjusted SE	Lower CI	Upper CI	AICω
Intercept	-12.60	1.87	-16.30	-8.92	
Snowmelt	-0.19	0.03	-0.24	-0.13	1.00
Moose change	0.012	0.001	0.009	0.015	1.00
TSR	3.93	0.63	2.70	5.17	1.00
TSR^2	-0.19	0.06	-0.31	-0.08	0.98

Snowmelt, date when the snowpack decreased to <100mm snow-water equivalent. An index of spring onset.
Moose change, annual change in moose abundance.
TSR, Time since moose reduction (years). Squared term is also included.

Table 6.6. Averaged coefficients for parameters used to predict the wolf use of caribou habitat (i.e. a caribou RSF value linearized to ln[p/(1-p)]) for the **summer** season in the **treatment** area, 2004 - 2011. Linear mixed effects models were used with random effect as wolf (N=22) nested within pack (N=5). The effect of TSR and TSR^2 is represented in Fig. 6.5.

Parameter	Coefficient	Adjusted SE	Lower CI	Upper CI	AICω
Intercept	-7.13	1.62	-10.30	-3.96	
Snowmelt	-0.25	0.06	-0.36	-0.13	1.00
Moose change	-0.004	0.004	-0.01	0.0003	0.72
TSR	1.76	0.60	0.58	2.93	1.00
TSR^2	-0.03	0.05	-0.14	0.08	0.39

Table 6.7. Averaged coefficients for parameters used to predict the wolf use of caribou habitat (i.e. a caribou RSF value linearized to ln[p/(1-p)]) for the **early winter** season in the **treatment** area, 2004 - 2011. Linear mixed effects models were used with random effect as wolf (N=19) nested within pack (N=5). The effect of TSR and TSR^2 is represented in Fig. 6.5.

Parameter	Coefficient	Adjusted SE	Lower CI	Upper CI	AICω
Intercept	-5.51	1.25	-7.97	-3.05	
Snowmelt	-0.06	0.02	-0.09	-0.03	1.00
Moose change	-0.001	0.001	-0.002	0.000	0.90
TSR	1.76	0.29	1.19	2.33	1.00
TSR^2	-0.11	0.03	-0.17	-0.05	1.00

Table 6.8. Averaged coefficients for parameters used to predict the wolf use of caribou habitat (i.e. a caribou RSF value linearized to ln[p/(1-p)]) for the **summer** season in the **reference** area, 2005 - 2010. Linear mixed effects models were used with random effect as wolf (N=11) nested within pack (N=5). The effect of TSR and TSR^2 is represented in Fig. 6.5.

Parameter	Coefficient	Adjusted SE	Lower CI	Upper CI	AICω
Intercept	-8.93	2.06	-13.00	-4.89	
Snowmelt	-0.04	0.08	-0.20	0.11	0.41
TSR	2.83	1.61	-0.32	5.98	0.96
TSR^2	-0.39	0.29	-0.97	0.18	0.76

Table 6.9. Averaged coefficients for parameters used to predict the wolf use of caribou habitat (i.e. a caribou RSF value linearized to ln[p/(1-p)]) for the **early winter** season in the **reference** area, 2005 - 2009. Linear mixed effects models were used with random effect as wolf (N=9) nested within pack (N=4). The effect of TSR and TSR^2 is represented in Fig. 6.5.

Parameter	Coefficient	Adjusted SE	Lower CI	Upper CI	AICω
Intercept	0.72	2.06	-3.31	4.76	
Snowmelt	0.03	0.04	-0.06	0.11	0.48
Moose change	-0.0004	0.001	-0.003	0.002	0.14
TSR	-2.16	0.71	-3.56	-0.76	1.00
TSR^2	0.05	0.09	-0.12	0.21	0.34

Snowmelt, date when the snowpack decreased to <100mm snow-water equivalent. An index of spring onset.

Moose change, annual change in moose abundance.

TSR, Time since moose reduction (years). Squared term is also included.

Table 6.10. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **spring** in the **treatment** area. Wolves were nested in packs as mixed effects (wolves = 15, pack = 5). The deviance for this model is 3515, and for the null model is 3520, and the likelihood ratio test indicated no improvement over the null.

Parameter	Estimate	Std. Error	z value	P-value
Intercept	-0.41	0.27	-1.52	0.13
Moose density	0.16	0.26	0.62	0.54
Snowmelt	-0.02	0.01	-1.91	0.06

Snowmelt, date when the snowpack decreased to <100mm snow-water equivalent. An index of spring.

Table 6.11. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **summer** in the **treatment** area. Wolves were nested in packs as mixed effects (wolves = 16, pack = 5). The deviance for this model is 16405, and for the null model is 16409, and the likelihood ratio test indicated no improvement over the null (p = 0.13).

Parameter	Estimate	Std. Error	z value	P-value
Intercept	-0.88	0.23	-3.85	<0.001
Moose density	0.41	0.20	2.01	0.04
Snowmelt	0.004	0.01	0.28	0.78

Snowmelt, date when the snowpack decreased to <100mm snow-water equivalent. An index of spring.

Table 6.12. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **early winter** in the **treatment** area. Wolves were nested in packs as mixed effects (wolves = 12, pack = 5). The deviance for this model is 3901, and for the null model is 3945 and the likelihood ratio test indicated an improvement over the null ($X^2 = 44.3$, $P<0.001$).

Parameter	Estimate	Std. Error	z value	P-value
Intercept	1.45	0.47	3.09	0.002
Moose density	-1.99	0.45	-4.38	<0.001
Snowmelt	-0.07	0.01	-5.71	<0.001

Snowmelt, date when the snowpack decreased to <100mm snow-water equivalent. An index of spring.

Table 6.13. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **late winter** in the **treatment** area. Wolves were nested in packs as mixed effects (wolves = 19, pack = 6). The deviance for this model is 10156, and for the null model is 10169 ($X^2 = 13.5$, $P < 0.001$).

Parameter	Estimate	Std. Error	z value	P-value
Intercept	-1.27	0.16	-7.90	<0.001
Moose density	0.75	0.20	3.68	<0.001

Table 6.14. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **early winter** in the **reference** area. Wolves were nested in packs as mixed effects (wolves = 7, pack = 4). The deviance for this model is 2239, and for the null model is 2250 ($X^2 = 11.2$, $P = 0.001$).

Parameter	Estimate	Std. Error	z value	P-value
Intercept	0.08	0.21	0.39	0.69
Moose density	-2.27	0.54	-4.19	<0.001

Table 6.15. Coefficients for parameters used to predict the proportion of long wolf movements using logistic regression for **late winter** in the **reference** area. Wolves were nested in packs as mixed effects (wolves = 9, pack = 6). The deviance for this model is 4291, and for the null model is 4303 ($X^2 = 12.1$, $P < 0.001$).

Parameter	Estimate	Std. Error	z value	P-value
Intercept	0.35	0.34	1.02	0.31
Moose density	-2.83	0.79	-3.60	<0.001

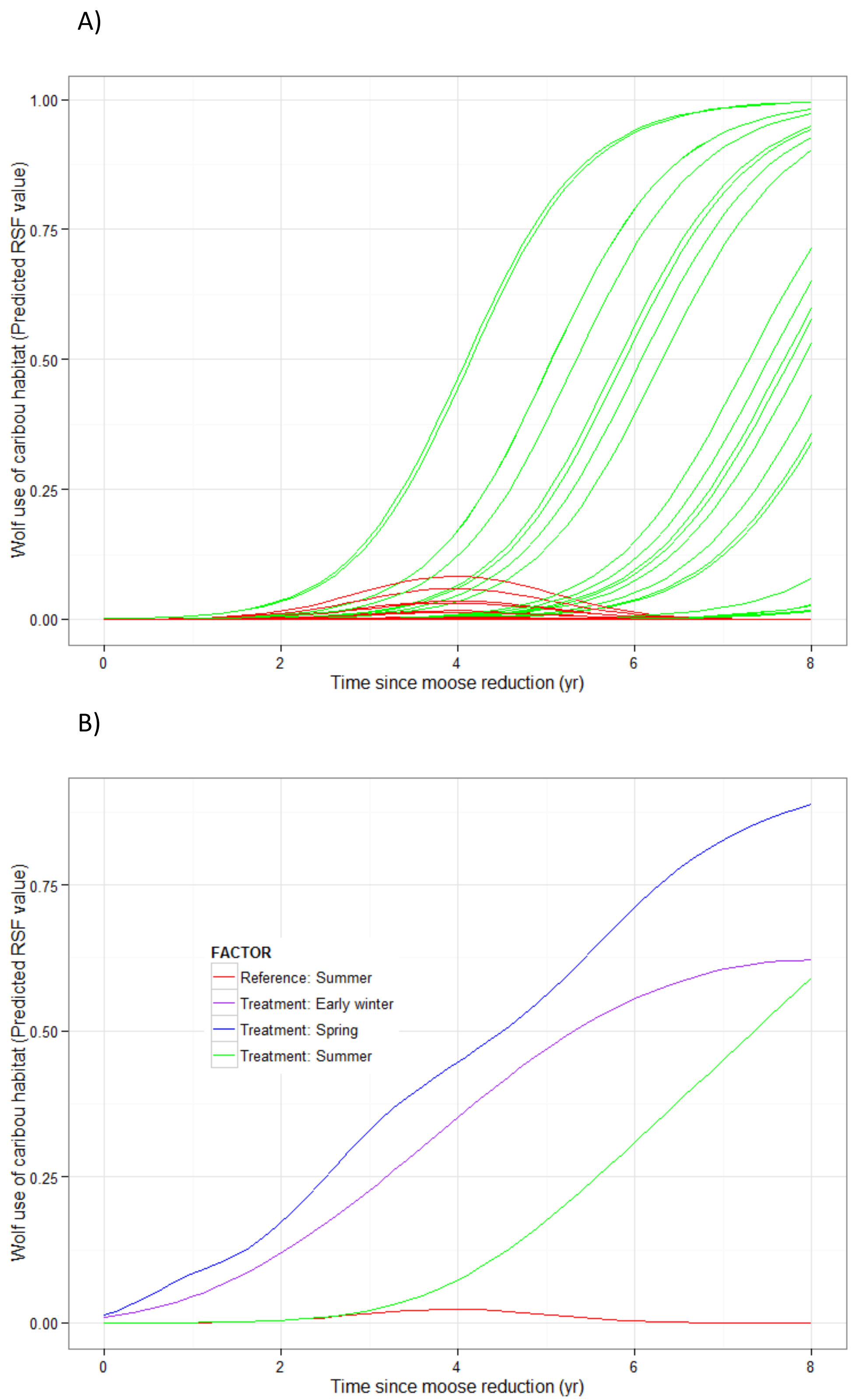


Figure 6.5. Wolf use of caribou habitat (i.e. a caribou RSF value (Apps et al. 2001)), as a function of the time since moose were reduced in the treatment area. Model averaged parameters from Tables 6.5 – 6.8. Panel A) Summer season for the treatment and

reference area: each line represents a wolf as predicted from the mixed effects model (Tables 6.6, 6.8), with wolf (nested within packs) as the random effect. Panel B) Prediction for the treatment and reference areas, averaged across all wolves. Only season/treatment combinations with a significant effect are shown, and where the effect of TSR was positive. The reference area had a significant effect of TSR in summer, but its magnitude was small compared to the treatment area.

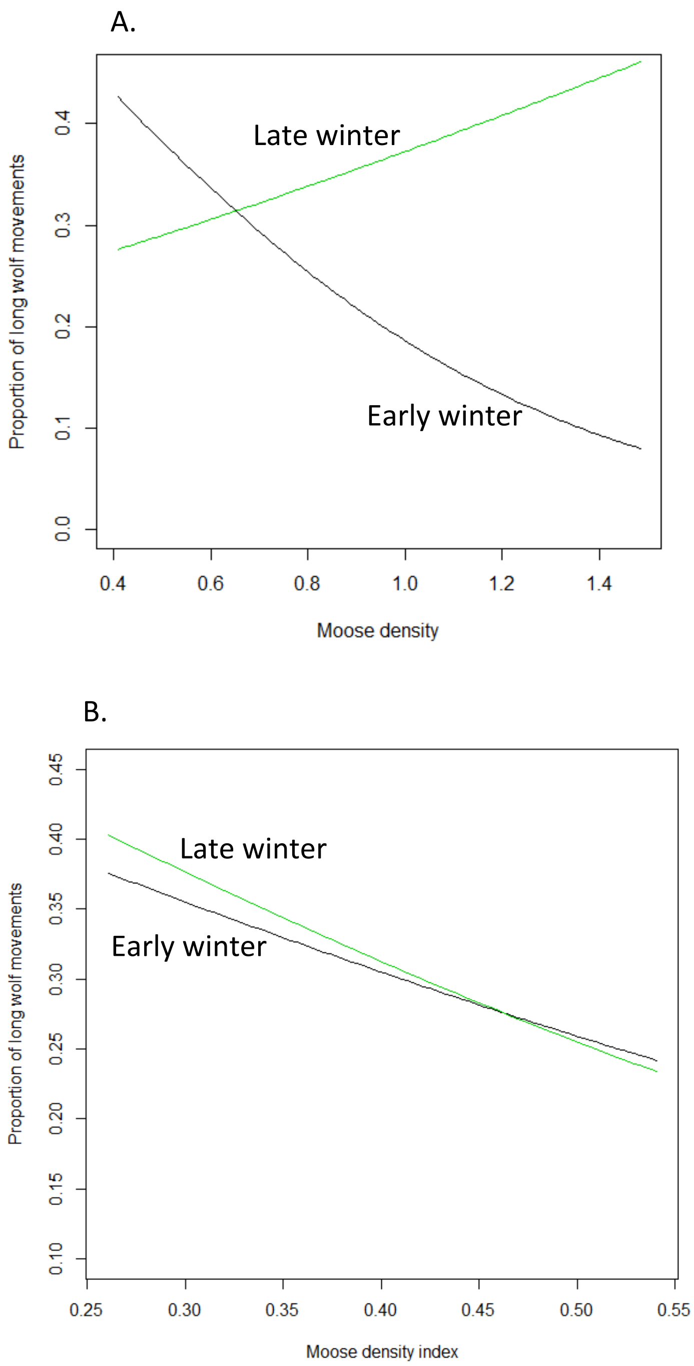


Figure 6.6. Predicted proportion of wolf movements that were “long movements”, as a function of moose density, in A) the treatment area, and B) the reference area. Only seasons with significant effects are shown. See tables 6.10 – 6.15.

The functional response based on kill rates

We visited the remains of 247 prey, 131 in winter and 116 in summer, though 16 of these were located just outside the primary treatment area. Moose remains were found at 204 (82.6 %) sites, followed by deer (*Odocoileus* spp; 4.0%), beaver (*Castor canadensis*; 3.6%), wolf (0.8%), bear (0.8%), marmot (0.8%; *Marmota caligata* and porcupine (*Erethizon dorsatum*; 0.8%). One mountain goat was found at a kill site. The remains of unknown prey were found at 13 sites, but most unknown kills consisted of old bone fragments and likely reflect scavenging. Two clusters were caused by trappers' bone piles or baits. Less than half the total kills investigated could be used for kill rate estimation (many kills were from short sampling sessions from wolves that dispersed or died, or were sampled outside the intended sampling seasons). Based on these data, a total of 17 kill-rate estimates were collected from six wolf packs, 11 in winter and six in summer. An additional estimate was calculated for summer based on the collar with 3 hr intervals, but was excluded because of the relatively long fix intervals compared to other studies (Metz et al. 2011, Knamiller 2011; though 16 kills were recorded including eight neonates over 81 days). Two estimates are provided for the Gothics pack in 2010 because GPS collars indicated a long-term split between members for the late summer and fall. Sampling sessions for estimates of kill rates averaged 46.9 days (range 29 – 82). Kill rates were collected across a 30-fold difference in moose density (Fig. 6.7), from 0.1 to 3.0/km^2, but this range was narrower for summer (0.1 – 0.3/km^2) than winter (0.6 – 3.0/km^2). The wolf with the lowest summer kill rate eventually left the treatment area, and packs with the next two lowest kill rates (Fig. 6.7) included four wolves that starved (three adults, two of which were collared, and one pup) the same summer that kill rates were estimated (Table 6.2).

With both seasons combined, kill rates were dependent on prey density and limited by handling time, indicating that a Type II functional response was a plausible explanation (Fig. 6.7), but the Type 0 functional response was the most parsimonious representation of the data (Table 6.16). When data were restricted to the winter season, kill rates were invariant to prey density, with the Type 0 functional response being clearly the most supported (Table 6.17, Fig. 6.7). There were insufficient data to repeat this analysis for the summer season.

The final approach was to use linear mixed models to contrast the effect of season with key factors that can affect the functional response, namely prey density and pack size. With uncorrected summer values, this analysis revealed that season was the best predictor (Table 6.18), with winter having higher kill rates (Fig. 6.7). However, using corrected summer kill rate values (*sensu* Metz et al. 2011), the difference between winter and summer kill rates was obviously diminished because of the positive effect that the correction factor had on summer kill rates, and no relationships were significant (P > 0.15).

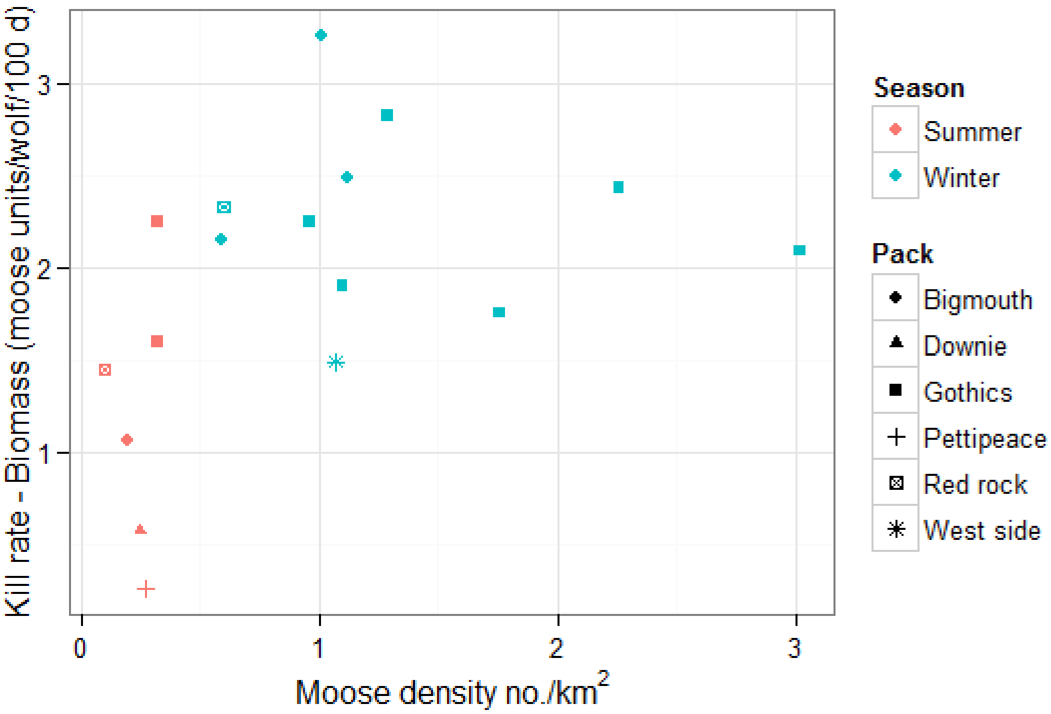


Figure 6.7. Wolf kill rates (biomass adjusted) as a function of moose density in the treatment area, 2004 – 2011. Moose abundance was experimentally reduced from 1650 to 480 during this time period.

Table 6.16. Functional response models to explain kill rates for **winter** and **summer** data (combined) in the treatment area. Non-linear mixed effects models were used to estimate the attack rate (*a*) and the handling time (*Th*), with wolf pack as the random effect. Standard errors are in brackets.

Model	df	AICc	a (se)	P-value	Th (se)	P-value
Type 0	**11**	**45.4**	**NA**	**NA**	**1.61(0.29)**	**<0.001**
Type I	11	59.8	1.86 (0.48)	0.002	NA	NA
Type II	10	50.6	11.1 (5.2)	0.06	0.37 (0.06)	<0.001
Type II ratio	10	57.0	56.8 (54.2)	0.32	0.43 (0.09)	<0.001

Table 6.17. Functional response models to explain kill rates for the **winter season** in the treatment area. Non-linear mixed effects models were used to estimate the attack rate (*a*) and the handling time (*Th*), with wolf pack as the random effect.

Model	df	AICc	a (se)	P-value	Th (se)	P-value
Type 0	**7**	**24.0**	**N/A**	**N/A**	**2.27(0.15)**	**<0.01**
Type I	7	43.3	1.84 (0.50)	0.01	N/A	N/A
Type II[a]						
Type II ratio[a]						

[a]The nlme package could not solve these equations. The lack of a numerical solution suggests that these models were not supported given the limited data.

Table 6.18 Linear mixed effects model used to explain wolf kill rates in the treatment area (See Fig. 6.7).
Using corrected summer values (x 1.32) renders all effects non-significant.

Parameter	Estimate	SE	DF	t-value	p-value
Intercept	0.96	0.32	8	3.02	0.02
Moose density	-0.30	0.31	8	-0.96	0.37
Season (Winter)	1.15	0.41	8	2.84	0.02
Pack size	0.13	0.10	8	1.26	0.24

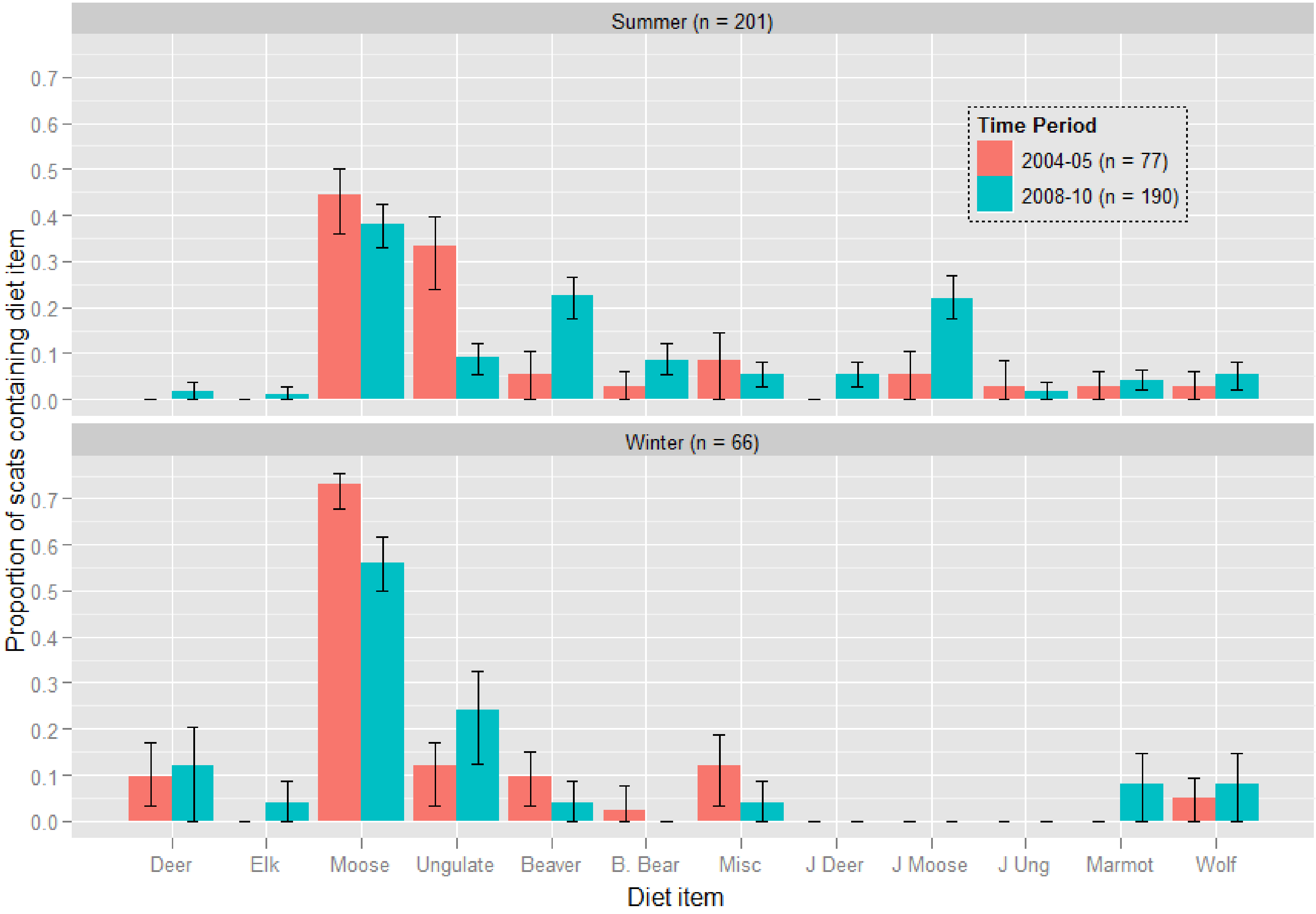

Summer (n = 201)
Winter (n = 66)
Time Period
2004-05 (n = 77)
2008-10 (n = 190)
Proportion of scats containing diet item
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Deer
Elk
Moose
Ungulate
Beaver
B. Bear
Misc
J Deer
J Moose
J Ung
Marmot
Wolf
Diet item

Figure. 6.8. Frequency of occurrence of prey items in wolf scats across two time periods and two seasons in the treatment area. Item preceded by a “J” indicates a juvenile. The moose density was *c*. 3 × greater during the 2004-05 time period. Error bars are bootstrapped 95% CIs. Sample sizes are shown in brackets.

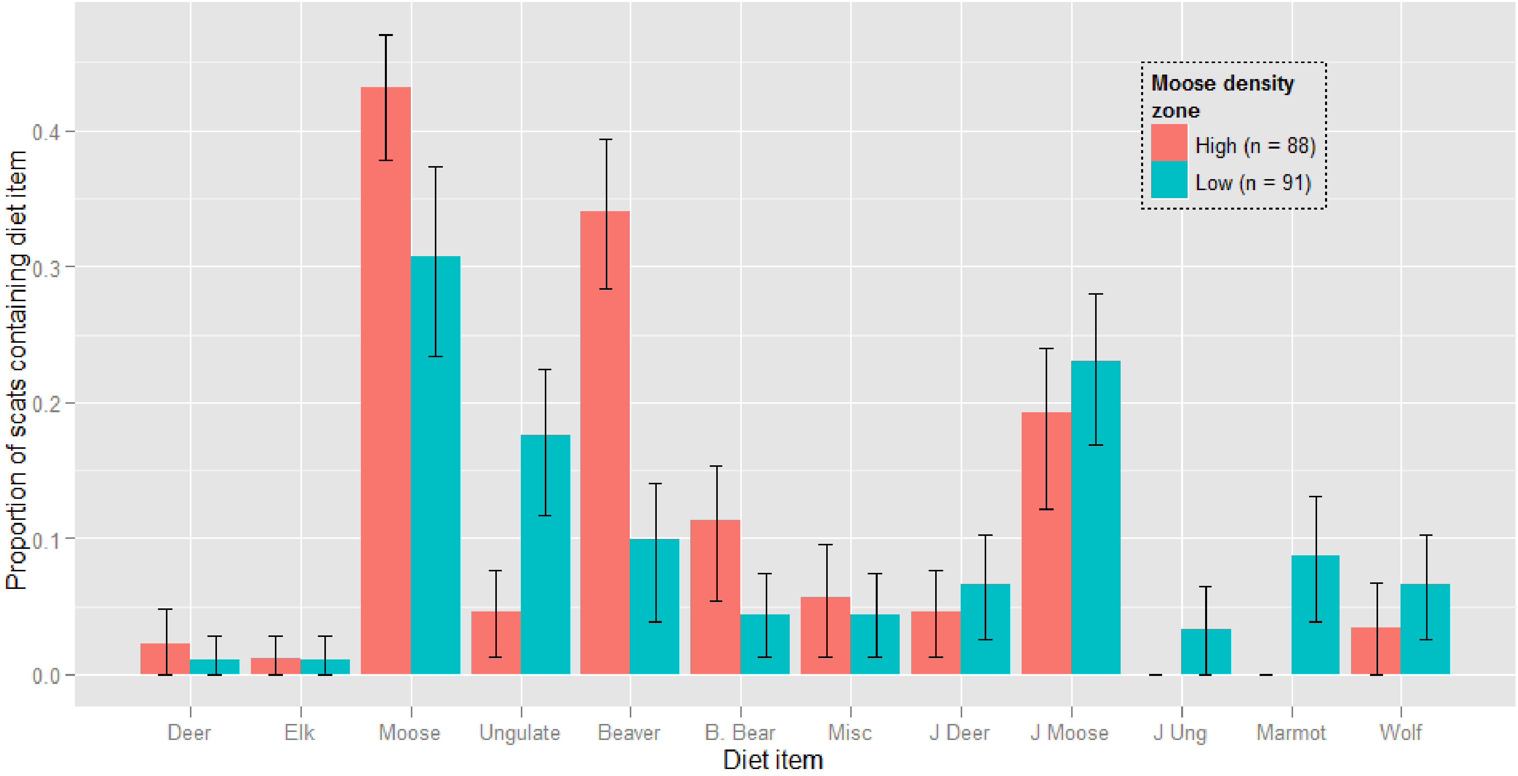


Figure 6.9. Frequency of occurrence of prey items in wolf scats from 2008 – 2010 in the treatment area, stratified by zones of two different moose densities. Items preceded by a “J” indicates a juvenile. Error bars are bootstrapped 95% CIs. Sample sizes are shown in brackets.

Changes in diet based on wolf scat analyses

For the temporal contrast (2004 – 2005 vs. 2008 – 2010), 267 scats were collected in the treatment area, with 77 of these collected during the high moose density period (2004 – 2005), and 190 during the low period (2008 – 2010). The seasonal breakdown was 201 scats from summer and 66 from winter. These scats were collected from five packs, including the Gothics, Adamants, Bigmouth, Downie, and West side. I used a subset of these scats for the spatial contrast, because I restricted the comparison to the summers of 2008 – 2010, and added 14 scats collected just outside the treatment area but suitable to include for the spatial contrast because of similarly low moose densities in that area. This comparison included 179 scats, 88 from the high moose density zone, and 91 from the low zone.

We recorded 18 different prey species (Fig. 6.8), but lumped those with fewer than five occurrences, and small rodents (n=9), into the “miscellaneous” category. Miscellaneous prey included mountain goat (n=1), pika (1), porcupine (1), squirrel (2), and snowshoe hare (3). After careful examination, three samples were classified as caribou but were later confirmed to be deer based on the mtDNA test. The adult ungulate category consisted of samples that failed the genetic test due to insufficient mtDNA, and were too difficult to discern with microscopic approaches. We surmise that they were deer or caribou but were too degraded to classify.

Temporal comparison

Wolf summer diets differed significantly between the high and low moose density time periods, (Fig. 6.8a; G = 29.1, 11 df, p = 0.002), but winter diets did not differ between the two time periods (G = 11.1, 8 df, p = 0.20). However, adult moose were eaten less frequently during the low density period in winter (bootstrapped CIs did not overlap; Fig. 6.8b), even though the G-test revealed no difference of the overall distribution between the two time periods.

In summer, at least five diet items differed between the two time periods (Fig. 6.8a). The most notable was four-fold increase in the consumption of calf moose and beaver during the low-density period. Juvenile deer were absent from the diets during the high moose density period, but consumed at a significantly higher frequency when moose were reduced. In all instances, adult moose were the most common prey item, regardless of season or time period (Fig. 6.8).

Spatial comparison

The spatial comparison of the 2008 – 2010 summer diets also revealed differences in consumption by packs that were located in areas of high vs. low moose density (Fig. 6.9; $G = 41.1$, 11 df, $p < 0.001$). In the low moose density zone, fewer adult moose and beaver were consumed, but more marmots, unclassified ungulates (likely not moose), and unclassified juvenile ungulates were consumed.

DISCUSSION

Wolves changed their foraging patterns and behaviour in response to the moose reduction treatment. Reducing the wolves' primary prey resulted in both a shift in diet and a change in habitat use resulting in increased use of caribou habitat. The latter pattern occurred in the treatment but not the reference area, strengthening the inference that the change in behaviour was caused by reducing moose abundance. My prediction that wolf movement rates would increase as a result of lower inter-annual prey density was only partially supported, with the pattern occurring in early winter in both treatment and reference areas. In late winter in the treatment area the result was contrary to prediction, although the magnitude of change was much less than the early winter result (Fig. 6.6). Early winter corresponds roughly with the period when wolves no longer use rendez-vous sites and begin to hunt collectively as a pack (Mech 1998), so this may explain why movements increased with less prey density during that season. In summer wolves are constrained by denning and localize at rendez-vous sites, perhaps reducing the validity of this metric as a response to changing moose density. The intra-annual seasonal influence on movements suggested that summer produced the highest proportion of long movements. This effect can be attributed to either a markedly lower prey density during summer, or a lack of snow that increases mobility, and therefore provides only equivocal support for my prediction. However, these seasonal differences indicate that the metric (proportion of long movements) was at least sensitive to changing biotic (prey abundance) and/or abiotic conditions (snow) that are known to affect wolf space use (Messier 1985a).

A number of studies have used spatial (Messier and Crête 1985) or temporal (Latham et al. 2011) comparisons to demonstrate how wolf diets can shift in relation to changing prey availability. In my case, the experimental moose reduction produced a temporal shift in diet that was most pronounced in summer when consumption rates are naturally lower, consistent with my final prediction. In situations where large mammalian prey are scarce, wolves tend to consume smaller and more diverse prey (Messier and Crête 1985). The switch from adult to calf moose at lower moose density matches this pattern and could be in response to the density dependent increase in calf recruitment (Chapter 3). My spatial comparison also suggests that wolves consumed fewer adult moose in the low moose density zone, and more alternative prey. This result parallels the lower wolf recruitment observed in the low moose density zone (Chapter 6a). Collectively, these findings provide a plausible mechanism for why a predator’s numerical response may lag behind declines in abundance of primary prey (Mech 1977, Gasaway et al. 1983). With few exceptions, wolves are obligate carnivores, usually consuming large mammalian prey (Fuller et al. 2003) and have relatively high daily metabolic requirements (0.1 – 0.2 /kg meat/kg wolf/day) that are 27% greater than theory predicts for placental mammals (Kreeger 2003). Therefore, a reduction in their primary prey should result in a rapid and proportional reduction in wolf numbers, either through dispersal or starvation (Chapter 6a). Yet, because wolves can also capture less profitable prey that may be less abundant or smaller in size, they can still exist in a given area but are less likely to have stable packs with successful recruitment (Messier 1985a, b).

Kill rates did not vary with prey density in the winter season and diets did not shift substantially in winter despite a sharp decline in moose abundance. Therefore, it appears that winter is the less relevant season to study food limitation in wolves because acquiring prey is comparatively easier during that time of year (Knamiller 2011, Metz et al. 2012). Although summer consumption rates were lower, once corrected for pack cohesion, the effect was not as pronounced. However, I expect that the pattern of lower kill rates in summer to be strongest in mountainous areas where prey densities change markedly across seasons, but may also extend to boreal systems where the rate of effective search (*a*) is more efficient in winter. Studies of other carnivores in boreal systems support the hypothesis that foraging efficiency is higher in winter (Nilsen et al. 2009), possibly because of differential mobility between predator and prey, cues that assist with prey detection in winter, or poor body condition of prey.

It is certain that small ungulate kills were missed in summer because of a less intensive GPS fix frequency compared to other studies (Metz et al. 2011, Knamiller 2011). However, the fact that the three packs with very low kill rates experienced starvation or left the treatment area suggests that I did not grossly underestimate prey acquisition. Furthermore, both the kill site investigations and the scat composition roughly correspond to the ratio of moose to deer in the study area (~ >8:1), suggesting that I did not underestimate the amount of small ungulate prey (i.e., deer) in the diet.

Beyond the theoretical aspect of this work, my results have practical implications for conservation. I monitored the outcome of a change in policy that eventually became a test to reduce the level of apparent competition between moose and caribou. In this chapter I found that any reduction in wolf abundance may not reflect a proportional reduction in predation risk to caribou. At least in early winter, wolves used more long movements when there were fewer moose, had an increased use of caribou habitat during most of the year, and consumed less moose based on diet analyses. This change in behaviour could partially offset an effect of having fewer wolves, and may explain why caribou population growth was not more pronounced following the treatment (Chapter 6a). Wittmer et al. (in press) suspected a similar process when 30,000 sheep were removed to reduce apparent competition with huemul in Patagonia, but predation rates by pumas on huemul markedly increased following the treatment. These behavioural changes should be considered by management agencies when attempting to reduce predators by reducing their primary prey, particularly when predator reduction is not done concurrently (Chapter 4, Chapter 6a).

Despite the greater potential risk posed by wolves altering their foraging patterns, there was no evidence that wolves increased their consumption of caribou as a result of the moose reduction treatment. Scat analyses and kill site investigations showed little or no use of caribou throughout the experiment. Stotyn (2008) found similar results in the treatment area using stable isotopes, but also found that one pack had likely recently consumed caribou (Stotyn 2008). Furthermore, the predicted use of caribou habitat by wolves was largely determined during 2006 – 2009 period, when GPS data were most abundant. The tail ends of the relationship (i.e. 2003 – 2005) were based on less data and thus the extrapolations are less precise, perhaps exaggerating the change in risk over time. Nonetheless, the comparison between the treatment and reference area suggest that the effect of increased use of caribou habitat was most pronounced in the treatment area.

However, I suggest that the amount of caribou in wolf diets is an imprecise metric to gauge risk based on the apparent competition phenomenon (Boutin et al. 2012). Rare prey can still be driven to extinction even though they comprise a very small component of the predator’s diet, due to the lack of a numerical relationship between the rare prey and the predator that is supported by primary prey. The amount of caribou in wolves’ diet in the treatment area may even have declined compared to the 1990s when caribou populations were 3 times more abundant. Allison (1998) found that wolf summer diets consisted of 18.9% caribou for two wolf packs in the central portion of the treatment area in the mid-1990s. As an alternative to measuring predator diets, monitoring mortalities from radio-collared caribou provides a more objective evaluation of risk factors (Marshal and Boutin 1999), which had been done intensively from 1992 – 2003 (Wittmer et al. 2005a) in this system. However, with declining caribou populations and correspondingly smaller sample sizes, this approach was not possible in recent years. A modest shift in cause-specific mortality could have a major impact on caribou populations, but would be difficult to estimate precisely with limited sample sizes that are inherent when dealing with an endangered species.

By combining the information obtained from numerical and functional aspects of predator-prey ecology, I gained a more complete understanding of how the system responded to the moose reduction treatment. Numerical responses alone can provide an incomplete picture of the complex and indirect trophic interactions in multi-prey systems (Krebs 2002). There appears to have been a decrease in wolf abundance caused by dispersal and perhaps starvation, similar to what Messier (1985a), and Messier and Crête (1985) observed in low moose density areas (< 0.2 / km^2). A shift in diet and habitat use by wolves accompanied these patterns, suggesting caution when using this approach as a primary tool for conserving endangered prey affected by apparent competition (Courchamp et al. 2003, Wittmer et al. in press), because of altered foraging behaviour of predators. The main uncertainty that remains is whether the reduced wolf numbers will outweigh the risk of having wolves cover more ground when hunting, and whether this behaviour will change with time. Over the long term, it will be important to continue monitoring the outcome of the moose reduction treatment, but not at the expense of addressing proximate and ultimate limiting factors linked to high predation rates and ecosystem change.

LITERATURE CITED

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

Allee, W. C. 1931. Animal Aggregations. University of Chicago Press, Chicago, Illinois.

Allison, B.A. 1998. The influence of wolves on the ecology of mountain caribou. M.Sc. Dissertation. University of British Columbia, Vancouver, British Columbia.

Anderson, C. R. and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management **67**:307-316.

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. D., B. N. McLellan, R. Serrouya, and J. P. Flaa 2007. A revised and expanded analysis of multi-scale habitat selection and predictive model development for mountain caribou in the north Columbia Mountains and environs. Unpublished report prepared for Parks Canada and the BC Ministry of Forests, Research Branch.

Armstrong, D. P. and H. U. Wittmer. 2011. Incorporating Allee effects into reintroduction strategies. Ecological Research **26**:687-695.

R. H. Baayen. 2007. Analyzing Linguistic Data: A practical introduction to statistics using R, Cambridge: Cambridge University Press.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs **98**:1-54.

Bartoń, K. 2011. Package MuMin. Multi-model inference. R package.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376-382.

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

Bird, C., R. Clarke, D. Lewis, and R. Serrouya. 2010. Cougar ecology, predation, and caribou in the Columbia Mountains of British Columbia. Fish and Wildlife Compensation Program – Columbia Basin, Nelson, British Columbia.

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management **74**:917-928.

Boutin, S. 1992. Predation and moose population dynamics - a critique. Journal of Wildlife Management **56**:116-127.

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.

Brown, T. L., D. J. Decker, S. J. Riley, J. W. Enck, T. B. Lauber, P. D. Curtis, and G. F. Mattfeld. 2000. The future of hunting as a mechanism to control white-tailed deer populations. Wildlife Society Bulletin **28**:797-807.

Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. Science **269**:324-327.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications **9**:751-771.

Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. Science **302**:1532.

Creel, S. and J. A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour **69**:1181-1189.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, *Odocoileus virginianus*, in the boreal forest of northern Alberta, Canada. PhD Thesis, University of Alberta, Edmonton.

D'Eon, R.G., R. Serrouya, G. Pavan. 2003. Moose damage on cedar seedlings in the Lake Revelstoke Valley: Year 2 summary. Report for the BC Forest Investment Account.

Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: are major surprises inevitable? Ecology **89**:952-961.

Flaa, J.P., and B.N. McLellan. 2000. Population characteristics of the Lake Revelstoke caribou. Pages 639-642. *In* At Risk: Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk. February 15-19, 1999, Kamloops, British Columbia. Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161-191 *in* D. L. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

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

Gasaway, W. C. 1986. Estimating moose population parameters from aerial surveys. Institute of Arctic Biology, Fairbanks.

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

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

Gleditsch, J. M. and T. A. Carlo. 2011. Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. Diversity and Distributions **17**:244-253.

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. PhD Thesis, University of British Columbia, Vancouver.

Hayes, R. D., A. M. Baer, U. Wotschikowsky, and A. S. Harestad. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology **78**:49-59.

Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the

Yukon: Ungulate responses and management implications. Wildlife Monographs **152**:1-35.

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

Heard, D.C. 2012. Presentation to the North American Caribou Conference, Sept 2012, Ft. St. John, BC.

Hebblewhite, M. 2013. Consequences of ratio-dependent predation by wolves for elk population dynamics. Population Ecology. **In press**.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. Oikos **111**:101-111.

Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. Wildlife Society Bulletin **31**:933-946.

Hebblewhite, M., C. White, and M. Musiani. 2010. Revisiting extinction in national parks: mountain caribou in Banff. Conservation Biology **24**:341-344.

Heisey, D. M. and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management **49**:668-674.

Holling, C. S. 1959a. Some characteristics of simple types of predation and parasitism. Canadian Entomologist **91**:385-398.

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

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

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management **57**:382-388.

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

Jones P., S. Sfez, P. Knamiller, and E. Merrill. 2009. Mammalian hair key with special reference to adult and juvenile ungulates on the Eastern slopes of the Canadian Rocky Mountains. University of Alberta. Edmonton, Alberta.

Kay, C. E. 1997. Aboriginal overkill and the biogeography of moose in western North America. Pages 141-164 *in* 32nd North American Moose Conference and Workshop, Banff, Canada.

Kennedy A. J. and L.N. Carbyn. 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian national parks. Canadian Wildlife Service. Edmonton, Alberta.

Klafki, R., K.G. Poole, and R. Serrouya. 2009. Moose inventory of MU 3-40, Thompson Region, January-February 2009. BC Ministry of Forests and Range – Research Branch, Victoria BC.

Knamiller, P.T. 2011. Seasonal wolf predation in a multi-prey system in west-central Alberta. M.Sc. Thesis, University of Alberta.

Knopff, K. H. 2010. Cougar predation in a multi-prey system in west-central Alberta. PhD Thesis, University of Alberta.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. Journal of Wildlife Management **73**:586-597.

Krebs, C. J. 2002. Beyond population regulation and limitation. Wildlife Research **29**:1-10.

Kreeger, T.J. 2003. The internal wolf: physioloy, pathology, and pharmacology. Pages 192-217 *in* D. L. Mech and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago.

Kulldorff, M., R. Heffernan, J. Hartman, R. Assunção, and F. Mostashari. 2005. A space–time permutation scan statistic for disease outbreak detection. PLoS Medicine **2**:e59.

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.

Lebel, F., C. Dussault, A. Masse, and S. D. Coté. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. Journal of Wildlife Management **76**:1431-1440.

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

Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. Generalized functional responses for species distributions. Ecology **92**:583-589.

McDonald, J. E., D. E. Clark, and W. A. Woytek. 2007. Reduction and maintenance of a white-tailed deer herd in central Massachusetts. Journal of Wildlife Management **71**:1585-1593.

McLellan, B. N. 2010. An historic perspective of mountain caribou distribution and abundance. BC Ministry of Forests, Research Branch, Victoria, British Columbia.

McLellan, B. N. 2011. Implications of a high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Canadian Journal of Zoology **89**:546-558.

McLellan, B. N., R. Serrouya, J. Flaa. 2006. Population censuses of caribou in the north Columbia Mountains. Unpublished report for the BC Ministry of Forests, Research Branch.

McLellan, B. N., R. Serrouya, H. U. Wittmer, and S. Boutin. 2010. Predator-mediated Allee effects in multi-prey systems. Ecology **91**:286-292.

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

McPhee, H. M., N. F. Webb, and E. H. Merrill. 2012. Time-to-kill: measuring attack rates in a heterogenous landscape with multiple prey types. Oikos **121**:711-720.

Mech, L. D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. Journal of Mammalogy **58**:559-574.

Mech, L. D. 1998. The wolves of Denali. University of Minnesota Press. Minneapolis.

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

Messier, F. 1985b. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology **63**:239-245.

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

Messier, F. and M. Crête. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia **65**:503-512.

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**: 553–563.

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.

Mills, K. J., B. R. Patterson, and D. L. Murray. 2008. Direct estimation of early survival and movements in eastern wolf pups. Journal of Wildlife Management **72**:949-954.

Moore T.D., L.E. Spence, C.E. Dugnolle and W.G. Hepworth. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming game and fish department. Cheyenne, Wyoming.

Mosnier, A., D. Boisjoly, R. Courtois, and J. P. Ouellet. 2008. Extensive predator space use can limit the efficacy of a control program. Journal of Wildlife Management **72**:483-491.

Nilsen, E. B., J. D. C. Linnell, J. Odden, and R. Andersen. 2009. Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. Journal of Animal Ecology **78**:741-751.

Orians, G., P. A. Cochran, J. W. Duffield, T. K. Fuller, R. J. Gutierrez, W. M. Henemann, F. C. James, P. Kereiva, S. R. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, bears, and their prey in Alaska. National Academy Press, Washington.

Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy **79**:828-841.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs **88**:3-52.

Polfus, J. L. and P. R. Krausman. 2012. Impacts of residential development on ungulates in the Rocky Mountain west. Wildlife Society Bulletin **36**:647-657.

Post, E. and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology **67**:537-543.

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.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology **67**:613-619.

Santomauro, D., C. J. Johnson, and G. Fondahl. 2012. Historical-ecological evaluation of the long-term distribution of woodland caribou and moose in central British Columbia. Ecosphere **3:**37.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology **70**:1494-1503.

Seip, D. R. 2008. Mountain caribou interactions with wolves and moose in central British Columbia. Alces **44**:1-5.

Serrouya, R., B. N. McLellan, S. Boutin, D. R. Seip, and S. E. Nielsen. 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., D. Paetkau, B. N. McLellan, S. Boutin, M. Campbell, and D. A. Jenkins. 2012. Population size and major valleys explain microsatellite variation better than taxonomic units for caribou in western Canada. Molecular Ecology. **21**:2588–2601.

Serrouya, R. and H. U. Wittmer. 2010. Imminent extinctions of woodland caribou from national parks. Conservation Biology **24**:363-364.

Simard, M. A., C. Dussault, J. Huot, and S. D. Côté. 2013. Is hunting an effective tool to control overabundant deer? A test using an experimental approach. Journal of Wildlife Management.

Sinclair, A. R. E. 1995. Population limitation of resident herbivores. Pages 194-219 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: Dynamics, management, and conservation of an Ecosystem. The University of Chicago Press, London.

Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology **12**:564-575.

Smith, A. P. and D. G. Quin. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biological Conservation **77**:243-267.

Solomon, M. E. 1949. The natural control of animal populations. The Journal of Animal Ecology **18**:1-35.

Spalding, D. J. 1990. The early history of moose (*Alces alces*): distribution and relative abundance in British Columbia. Contributions of Natural Science No. 11. Royal B.C.Museum, Victoria, British Columbia.

Steenweg, R. 2011. Interactions of wolves, mountain caribou, and an increased moose-hunting quota - primary-prey management as an approach to caribou recovery. M.Sc. Thesis, University of Northern British Columbia, Prince George, British Columbia.

Stotyn, S. 2008. Ecological interactions of mountain caribou, wolves and moose in the north Columbia Mountains, British Columbia. University of Alberta, Edmonton.

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.

van Oort, H., R. Serrouya, and B. N. McLellan. 2009b. Wolf movement patterns and kill rates in the Columbia Mountains. Unpublished report for the BC Ministry of Forests, Research Branch.

van Oort, H., C. Gaynor, C. Bird, G. Mowat, L. DeGroot. 2009a. Winter carnivore surveys in the Kootenay's mountain caribou recovery areas. Unpublished report prepared for the BC Ministry of Environment.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology **80**:1236-1245.

Walters, C. J. and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology **71**:2060-2068.

Webb, N. F. 2009. Density, demography, and functional response of a harvested wolf population in west-central Alberta, Canada. PhD Thesis, University of Alberta, Edmonton, AB.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Canadian Journal of Zoology **89**:744-752.

Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management **72**:798-807.

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.

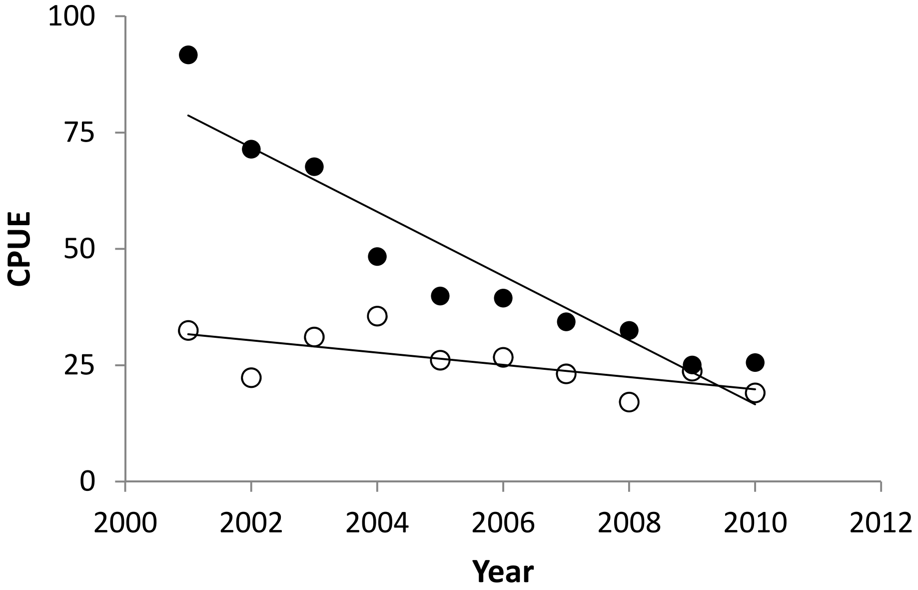
Wittmer, H. U., L. M. Elbroch, and A. J. Marshall. In press. Good intentions gone wrong: did conservation management threaten endangered huemul deer in the future Patagonia National Park. Oryx.

Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T. A. Kinley, G. S. Watts, and D. Hamilton. 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., R. Serrouya, L. M. Elbroch, and A. J. Marshall. 2013. Conservation strategies for species affected by apparent competition. Conservation Biology.

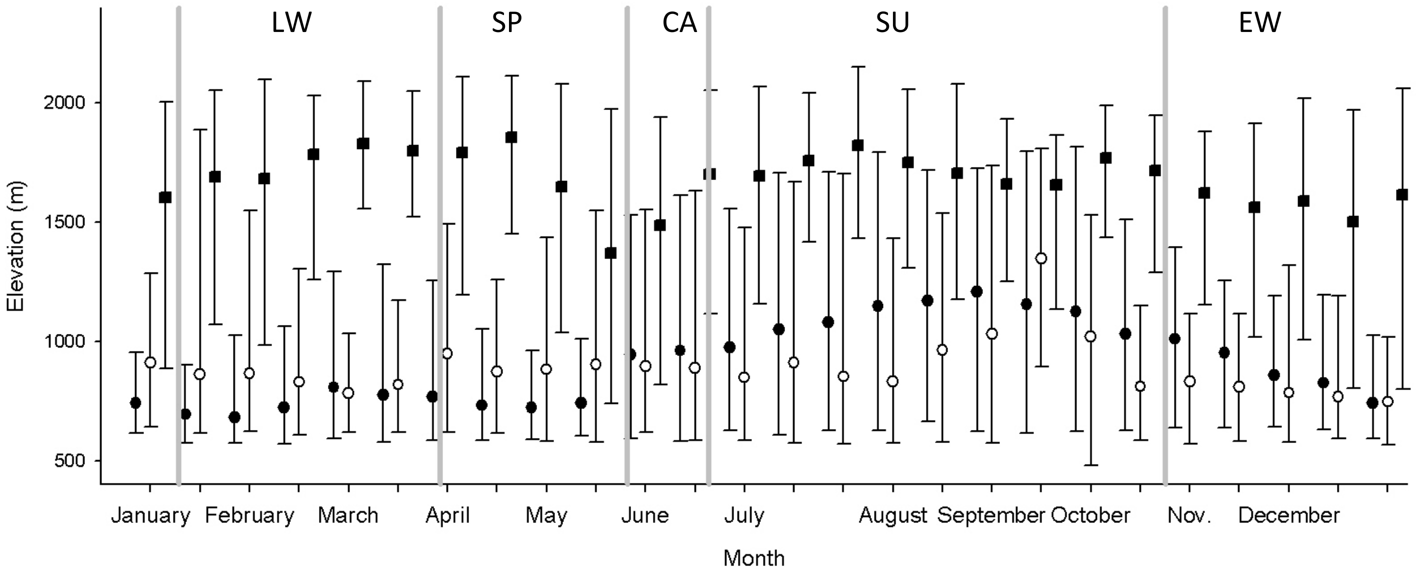
Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005b. The role of predation in the decline and extirpation of woodland caribou. Oecologia **144**:257-267.

APPENDIX 6.1. MOOSE POPULATION TREND COMPARISON BETWEEN THE TREATMENT AND REFERENCE AREAS.



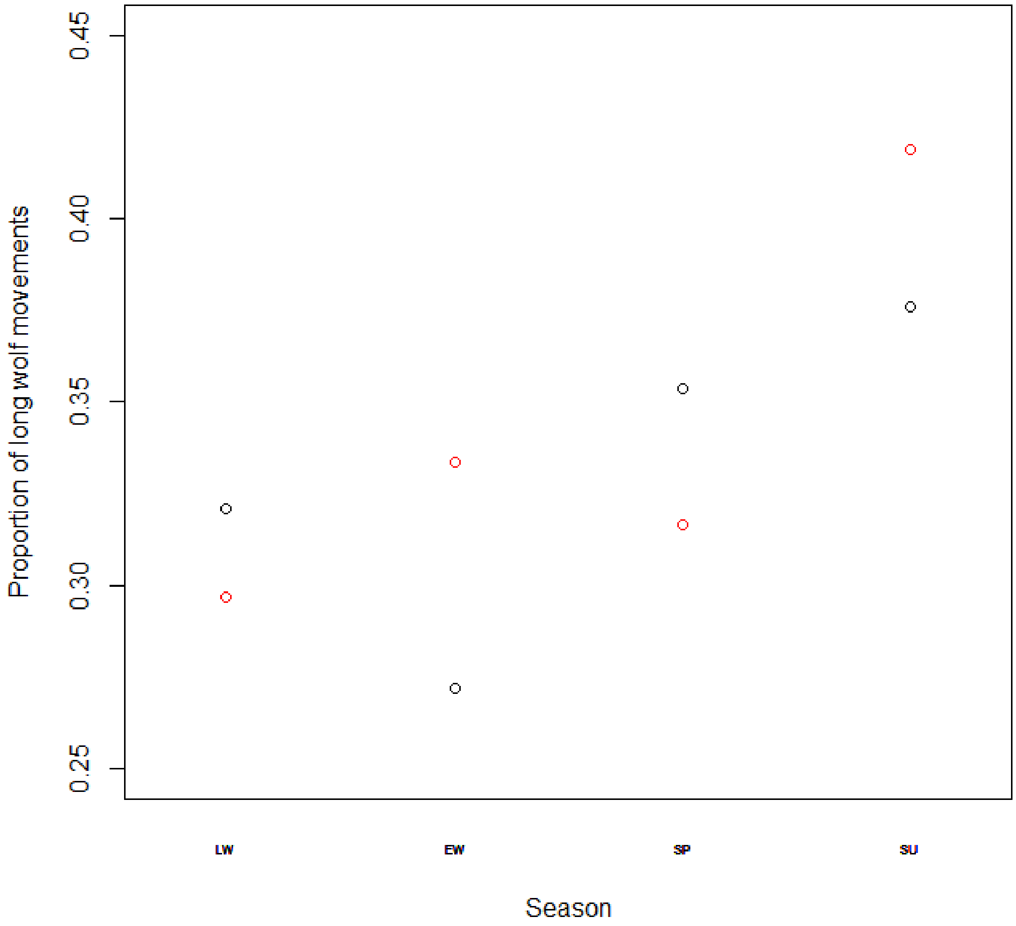
The slope of decline was more than five times greater in the treatment (solid circles) compared to the reference area (open circles; slopes were –6.88 [–9.02 to –4.68] compared to –1.32 [–2.46 to –0.26] for the respective treatment and reference areas; 1000 bootstrapped iterations). The slopes estimated here are slightly different from Chapter 5 because the reference area was larger to accommodate the wolf ranges and caribou subpopulations. Nonetheless, the ratio of the slopes between the two areas (i.e. comparing the magnitude of change between the treatment and reference) was similar when the smaller or larger reference area was compared to the treatment area.

APPENDIX 6.2. ELEVATIONAL USE PATTERNS OF MOOSE, WOLVES, AND CARIBOU



Mean biweekly use of elevation by moose (closed circles), wolves (open circles), and caribou (squares) in the treatment area. Error bars are 90th percentiles of use, calculated based on individual animals as the sample unit. Grey bars separate seasons. EW = early winter, LW = late winter, SP = spring, CA = calving, SU = summer. Updated from Stotyn 2008.

APPENDIX 6.3. THE PROPORTION OF LONG WOLF MOVEMENTS AS A FUNCTION OF SEASON



The effect of season on the proportion of long wolf movements was significant in both the treatment (black) and the reference areas (red), with most long movements occurring in summer. For the reference area, $\beta_{summer} = 0.53$ (SE = 0.051, $p < 0.001$), and in the treatment area, $\beta_{summer} = 0.24$, (SE = 0.031, $p < 0.001$). LW = late winter (reference category), EW = early winter, SP = spring, SU = summer. Analysis based on linear mixed effects models with wolf nested within pack as the random intercept.

CHAPTER 7

CONCLUDING REMARKS AND NEXT STEPS

Science progresses slowly, particularly when studying organisms with long generation times. This project represents the first cycle in the adaptive management process, and it took almost a decade before conclusions could be reached, especially for the caribou population responses following the moose reduction treatment. The cycle is even longer if we consider the time it took to determine and agree upon the agent of decline. In the meantime, caribou populations have continued to decline, both within and beyond the deep-snow mountain caribou ecotype (Boutin et al. 2012). Two mountain caribou subpopulations have recently gone extinct, and so has a neighbouring shallow-snow subpopulation in Banff National Park (Hebblewhite et al. 2010). These patterns raise the question of whether it is worth sacrificing scientific purity to conserve a species (Krebs 2009). By purity I mean removing one limiting factor at a time to evaluate the benefit of each option, compared to removing all suspected agents at once. Although there is a good understanding of limiting factors, we know less about how to recover these animals in a landscape that has been substantially altered by human development. If recovering the southernmost mountain caribou subpopulations is a societal goal, I reiterate the need to exceed all biological targets estimated by myself or others, particularly for critically endangered subpopulations that are affected by processes associated with small numbers.

I agree with Krebs (2009), who stated that it is worth compromising scientific purity to conserve a species. I suggest that all components of the ecosystem be addressed simultaneously, including moose and deer, and wolves and cougars. These dynamics can change unpredictably over space and time depending upon short-term weather trends and management values. In the Revelstoke area, the cougar-deer dynamic dominated in the mid 1990s, followed by an increase in moose and likely wolves, then the eventual moose reduction. If deer are allowed to recover, then the pattern may be repeated. Furthermore, climate change may be facilitating the northward expansion of deer and cougars (Dawe 2011) at the expense of moose (Murray et al. 2006). Maintaining primary prey at low numbers through year-round hunting seasons may be easier than reducing prey once they are established – and this logic may apply biologically and socially. Furthermore, the role of bear predation has been neglected because bears are considered to be within their natural range of variation in these ecosystems, so there was less of an ecological rationale to control bear numbers. Also, unlike neighbouring Alaska (Boertje et al. 2010), the social opposition to controlling bears would be insurmountable in British Columbia. To deal with this source of caribou mortality, at least for calves, maternity penning of pregnant female caribou could be considered. Transplanting caribou to smaller populations may be necessary in some cases, but only after the agent of decline – unsustainable predation, is dealt with. Addressing the agent of decline before transplanting is an obvious recommendation made by Caughley (1994) and recently reiterated by Pérez et al. (2012), but this caveat is sometimes overlooked (Pérez et al. 2012).

Perhaps when Krebs (2002) was criticising the population-based approach used to address problems such as declining caribou numbers, he was referring to what contemporary caribou researchers call proximate vs. ultimate limiting factors. The perception may have been that only the proximate factors were being addressed. However, we first had to identify the proximate factors (Bergerud and Elliot 1986, Seip 1992) before we could make correlative associations with climate (Dawe 2011) or landscape conditions that negatively affect caribou (Schaefer 2003, Vors et al. 2007, Wittmer et al. 2007, Sorensen et al. 2008). Both proximate and ultimate factors have been studied intensively, and lack of such knowledge cannot be used as an excuse to delay addressing both degrees of limiting factors, though social values will always be the final determinant. Addressing ultimate factors such as protecting old-growth forests will help to make the situation “less worse” for caribou, but populations will continue to decline unless proximate factors are also removed (Wittmer et al. 2010). Protecting old forests may also help garner public support to deal with proximate actions such as predator control (Serrouya, personal observation), which are often unpopular (Orians et al. 1997).

Although it is desirable to use ecological theory to make predictions and validate these predictions when possible, it is important to recognize the long time scales involved when studying organisms that reproduce slowly. Predictions from the differential equations suggested that an abrupt reduction in primary prey could be detrimental to caribou, and the deer – cougar case study appeared to validate this prediction. A more gradual decline in primary prey, as in the case of the moose – wolf reduction, was predicted to dampen the impact of wolves switching to caribou. In both these cases however, the predicted response to caribou transitioned over at least 10 years, and often our study periods are too short to monitor the full demographic responses. Indeed, the empirical data from Chapter 6 suggested support for the prediction that gradually reducing moose could benefit, or at least not severely reduce caribou abundance, but it took at least a decade to observe this pattern. Furthermore, no major shift in consumption from moose to caribou occurred, as estimated from the scat analyses and kill-site investigations. More importantly, the Columbia North subpopulation, where most of the wolf packs were located, did not experience a pronounced decline following the moose reduction and in fact caribou numbers increased. Again, this result suggests that wolves did not shift their foraging strategy to caribou as their primary prey were reduced. It is likely that because moose were gradually reduced, any potential switching effect was mitigated.

With the latest GPS, GIS, and genetic technology, it is comparatively easy to produce an abundance of data for analysis. Since some of the initial woodland caribou resource selection papers were published (Terry et al. 2000, Apps et al. 2001), many others have reached very similar conclusions, even when the latest statistical advances are incorporated. Caribou use or select old forests, and avoid most human developments. Similarly, genetic advances such as SNPs and microsatellites have facilitated many caribou genetic studies, including the one I conducted. It remains unclear, however, whether these tools contribute to previously existing knowledge about population limiting factors. If the goal is to address caribou conservation, I encourage researchers to engage with managers to implement active or passive management experiments, while at the same time incorporating the important technological improvements at our disposal (Hebblewhite and Haydon 2010).

A rewarding aspect of this thesis was the ability to test ecological theory but at the same time address an important conservation challenge. In Chapter 2 I outlined a potentially underappreciated aspect of landscape genetics where the role of population size can influence spatial structure, and in Chapter 3 I addressed an applied question to help set a management target. In the 4th chapter I made predictions based on predator prey theory, and in the 5th I was able to directly test theory with independent validation. The 6th chapter combined an applied experiment with theoretical predictions, particularly the behavioural chapter where I was able to test simple predictions relating to Holling's disc equation (Holling 1959). Results were not always as predicted, nor as were hoped, because some caribou subpopulations continued to decline. However, these disparities are precisely what make science interesting, and conservation challenging.

LITERATURE CITED

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.

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

Boertje, R. D., M. A. Keech, and T. F. Paragi. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management **74**:917-928.

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.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**:215-244.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, Odocoileus virginianus, in the boreal forest of northern Alberta, Canada. PhD Thesis, University of Alberta, Edmonton.

Hebblewhite, M. and D. T. Haydon. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2303-2312.

Hebblewhite, M., C. White, and M. Musiani. 2010. Revisiting extinction in national parks: mountain caribou in Banff. Conservation Biology **24**:341-344.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist **91**:385-398.

Krebs, C. J. 2002. Beyond population regulation and limitation. Wildlife Research **29**:1-10.

Krebs, C. J. 2009. Ecology: the experimental analysis of distribution and abundance. 6th edition. Benjamin Cummings, San Francisco, Calif. ; London.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs **166**:1-29.

Orians, G., P. A. Cochran, J. W. Duffield, T. K. Fuller, R. J. Gutierrez, W. M. Henemann, F. C. James, P. Kereiva, S. R. Kellert, D. Klein, B. N. McLellan, P. D. Olson, and G. Yaska. 1997. Wolves, bears, and their prey in Alaska. National Academy Press, Washington.

Pérez, I., J. D. Anadón, M. Díaz, G. G. Nicola, J. L. Tella, and A. Giménez. 2012. What is wrong with current translocations? A review and a decision-making proposal. Frontiers in Ecology and the Environment **10**:494-501.

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

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.

Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management **72**:900-905.

Terry, E. L., B. N. McLellan, and G. S. Watts. 2000. Winter habitat ecology of mountain caribou in relation to forest management. Journal of Applied Ecology **37**:589-602.

Vors, L. S., J. A. Schaefer, B. A. Pond, A. R. Rodgers, and B. R. Patterson. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. Journal of Wildlife Management **71**:1249-1256.

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, R. Serrouya, and C. D. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology **76**:568-579.