INTERACTIONS OF WOLVES, MOUNTAIN CARIBOU AND AN INCREASED MOOSE-HUNTING QUOTA – PRIMARY-PREY MANAGEMENT AS AN APPROACH TO CARIBOU RECOVERY

by

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B.Sc., McGill University, 2005

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ABSTRACT

Mountain caribou (*Rangifer tarandus caribou*) are endangered across their range. The leading cause of their decline is increased apparent competition with other ungulates, mainly moose (*Alces alces*), because of increases in densities of predators such as wolves (*Canis lupus*). I tested some assumptions of, and evidence for, moose management as an approach to caribou recovery through the indirect reduction in wolf numbers. Increased hunting quotas drastically reduced moose densities in the Parsnip River Study Area of northern British Columbia, and I monitored 31 collared wolves during this decline. Despite wolf selection for vegetation types associated with moose and avoidance of areas selected by caribou, wolves occasionally forayed during snow-free months to elevations where caribou were more common. Wolf diets were comprised of >80% moose, with little caribou and other prey items. Annual dispersal rates of wolves increased compared to rates before moose reduction, and compared to a control study area. In systems where moose comprise the majority of wolf diets and caribou are at low densities, reductions in moose numbers may help to facilitate caribou recovery.

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CHAPTER 1: INTRODUCTION

CONTEXT

Woodland caribou (*Rangifer tarandus caribou*) are 1 of 5 extant sub-species of caribou in North America and 1 of 9 across the globe (Banfield 1961). They are essentially endemic to Canada with the exception of ~750 caribou found in the Chisana herd that regularly crosses the Alaska-Yukon border (Adams and Roffler 2007) and ~2 caribou in the South Selkirks herd that cross from British Columbia (BC) into Idaho (Mark Hurley, Idaho Fish and Game, personal communication). In BC, woodland caribou have been grouped into 3 ecotypes (Figure 1.1) according to ecological and behavioural characteristics: northern, boreal, and mountain (Heard and Vagt 1998).

Mountain caribou almost exclusively inhabit the interior wet belt of BC (Heard and Vagt 1998, Wittmer et al. 2005*a*). Their range stretches from the northern tip of Idaho, through the Columbia Mountains to the Central Rockies, north-east of Prince George, BC (Hatter 2006). They are distinguished from northern and boreal ecotypes by their diet and habitat use. In winter, when the deep snowpack prevents terrestrial foraging, mountain caribou forage primarily on arboreal lichens in subalpine old-growth forests (Stevenson and Hatler 1985). In contrast, northern caribou inhabit the northern mountainous regions of BC where snow fall is lower and caribou can continue to rely on terrestrial lichens in low-elevation mature coniferous forests or on wind-swept alpine ridges (Bergerud 1978). Boreal caribou inhabit the flatter, north-eastern portion of the province and also forage on terrestrial lichens throughout the winter.

Caribou are in global decline (Vors and Boyce 2009) and mountain caribou have been decreasing in numbers and range for many decades (Spalding 2000). Currently, mountain

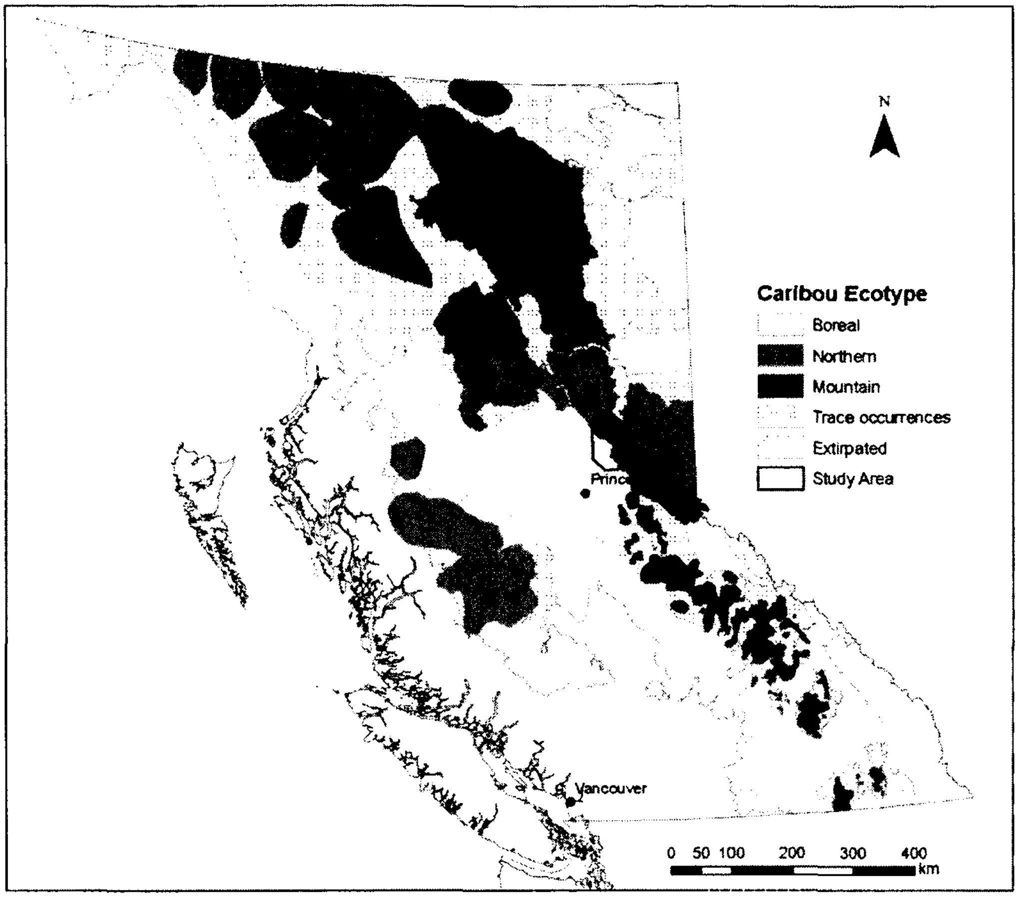

Figure 1.1 Location of Parsnip River Study Area relative to the distribution of 3 ecotypes of woodland caribou (*Rangifer tarandus caribou*) in British Columbia. Data courtesy of BC Ministry of Environment.

caribou are listed by the Canadian government as threatened (Committee on the Status of Endangered Wildlife In Canada 2002) and are red-listed by the BC government (BC Conservation Data Centre 2010). The total population numbers <2000 individuals, with 12 of the 16 sub-populations now at >50% risk of extirpation within 20 years (Wittmer et al. 2005*a*, Hatter 2006). Two herds have been extirpated very recently: the George Mountain herd (Seip 2008) and the Purcells-Central herd (DeGroot 2010). Furthermore, even in protected areas, such as national parks (NP), caribou are not immune to extirpation. For example, extirpation of mountain caribou in Mount Revelstoke-Glacier NP appears imminent (Serrouya and Wittmer 2010), just as caribou were extirpated from Banff NP in 2009 (Hebblewhite et al. 2009).

Habitat loss and fragmentation (Apps and McLellan 2006), direct human disturbance (Seip et al. 2007), and predation (Wittmer et al. 2005*b*) have all contributed to this decline. In recent years, researchers have identified predation as the number one proximate cause of mortality, ultimately due to shifts in the predator-prey community (Bergerud and Elliot 1986, Seip 1992, Hatter 1999, Wittmer et al. 2005*a,b*). Common predators of mountain caribou include grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), cougars (*Puma concolor*) and wolverines (*Gulo gulo*) (Wittmer et al. 2005*a*). In southern BC, cougars are the top predator of collared caribou. In northern BC, wolves are the top predator and, therefore, are one of the main focuses of caribou recovery initiatives (Wilson 2009).

Forest harvesting is common across much of the range of woodland caribou and has led to a considerable increase in both density and range of other ungulates, mainly moose (*Alces alces*) (Peterson 1955, Spalding 1990, Rempel et al. 1997), but also elk (*Cervis elaphus*) and deer (*Odocoileus spp.*) in southern BC (Kinley and Apps 2001). As moose densities have increased, caribou densities have declined (Bergerud and Elliot 1986, Rettie and Messier 1998, Wittmer et al. 2005*a*). They are not, however, in direct competition for food, space or any other resource, but rather, moose and caribou share at least one common predator. They are, therefore, considered to be in *apparent competition* — where an increase in one prey species leads to a decrease in the other, but only through an increase in predator numbers (Holt 1977). Densities of predators, such as wolves, have increased considerably due to the increase in moose (Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005*b*), and as a result, predation on caribou also has increased. Wolf numerical response, however, remains linked to the abundance of their primary prey, moose in my study area, and not to caribou abundance (Hebblewhite et al. 2007). Thus, even as caribou numbers decline, there is no feedback to wolf numbers. It is this asymmetric relationship that has led to the endangerment of many woodland caribou populations (DeCesare et al. 2010).

Wolves occupy low elevations similar to moose. To a large extent, caribou are spatially separated from both wolves and moose because they select for high-elevation areas (Bergerud and Page 1987, Seip 1992, James et al. 2004, Jones 2007, Stotyn 2008). This general elevational separation, although not complete, can be readily seen by plotting locations of collared caribou and wolves (Figure 1.2). Despite this separation, wolves remain a top predator of adult female caribou (Wittmer et al. 2005*a*) and caribou calves (Gustine et al. 2006*a*). Therefore, with the increases in moose densities following forest harvest, caribou spatial separation may be reduced (Stotyn 2008, Latham 2009).

In BC, a recent management initiative was implemented to mitigate the first 2 causes of mountain caribou decline: habitat loss and human disturbance. A moratorium on logging and road building has been placed on 2.2 million ha and a moratorium on snowmobile activity has been implemented on 1 million ha of mountain caribou habitat, essentially restricting all such activity above 1100 m (BC Ministry of Environment Species At Risk

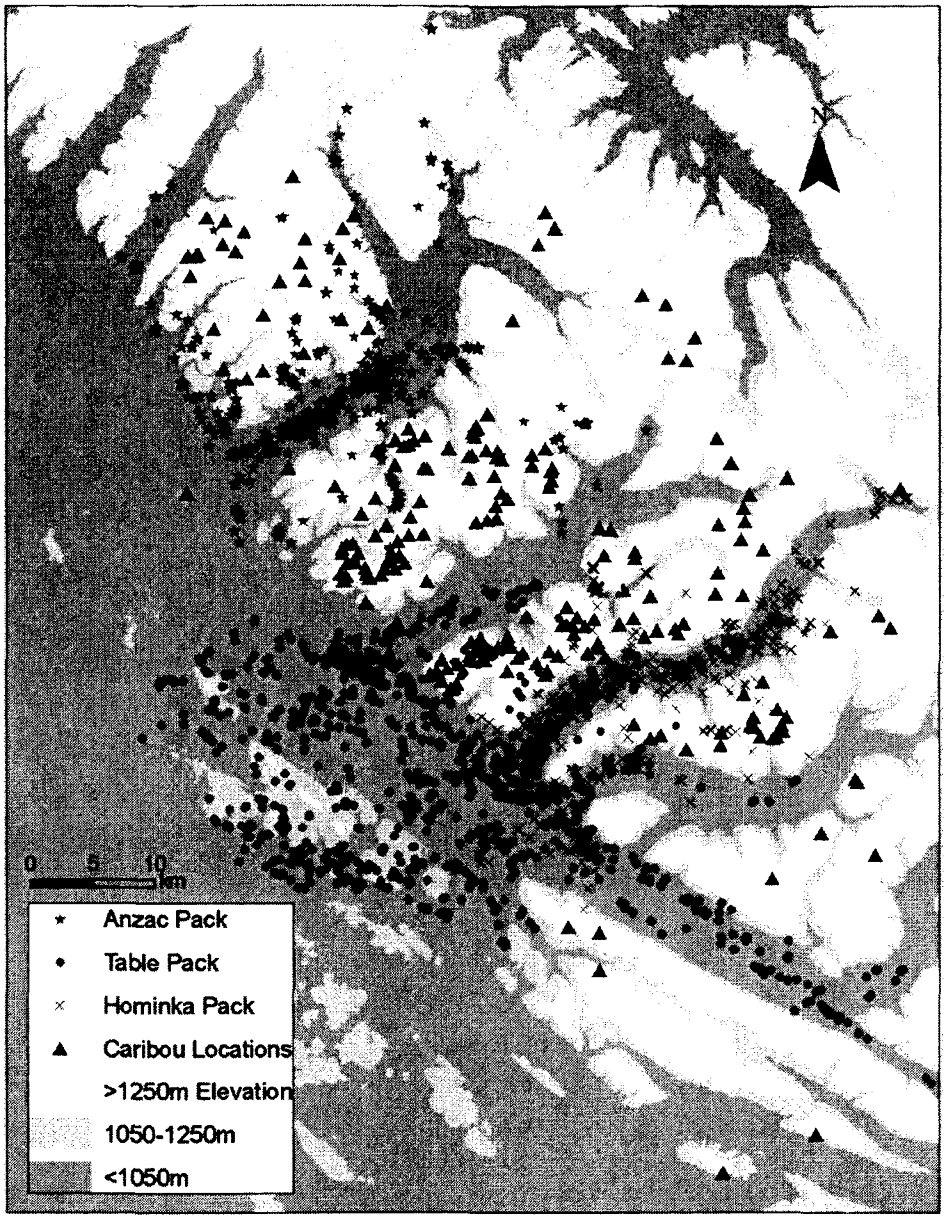

Figure 1.2 Relative spatial separation of wolves and caribou in the Parsnip River Study Area, BC. Locations from VHF-collared caribou ($n = 28$) and GPS-collared wolves ($n = 3$), 2007–2009.

Coordination 2009).

Options for dealing with the shift in predator-prey dynamics include managing predators at 3 different temporal scales (Seip 2008). Firstly, predators could be directly reduced in the short term (i.e., controlled) in order to try to directly decrease predation on caribou. Secondly, predators could be reduced indirectly through the management of their primary-prey species over the medium term, inducing a numerical response. Thirdly, management could be focused over the long term by managing the landscape to reduce the amount of early-seral forest available to primary prey of caribou predators and again leading indirectly to lower predator densities. In my study, I tested assumptions and predictions of the second, medium-term approach to caribou recovery.

The Parsnip River Study Area (PRSA) is located 100 km north-east of Prince George, BC (Figure 1.1). Until 2006, moose were abundant and near carrying capacity (Walker et al. 2006). In 2005, the population was estimated at 3000 ± 440 individuals ($\overline{X}$ ± SE; Walker et al. 2006) with a density of 1.18 moose / km^2 and had changed little since the 1998 estimate (2600 ± 600 individuals; 1.1 moose / km^2; Heard et al. 1999). With the support of local First Nations, guide outfitters and the hunting community, the BC Ministry of Environment increased moose-hunting allocations in the PRSA starting in fall 2006, as recommended by the caribou-recovery-implementation plan (Seip 2005, Wilson 2009). Following this change, moose density was approximately halved. By winter 2008–2009, the total moose abundance and density was estimated at 1818 ± 297 individuals and 0.73 moose / km^2 (Steenweg et al. 2009). In fall 2009 moose were estimated at 1181 ± 151 individuals and 0.47 moose / km^2 (Gillingham et al. 2010).

OBJECTIVES

Given the context of a declining moose density, my general objectives were:

1) To understand the potential for contact between wolves and caribou. To do so, I characterized resource selection of wolves and movements of wolves relative to caribou and moose, and assessed the degree of overlap between wolves and caribou.
2) To determine the prevalence of moose and caribou in wolf diet. To do so, I quantified wolf diet during summer when caribou are more likely to constitute a common prey species of wolves.
3) To examine evidence for the expected numerical response in the wolf population following this decline in moose density. To do so, I calculated annual mortality and dispersal rates of collared wolves during this experiment.

THESIS ORGANIZATION

My thesis is organized into 5 chapters. Chapter 1 is an introduction to the background and issues surrounding mountain caribou decline, including a discussion on current management initiatives and options. This introductory chapter is followed by 3 data chapters and a concluding chapter.

In Chapter 2, I examine interactions among wolves, caribou, and moose at 3 distinct scales. At the coarsest scale, I examined the use of elevation by moose, caribou and wolves across seasons. Secondly, I created a resource selection model to examine selection by wolves within their home ranges for areas associated with moose and caribou (i.e., third-order selection, Johnson 1980). Thirdly, I characterized movements of Global Positioning System (GPS) collared wolves in 2 ways: through the quantification of movements between areas selected by moose and areas selected by caribou to understand when and how often wolves are likely hunting for caribou, and through the examination of clusters of wolf GPS locations to estimate the relative success rate of wolves when likely hunting for caribou.

In order for a decline in moose density to have a strong effect on wolf density, moose should comprise a major portion of wolf diet. Furthermore, for a decrease in wolf density to translate into a decrease in wolf predation on caribou, caribou should constitute some portion of wolf diet. In Chapter 3, I examine summer diet of wolves and quantify the relative contributions of moose, caribou, beaver (*Castor canadensis*), and minor prey species. I analyzed wolf scats that were collected at wolf homesites (i.e., dens and rendezvous sites where pups remain when adults leave to hunt; Joslin 1967) and from roads within home ranges. I also used stable isotopes to compare hairs collected from captured wolves with hairs of common prey species known to be in the study area.

In Chapter 4, I examine evidence for a numerical response by wolves to the decline in moose density. I predicted that wolf mortality, dispersal, or both, would increase due to a decreased food supply. I calculated annual wolf-mortality rates and annual dispersal rates for 31 collared wolves, and compared them to a control study area 60 km northeast of the PRSA, where no changes to moose hunting quotas were made.

In Chapter 5, I summarize the results from the 3 data chapters in the context of current and future research and management. I relate the results from this research to concurrent work in the study area, discuss long-term expectations from this large-scale manipulation, and discuss some areas in mountain caribou conservation and management where knowledge gaps should be addressed with future research.

NOTE ABOUT CONTRIBUTIONS

A large-scale project like this one is fundamentally an exercise in collaboration and I respectively acknowledge the contributions of my co-authors with the use of the 1st person plural, ‘we’, throughout the remainder of this thesis. Although the project is ongoing, the end date for data collection for this thesis was 31 Mar 2010.

CHAPTER 2: ON APPARENT COMPETITION AND THE SPATIAL OVERLAP OF AN ENDANGERED SPECIES WITH PREDATORS AND A DECLINING PRIMARY-PREY POPULATION[1]

INTRODUCTION

Many caribou (*Rangifer tarandus*) herds around the globe have declined in the past 20 years due to climate change and landscape alteration by humans, which have led to trophic mismatches, increased insect harassment and increased predation (Vors and Boyce 2009). Migratory caribou, including *R. t. groenlandicus* and *R. t. granti* in the arctic, and the northern-most woodland caribou (*R. t. caribou*) in eastern Canada, aggregate annually at calving grounds north of tree line, away from common predators, primary prey of predators, and non-calving caribou (Bergerud 1988, Heard and Williams 1992, Heard et al. 1996). This long-distance-migration strategy reduces the limitation of ungulate populations by predation at coarse scales (Fryxell et al. 1988). Due largely to this seasonal restriction of overlap with predators, these caribou populations are thought to be primarily limited by processes independent of predation (Messier et al. 1988, Vors and Boyce 2009, but see Heard and Williams 1992). Predation remains, however, an important limiting factor for sedentary woodland caribou, which do not migrate long distances to refuges (Edmonds 1988, Rettie and Messier 1998, Wittmer et al. 2005*b*).

Sedentary woodland caribou inhabit most of the Canadian boreal forest and parts of southern British Columbia (BC) (Bergerud 2000). These caribou employ many different life-history strategies to increase distances from their predators and, therefore, they show spatial separation from predators at smaller scales than migratory caribou (Bergerud and Page 1987).

---

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In contrast to the *spacing-away* tactic of migratory caribou described above, sedentary woodland caribou *space out* during calving. Caribou disperse to calve alone or in small groups, often at the expense of forage quality, thereby increasing the predator search time, which should decrease encounter rates of caribou by wolves (*Canis lupus*). Such areas include island refuges or shorelines (Shoesmith and Story 1977, Darby and Pruitt 1984, Bergerud 1985, Seip and Cichowski 1996), open peat lands (Brown et al. 1986, Bergerud 2000) and higher-elevation terrain with less vegetation in mountainous areas (Bergerud et al. 1984). At even smaller spatial scales, caribou select calving sites of relatively low forage abundance within larger calving areas (Gustine et al. 2006*b*). Furthermore, caribou have shown differential resource selection across seasons, in order to decrease predation risk. In north-eastern Alberta, for example, caribou occupy low-lying, bog-fen complexes while wolves select for uplands (James et al. 2004). In mountainous areas of BC, caribou select for higher elevations, while wolves mainly occupy valley bottoms (Bergerud and Page 1987, Seip 1992). The relative low density of sedentary caribou has been hypothesized to enhance predator avoidance at the species level by minimizing encounters with predators (Bergerud 1992, but see McLellan et al. 2010). Studies also have shown that caribou modify their movements to minimize predation risk, resulting in increased predator search times and effectively reducing encounter rates with predators (Rettie and Messier 2001, Johnson et al. 2002).

Forest harvesting is common across much of the range of sedentary woodland caribou and has led to a considerable increase in both density and distribution of moose (*Alces alces*) (Peterson 1955, Spalding 1990, Rempel et al. 1997). As moose densities have increased, caribou populations have declined, but they are not in direct competition for food, space or any other resource (Bergerud and Elliot 1986, Rettie and Messier 1998, Wittmer et al.

2005*a*). Rather, because moose and caribou share at least one common predator, they are considered to be in *apparent competition* — where an increase in one prey species leads to a decrease in the other, but only through an increase in predator numbers (Holt 1977). Therefore, due to this increase in moose, as well as the release from government-sponsored predator control programs that were in place until the mid-20th century, wolf densities have increased, causing an increase in predation on caribou (Bergerud 1974, Bergerud and Elliot 1986, Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005*a*).

Spatial separation between apparently competing prey species is one of a few mechanisms that have been shown to prevent extinction of a secondary prey species at low densities (Sinclair et al. 1998, but see McLellan et al. 2010). Wolves occupy similar areas as their primary prey, moose, and caribou have many strategies to separate themselves from major predators; caribou, therefore, are to a large extent spatially separated from both wolves and moose (Bergerud and Page 1987, Seip 1992, James et al. 2004, Stotyn 2008). Wolves, however, still remain a top predator of adult female caribou (Wittmer et al. 2005*a*) and caribou calves (Gustine et al. 2006*a*). Therefore, with the increases in moose densities following forest harvest, caribou spatial separation by caribou from wolves may be declining (Stotyn 2008, James et al. 2004).

The issue of scale is important when investigating selection because animals interact with their environment differently at different scales (Johnson 1980). Further, different conclusions can be drawn at different scales of analysis (Levin 1992). At the largest scales, animals should avoid factors that have the greatest negative effect on their fitness, and caribou have been shown to avoid predation risk at these coarse scales, while selecting for forage availability at smaller scales (Rettie and Messier 2000). To fully understand caribou separation from wolves and moose, these interactions should be examined at multiple scales.

To mitigate the indirect effects of forest harvesting on caribou, many authors have recommended the reduction of moose (e.g., James et al. 2004, Messier et al. 2004, Wittmer et al. 2005*b*, Seip 2008). In order to understand predator response to declining prey densities in systems characterized by apparent competition, researchers need to understand the spatial separation of these species and, therefore, how predators move in relation to their prey (Holt and Lawton 1994).

Many tools are available to examine the interaction of wolves and caribou. Spatially-explicit analysis of caribou selection relative to predation risk, and resource selection functions (RSFs) have been used to examine caribou-wolf interactions at the landscape scale (Gustine et al. 2006*b*, Stotyn 2008, Courbin et al. 2009). With high-precision Global Positioning System (GPS) technology, analysis of animal movements creates an important link between landscape-level ecology and population dynamics (Morales et al. 2010) and thus movements of wolves may help the understanding of wolf-caribou separation. Cluster analysis of GPS-collared animals can to some extent elucidate kill rates (Merrill et al. 2010). We used a combination of these approaches to understand wolf-caribou interactions at the northern extent of mountain caribou range.

In fall 2006, with the support of local First Nations, guide outfitters, and the hunting community, moose-hunting quotas were increased in the Parsnip River Study Area (PRSA), BC, as recommended by the caribou-recovery-implementation plan (Seip 2005, Wilson 2009). The diet of wolves in the PRSA is simple, consisting mostly of moose with some caribou and beaver (*Castor canadensis*) (see Chapter 3). Moose were at very high densities in valley bottoms (1.18 moose / km^2 in 2005; Walker et al. 2006) with relatively low hunting pressure prior to changes in quota, whereas caribou were at low density and highly selective for upper elevations across seasons (Jones et al. 2007). These characteristics made the PRSA ideal to study apparent competition, spatial separation, and the movements of wolves during a decline in primary-prey density.

Our overall objective was to characterize the spatial relations of wolves with caribou and moose during a period of moose population decline. To do so, we examined the interactions among wolves, caribou, and moose at 3 distinct scales. At the coarsest scale, we examined the use of elevation by moose, caribou and wolves across seasons and predicted that caribou would be predominantly spatially separated from wolves and moose in all seasons but summer. At the scale of the wolf home range, we created an RSF to examine third-order selection by wolves for areas associated with moose and caribou (Johnson 1980). We hypothesized that wolves would select for features of the landscape associated with moose and avoid features selected by caribou within their home ranges. At the finest scale, we characterized movements of GPS-collared wolves in 2 ways: through the quantification of movements between areas selected by moose and areas selected by caribou to understand when and how often wolves were likely hunting for caribou, and through the examination of clusters of wolf GPS locations to estimate the relative success rate of wolves when likely hunting for caribou. We expected that, although infrequent across all seasons, wolves would be more likely to hunt for and kill caribou during snow-free months.

STUDY AREA

The PRSA is located 100 km north-east of Prince George, BC (see Chapter 1). The Parsnip River bisects the study area such that to the south-west lies a plateau of rolling hills of largely mixed forests in the sub-boreal spruce (SBS) biogeoclimatic (BEC) zone (Meidinger and Pojar 1991) with elevations ranging from 600–1650 m. Common tree species include hybrid white spruce (*Picea englemanni x glauca*), sub-alpine fir (*Abies lasiocarpa*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*), with some stands of lodgepole pine (*Pinus contorta*). Riparian areas were abundant with cottonwood (*Populus balsamifera*), willow (*Salix spp.*), alder (*Alnus spp.*) and red-osier dogwood (*Cornus stolonifera*). To the north-east of the Parsnip River lie the Central Rocky Mountains with valleys that run down to the Parsnip River characterized by the SBS BEC zone at lower elevation (~700–1100 m). Upper elevations (1100–2500 m) are characterized by the Engelmann spruce-subalpine fir (ESSF) BEC zone (Coupe et al. 1991), which consists mostly of Engelmann spruce and subalpine fir.

The study area has a long history of logging and much of the area is in early-seral growth stages throughout the plateau and up the valleys into the mountains, although little logging has occurred above 1100 m. On the north-east (Central Rockies) side of the Parsnip River, ~4% of the PRSA has been cut in the past 40 years; on the south-east (plateau) side, 21% has been cut in the past 40 years (calculated based on Vegetation Resource Index (VRI) data, BC Ministry of Sustainable Resource Management, Land and Resource Data Warehouse 2005).

The PRSA has a full complement of large carnivores, including grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), lynx (*Lynx canadensis*) and wolverines (*Gulo gulo*). Main prey for wolves are moose, caribou, and beaver (see Chapter 3). Mountain caribou occupy the mountainous terrain in the PRSA away from roads and cutblocks, selecting for mid-to-high elevations across all seasons and rarely descending below 1100 m (Jones 2007, Jones et al. 2007). They were at low density (0.048 caribou / km^2; Steenweg et al. 2009, updated as per D. C. Heard, unpublished data) with a relatively stable population of ~180 caribou inhabiting the study area (Wittmer et al. 2005*a*, Hatter 2006, Gillingham et al. 2010). Moose densities were high in this study area with 2600 ± 1200 moose in 2005 ($\overline{X} \pm 95$ CI) (Walker et al. 2006). In 2006, changes were made to increase the moose-hunting quotas and the moose population subsequently declined to 1200 ± 300 by 2009 (Gillingham et al. 2010). Reports from local trappers indicate that beaver were abundant (F. Booker, personal communication). They occupy ubiquitous riparian areas surrounding the major rivers in the study area (i.e., the Parsnip River and tributes). Other ungulates available to wolves, such as elk (*Cervus elaphus*), deer (*Odocoileus* spp.), mountain sheep (*Ovis* spp.) and mountain goats (*Oreamnos americanus*) are rare.

Snowpack in the PRSA can be deep because the area receives ~700 cm of snow annually (Delong et al. 1994). Snow depth data are available from the Hedrick Lake weather station, ~60 km SE of the center of the PRSA at 1118 m elevation. Average snow depth is calculated only for full years of this study (2007–2009) from an automated snow pillow recorder as daily water equivalent (mm) (data available at http://a100.gov.bc.ca/pub/aspr/).

METHODS

During 2007–2010, we captured wolves in winter by aerial darting from a Bell 206 helicopter (Altoft Helicopters, Prince George, BC) and in summer by ground trapping using a modified padded leg-hold trap (Braun -Wolf Traps; Wayne's Tool Innovations, Inc., Campbell River, BC). Wolves were immobilized with Telezol and fitted with a Very High Frequency (VHF) collar (Lotek Wireless Inc., Newmarket, ON, $n = 18$) or a GPS collar (Lotek model: 4400S, $n = 11$, or Telemetry Solutions, Concord, CA, model: GPS-Pod, $n = 2$) in accordance with the guidelines of the Canadian Council on Animal Care (2003). Lotek GPS collars obtained locations every 2–8 hours and were remotely downloaded from aircraft. GPS-Pod collars obtained locations every 3 hours and were downloaded after recovery of the wolf collar. We considered 3D locations with DOP > 25 m and 2D locations with DOP > 10 m to have poor accuracy and removed them from analysis (Rempel and Rogers 1997, Dussault et al. 2001).

Pack membership was assigned to wolves based on telemetry locations (see Appendices E and F). Some packs had multiple GPS-collared wolves used for resource selection analysis, but packs never had >1 wolf with a GPS collar in a given year. Because of mortality and dispersal, no wolves were GPS-collared for >1 year in the study area. Identification of individuals consisted of pack membership and year collared.

To examine wolf selection across seasons, we split wolf locations into 3 seasons based on wolf biology, movement, and snow conditions. Denning (1 April–14 June) corresponded to when wolves have high fidelity to homesites (dens and rendezvous sites) where pups remain when adults leave to hunt (Joslin 1967). Late summer (15 June–31 October) corresponded to when wolves have less fidelity to homesites and pups start following pack members on hunts. Winter (1 November–31 March) corresponded to snow-covered months during which there is also less high-elevation movement by wolves (Steenweg et al. 2009).

Use of elevation by wolves, caribou and moose

To compare the use of space on the landscape by wolves relative to moose and caribou at a coarse scale, we contrasted use of elevation by wolves to use of elevation by moose and caribou. A concurrent study in the PRSA looked at survival of VHF-collared moose and caribou (*n* = 23 and 28, respectively). Although monthly flights allowed for regular monitoring of mortality signals for wolves, caribou and moose, locations on the latter two species were acquired non-systematically during the study period (*n* = 101 and 251 locations, respectively). In addition, locations from moose collared during a previous study in the PRSA (*n* = 16, 1996–1998) were included in this analysis to increase sample size of moose locations ($n = 319$, D. C. Heard, unpublished data). Use of elevation by moose and caribou was stratified across wolf seasons and compared to the use of elevation by wolves.

Selection of landscape features by wolves

In advance of developing RSF models for wolves, we assembled Geographic Information Systems (GIS) layers of landscape characteristics (Table 2.1) that we hypothesized would influence wolf selection based on previous wolf-selection studies (Arjo and Pletscher 2004, Kuzyk et al. 2004, Oakleaf et al. 2006, Milakovic et al. 2011). We classified the landscape into vegetation classes using multispectral images from SPOT 4/5 satellites (available at www.geobase.ca). We used 3 wavelengths, each at 20-m resolution: mid-infrared, near-infrared (NIR), and red. The Normalized Difference Vegetation Index (NDVI = (NIR-Red) / (NIR + Red)) was also included in the classification to filter out the effects of shadows, which are common in late season imagery (September–October in the PRSA) (Bannari et al. 1995). We compiled satellite image tiles (40 x 40 km) into a mosaic (PCI Orthoengine, Richmond Hill, ON, Canada) and we used a supervised classification to separate the signatures of distinct classes (PCI Focus, ibid). We used areas of known vegetation types from field investigations as a basis for the raster-seeded supervised classification. We created a mask of open water (rivers and lakes) to remove this class from the classification because water was often confused with dark shadows in preliminary classifications (data from VRI). We then filtered the final classification with a 3x3-pixel sieve to remove inconsistent pixels from otherwise homogenous areas (Lay 2005). The vegetation classes created were: alpine, coniferous (conif), non-vegetated (non_veg), open-vegetated (open), shrub-deciduous (shr_decid), water, and wetland (see Appendix A for details on plant communities included in vegetation classes and abundance of classes on the landscape). We split conifer, open-vegetated and shrub-deciduous classes into lower (lo) and

Table 2.1 Explanation of, and rational for, variables included in resource selection models for wolves in the Parsnip River Study Area, BC. All variables were continuous except Inctbk and Vegcl, which were categorical.

Variable	Extended Name	Explanation	Biological Reason for Inclusion
Elev	Elevation		Topographical feature of mountainous landscape
Slope	Slope		Topographical feature of mountainous landscape
North	Northness	Cosine of aspect	Topographical feature of mountainous landscape
East	Eastness	Sine of aspect	Topographical feature of mountainous landscape
D2rd	Distance to Road	Distance to line feature	Travel corridor for wolves, human disturbance
D2strm	Distance to Stream	Distance to line feature	Surrogate for beaver surrogate
InctBk	In ≤40yr cutblock	2 levels: 0,1	Moose forage surrogate, human disturbance
Vegcl	Vegetation class	10 levels (see text)	Vegetation classes different prey may select for
Qual	Vegetation Quality	Late summer NDVI	Smaller scale refinement of what prey may select

upper (hi) elevation strata using 1050 m as the threshold, corresponding to the elevation where the Biogeoclimatic Zone most frequently changes from SBS to ESSF in the study area (Meidinger and Pojar 1991). Splitting these 3 vegetation classes allowed us to differentiate among: fir-dominated stands that are more common in higher elevations and spruce-dominated stands in lower regions; alpine meadows and forb-dominated recent cutblocks; and avalanche chutes and riparian shrubs. We ground truthed all vegetation classifications by verifying that locations visited for kill sites (*n*=54), rendezvous sites and other known areas in the study area were correctly classified.

The creation of other GIS layers was based on wolf and prey ecology. Wolf diet consisted mostly of moose in the PRSA (see Chapter 3). Moose densities are higher in younger forest stands due to increased forage availability (Schwartz and Franzmann 1989, Courtois et al. 1998, Potvin et al. 2005). Cutblocks ≤40 years old have higher stem densities than older forested areas and represent areas of higher forage availability for moose (Collins and Schwartz 1998). It was not possible, however, to separate recent cutblocks from other shrubby areas, such as avalanche chutes and riparian areas on satellite imagery, due to similar reflectance from their leaves. We, therefore, created a cutblock layer in order to examine wolf selection for areas assumed to be selected by moose. The in-cutblock category was created by extracting <40 year-old cutblocks from multiple GIS layers (sources: VRI, Canfor Inc., and manual extraction from satellite imagery).

Beavers were also consumed by wolves (see Chapter 3). Beavers select for rivers and streams for shelter and food (Nagorsen 2005) as do moose (Boer 1998). We created a distance-to-stream layer to examine selection for riparian areas by extracting streams from VRI data, including stream order classes of 7 (the Parsnip River) to 3 (tributes of tributes of major rivers) using IDRISI (Clark Labs, Clark University Worcester MA, USA).

As well as using NDVI to help classify the landscape into larger vegetation classes, we included the NDVI as a layer (quality) to provide some small-scale discrimination of vegetation productivity that wolf prey, such as moose, may be selecting for and that vegetation classification may have smoothed over. NDVI is associated with photosynthetic activity such that the reflectance of red wavelengths decreases as chlorophyll concentration increases due to absorption, and reflectance of NIR wavelengths increases due to leaf structure (Bella et al. 2004). NDVI is thus proportional to annual net primary productivity of the landscape (Paruelo et al. 1997). In general, low values of NDVI are associated with low-productivity areas that lack terrestrial vegetation (i.e., ice, rock, water); medium NDVI values are associated with medium-productivity areas including conifer trees and open senescing meadows; and high NDVI values are associated with high-productivity areas including shrubs and deciduous trees in avalanche chutes and cutblocks.

Wolves use linear features such as roads for travel (James et al. 2004). We created a distance-to-road layer using IDRISI of all past and present roads in the study area (data from: Resource Tenures and Engineering 2009, BC Ministry of Forests and Range Data Models, Victoria, BC, Canada).

Elevation, slope, and aspect are common variables in selection models for animals in mountainous areas (e.g., Copeland et al. 2007, Jones et al. 2007, Milakovic 2008) largely because they heavily influence productivity and community structure through their co-variation with temperature, precipitation and solar exposure. Elevation, slope and aspect were extracted from a Digital Elevation Model (BC Ministry of Sustainable Resource Management Base Mapping and Geomatic Services Branch, 2005). Both slope and elevation were modeled as continuous variables. Elevation was modeled as a quadratic, requiring the inclusion of elevation^2 in order to test for selection for mid elevations. Aspect was modeled as 2 continuous variables, northness and eastness (Roberts 1986) to minimize issues of perfect separation between used and available data sets. Northness and eastness were calculated by taking the cosine and sine of the aspect, respectively. For areas of zero slope, both northness and eastness were set to zero.

Nine candidate models for the RSF analysis were created a priori (Table 2.2). They consisted of 4 distinct models with nested variants. These 4 base models were: a topographical model that included only elevation, slope and aspect; a human-dominated model that only included features affected by humans; a vegetation model that only consisted of the vegetation classifications; and a vegetation-prey model that included all vegetation variables that prey may be selecting for. These last 3 models were also combined with the topographical model to create 3 more models, and separate models were created for winter which did not include the quality variable because of reduced vegetation productivity in winter.

To create a set of random available points, the 95th-percentile straight-line distance was first calculated for each wolf and for each season (Arthur et al. 1996). This approximates the distance a wolf can move between GPS fixes from a given location. Because time intervals between GPS locations varied for some wolves within seasons, different 95th-percentile distances were calculated for each fix frequency. Five random points were selected around each GPS location using the 95th-percentile distance as the radius. This set of pseudo-absence points served as a measure of availability at the movement scale in order to compare to use (GPS locations). Use and available points were then queried across all GIS layers, using Hawth Tools (Hawth's Analysis Tools for ArcGIS, available at http://www.spatialecology.com/htools) in ArcMap (Environmental Systems Research Institute, v9.3, Redlands, California, USA).

Table 2.2 Descriptions of 9 candidate models developed a priori for resource selection by wolves in the Parsnip River Study Area, BC, 2007–2010. Models included in the candidate model set vary by season. See Table 2.1 for rational for inclusion of variables in each model and descriptions for variable abbreviations.

										Season[a]		
Model name	**Variables Included in Model**									**D**	**LS**	**W**
Topographical						Elev	Slope	North	East	*	*	*
Human Dominated		Inctbk			D2rd					*	*	*
Human Dominated-Topo		Inctbk			D2rd	Elev	Slope	North	East	*	*	*
Vegetation	Vegcl									*	*	*
Vegetation-Prey	Vegcl	Inctbk	D2strm	Qual						*	*	
Vegetation-Topo	Vegcl					Elev	Slope	North	East	*	*	*
Vegetation-Prey-Topo	Vegcl	Inctbk	D2strm	Qual		Elev	Slope	North	East	*	*	
Vegetation-Prey-W[b]	Vegcl	Inctbk	D2strm									*
Vegetation-Prey-Topo-W[b]	Vegcl	Inctbk	D2strm			Elev	Slope	North	East			*

[a] D = Denning, LS = Late Summer, W = Winter.

[b] W refers to models included only in Winter

Logistic-regression models can create unreliable estimates if levels of categorical variables are nearly or completely avoided, or rarely available (i.e., complete or near-complete separation, Menard 2002). We did not use vegetation classes in models with ≤ 4 use or available locations and we dropped these classes from the analysis (Gillingham and Parker 2008) (see Figure 2.1). All variables were tested for multi-colinearity using a conservative tolerance of 0.20 (Hosmer and Lemeshow 2000). All logistic-regression analyses employed categorical deviation coding (Menard 2002) in STATA (Stata Corporation, v9.2, College Station, TX) using Desmat (Hendrickx 1999).

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c, Burnham and Anderson 2002) to determine the top models for each season. For each season, we calculated Akaike weights (w_i) and considered models with $w_i \geq 0.95$ to be top models (Burnham and Anderson 2002). When there was no single top model, we averaged all models with $\sum w_i \geq 0.95$. For all top models, and for models used to create averaged top models, we used k-fold cross validation to calculate Spearman's rank correlation coefficients (r_s) (Boyce et al. 2002). An $r_s >$ 0.648 corresponds to significance at $\alpha \leq 0.05$ (Zar 1999).

Movements of wolves relative to moose, caribou and snow depth

Caribou in the Parsnip herd selected for elevations above 1150 m in all seasons and were rarely located below 1100 m (Jones 2007). Summer wolf diet is composed of >90% moose and beaver, and little caribou or marmot (*Marmota caligata*), another high-elevation species (see Chapter 3). Therefore, we expected wolves to remain mostly in valley bottoms near where moose and beaver are mostly found. When wolves were above 1050 m elevation, we considered them to be potentially hunting for caribou. The average amount of time spent by wolves above 1050 m elevation per calendar month was calculated as the percentage of fixes above 1050 m, averaged

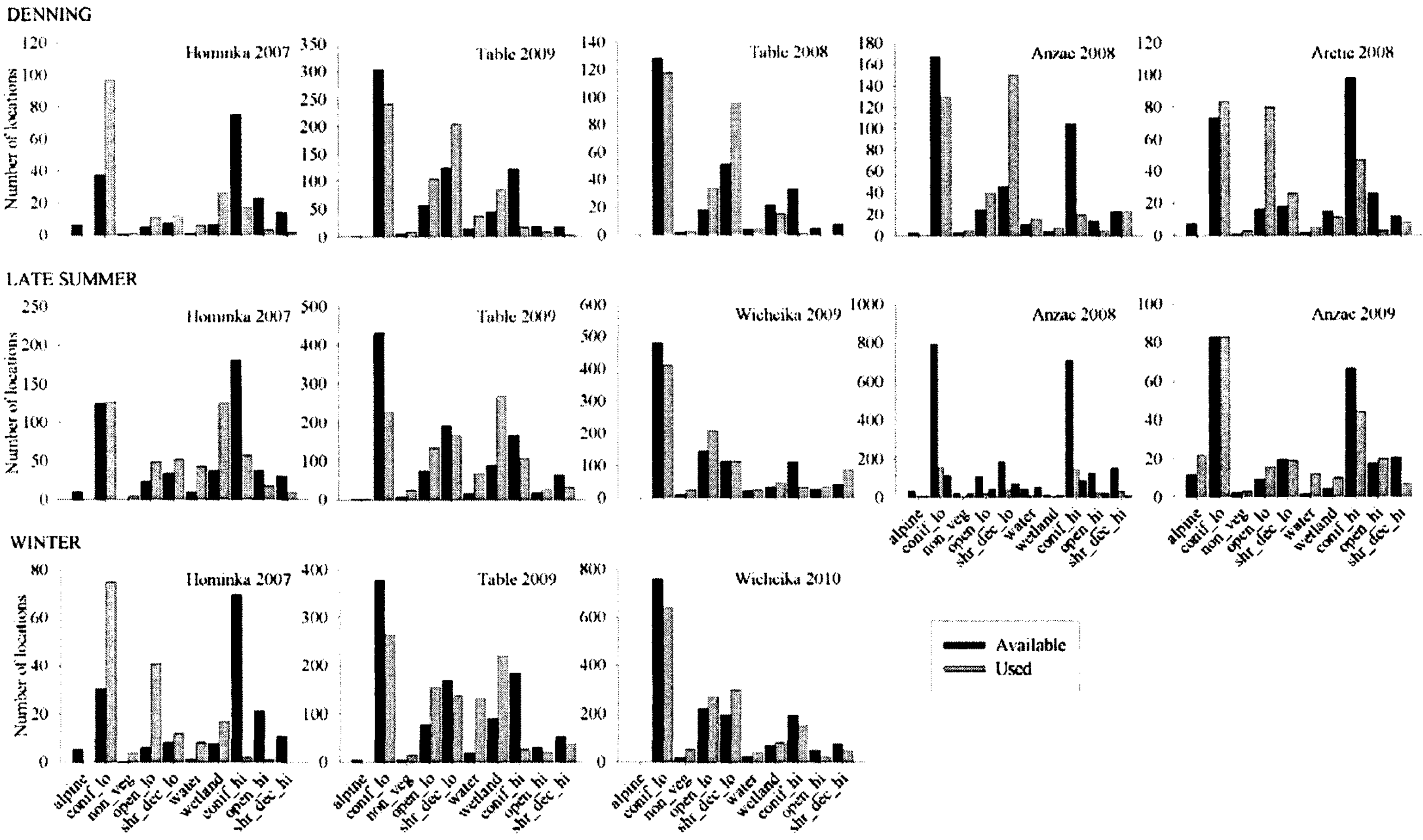

Figure 2.1 Number of locations used (GPS collar) and available (random, see text) among vegetation classes for wolf resource selection models in the Parsnip River Study Area, BC. Wolf pack and year are presented in the top right corner of each graph. Note that although 5 random locations were created per used location, totals were divided by 5 for comparison with use locations.

across all wolves collared during that month, and we compared that value to snow depth. Only wolves collared for the entire calendar month were used.

We defined a hunting foray as any excursion by a collared wolf above 1050 m (≥1 GPS location) and considered these hunting forays as occasions when wolves could be hunting caribou. Returns to high-elevation kill sites, or movements associated with low-elevation kill sites, were not considered distinct hunting forays and were removed from our analysis. While returning to kills, hunting was likely not the wolves' prime objective and, rather, signified returning from bed sites where wolves rested between feeding bouts. To describe the frequency of these forays, we examined fine spatial- and temporal-scale movements of wolves for which we had ~1 year of data (*n* = 3: Hominka 2007, Anzac 2008 and Table 2009 wolves). Forays were identified using ArcMap (Environmental Systems Research Institute, v9.3, Redlands, California, USA) and visually analyzed using Spatial Viewer (unpublished program by M. P. Gillingham). The probability of detecting a foray was likely affected by variable collar sampling rates (every 2–8 hours) and the number of wolves collared each month. To correct for monitoring intensity the frequency of forays was corrected using the total number of GPS locations collected for all 3 wolves during that month (i.e., total number of forays / total GPS locations, then times a constant for scaling). Monthly rate of forays was then compared to average monthly snow depth.

Cluster analysis is a means of calculating kill rates of prey (Anderson and Lindzey 2003, Sand et al. 2005, Franke et al. 2006, Zimmerman et al. 2007, Webb et al. 2008, Merrill et al. 2010). Although cluster analysis alone provides inaccurate estimates of kill rates, it can guide field investigations (Webb et al. 2008, Merrill et al. 2010). Automated classification algorithms for identifying kill sites and non-kill sites can have much higher commission than omission errors (Webb et al. 2008) leading to inflated estimates of kill rates. We used a similar technique, however, to estimate relative kill rates at high elevations across seasons. We used Point Finder (unpublished program by M.P. Gillingham) to identify clusters of GPS locations with given spatial and temporal thresholds of distance and time between GPS locations. We followed previous analyses on cluster investigations for large carnivores that indicated a 100-m distance between locations was sufficient for defining clusters associated with kill sites (Webb et al. 2008). Because we were also interested in clusters during summer when wolves spend much time at their homesites and returning to cluster locations, we did not incorporate a temporal threshold for time between GPS locations. Any 2 locations, therefore, within 100 m regardless of the time between the fixes, was considered a cluster.

Preliminary analyses indicated that wolves spent more time potentially hunting caribou during snow-free months than snow-covered months (Steenweg et al. 2009). For 4 GPS-collared wolves (each in a different pack) between June and August, we investigated all wolf clusters above 1050 m. Due to different lengths of time that wolves were collared, this represented 8 collar-months of clusters. We also visited a large sample of lower-elevation clusters to determine if caribou were being killed at low elevations. Investigation of these lower elevation clusters was stratified across cluster sizes, ranging from 2 to >25 GPS-collar locations.

To estimate success of forays (i.e., forays leading to the kill of a large-bodied prey, such as moose or caribou), we categorized clusters above 1050 m. Criteria for categorization were based on the minimum characteristics of the smallest large-bodied kill site found during field investigations and on natural breaks in the data (i.e., no clusters were found with diameters of 50–90 m and wolves never spent between 48 and 160 hours at a cluster). Of the 20 kill sites we visited, the smallest large-bodied prey found was a 13-month-old caribou in June; its cluster had the smallest temporal and spatial dimensions of all confirmed kill sites.

This cluster consisted of 4 GPS-locations (over 8 hours) with a maximum diameter of 90 m. Using this as minimum criteria for large-bodied prey kill sites, we assumed that if wolves spent <8 h at a cluster that was not investigated in the field, it was not likely a kill site of a large-bodied prey. After visiting bed sites associated with moose kill sites at lower elevation, we concluded that clusters ≤50 m in diameter over ≤18 hours were likely bed sites. Consequently, we classified the remaining clusters above 1050 m from the 4 collared wolves that were not visited in the field (*n* = 15) as follows: moose kill (time spent at kill >160 h, diameter of cluster ≥90 m), likely a caribou kill site (27–48 hours, ≥ 90 m), possibly a caribou kill site (9–24 hours, ≥90 m), or bed site (9–18 hours, ≤ 50 m). This procedure likely over-estimates kill rates (see above), but it remains informative as a relative measure of foray success across seasons and serves as a maximum kill rate.

RESULTS

We retrieved 8,370 GPS locations from 9 GPS-collared wolves in 6 packs: Anzac, Arctic, Hominka, Table, Upper Table and Wichcika packs (see Appendix E). Each pack had only one GPS-collared wolf at a time. Fix-success rates were high, averaging 86% (range: 73–97%). Six wolves had sufficient data to create RSF models for at least one season. One hundred GPS locations were dropped due to poor accuracy. GPS-fix success may vary among vegetation cover types (Frair et al. 2004) and with changes in animal behaviour (Heard et al. 2008), which can affects selection coefficients. Unfortunately, there is little consensus on how to deal with these issues (Frair et al. 2010), particularly when many categorical aspects of the terrain and habitat are being sampled. High fix rates and the removal of the worst fixes using DOP criteria likely means that such bias was low in this study.

Use of elevation by wolves, caribou and moose

Across all seasons, wolves used low elevations more than their availability and high elevations less than their availability (Figure 2.2). Elevational use by caribou and moose supported our assumption of relative spatial separation between moose and caribou, with moose using mainly lower elevations and caribou predominantly using higher elevations (Figure 2.3). Elevations used by caribou did not appear to change across wolf seasons, but moose tended to use higher elevations during late summer while remaining mostly at low elevations during wolf denning and winter. Use of elevation by wolves largely mirrored use by moose across seasons (Figure 2.3).

Selection of landscape features by wolves

Wolves used the coniferous-low vegetation class more than other classes and rarely used alpine or non-vegetated classes (Figure 2.1). Both alpine and non-vegetated classes were uncommon on the landscape (~1% each, see Appendix A) and had to be dropped from most wolf-season combinations due to near or complete separation. Open-vegetated-high and shrub-deciduous-high classes were used <4 times and were dropped from models of the Table 2008 wolf in denning and the Hominka wolf in winter. Shrub-deciduous-high was also dropped from the models of the Hominka wolf during denning due to complete or near separation. Coniferous-high was used by all wolves in late summer but less during denning, and rarely during winter (it was dropped from the models of the Table 2008 wolf in denning and the Hominka wolf in winter). Shrub-deciduous-low and open-vegetated-low were commonly used across seasons by all wolves. Use of water and wetland varied substantially among wolves and seasons. Use of the in-cutblock class was high, averaging 17% of wolf GPS locations in cutblocks <40 years old across wolves and seasons (range: 3–33%).

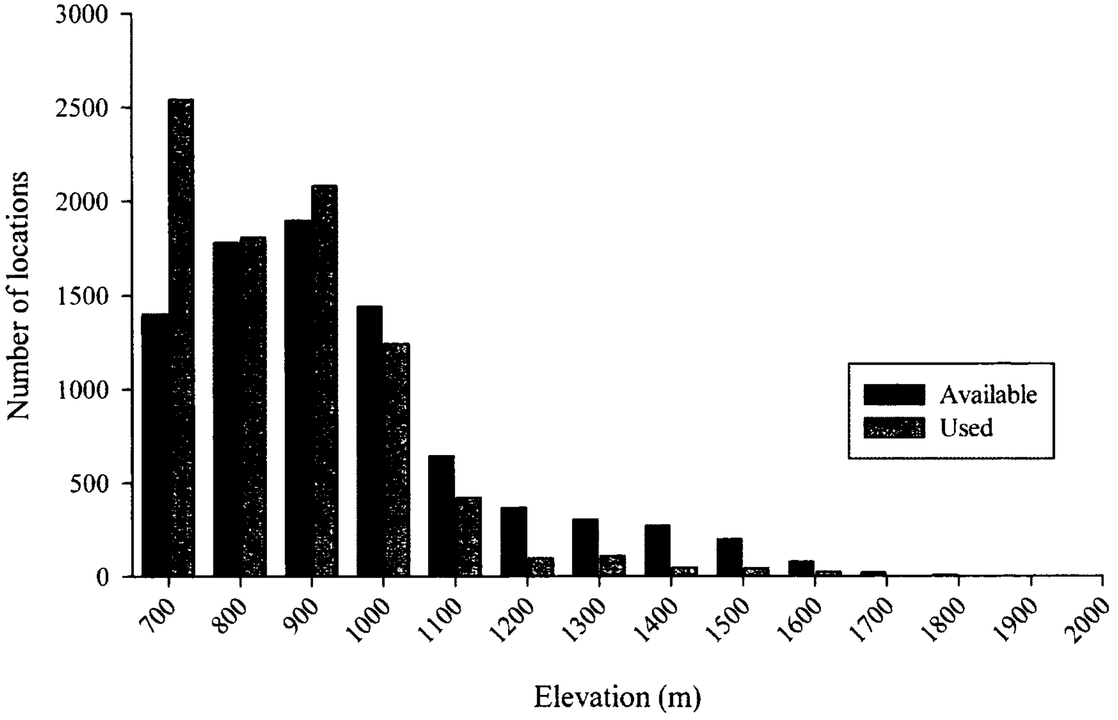

Figure 2.2 Use of elevation by wolves (*n* = 9) with respect to its availability in the Parsnip River Study Area, BC, 2007–2010. X-axis labels represent midpoint of interval (e.g., 1000 m represents 950–1049 m). Note that although 5 available points were created for every GPS location, the total available points were divided by 5 for display purposes.

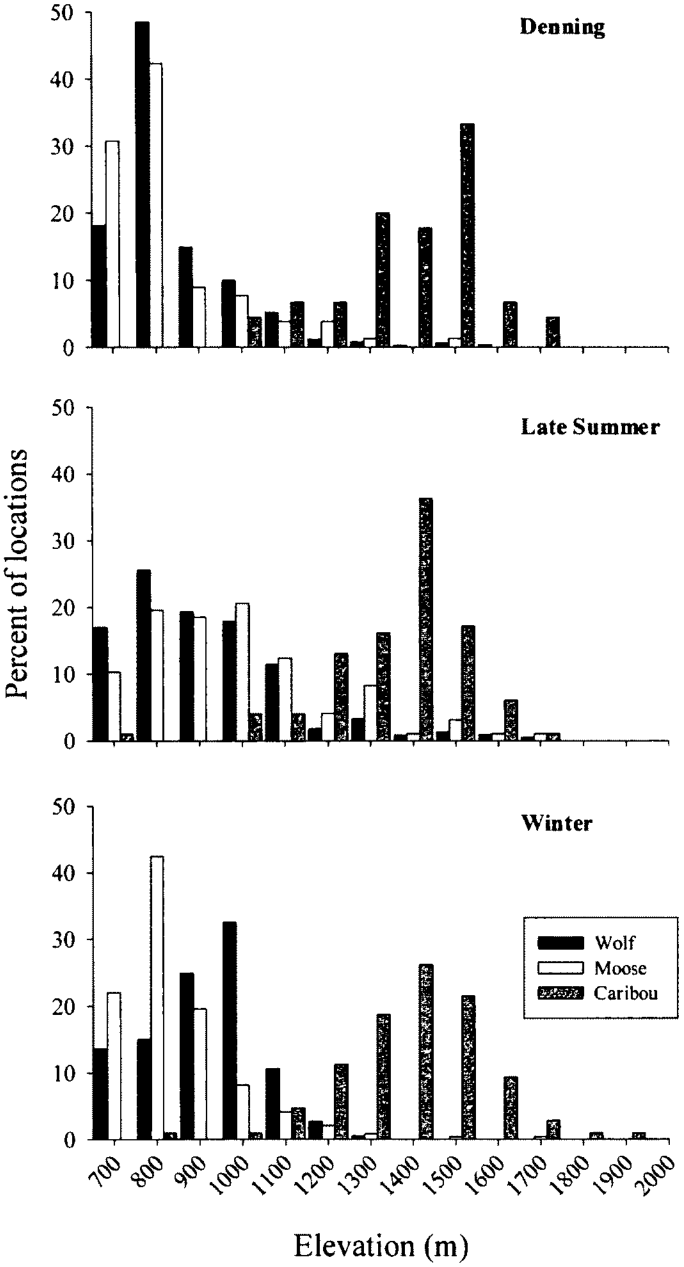

Figure 2.3 Use of elevation by GPS-collared wolves ($n = 9$) compared to VHF-collared caribou ($n = 28$) and VHF-collared moose ($n = 39$) by season in the Parsnip River Study Area, BC, 2007–2010. X-axis labels represent midpoint of interval (e.g., 1000 m represents 950–1049 m). Note that the only 2 caribou locations below 1000 m were mortality sites.

During denning and late summer, the Vegetation-Prey-Topo model was the top model, or one of the averaged top models, for all but one wolf (Table 2.3). The winter analogue (Vegetation-Prey-Topo-W) was the top model or one of the averaged top models for all wolves during the winter season. All top models validated by k-fold cross-validation except for the Hominka wolf in winter ($r_s = 0.590$ and 0.428, Table 2.3).

Vegetation classes removed from models (≤4 locations) included: alpine, non-vegetated, coniferous-high, open-vegetated-high and shrub-deciduous-high classes. When these classes had sufficient locations to be included in the model, wolves most often avoided them (Table 2.4). Non-vegetated areas, however, were selected for when included in the model and corresponded mostly to roads and exposed river shores, which are likely used as travel corridors (James et al. 2004). Most wolves completely avoided alpine across all seasons except the Anzac 2008 wolf, which selected for alpine during late summer. This selection, however, was driven by only 9 locations in the alpine and is, therefore, not likely of great importance to wolves.

Open-vegetated areas at low elevations (open-vegetated-low) and open-water classes (water) were selected for, as was proximity to streams, in 6 of 13 wolf-season models (Table 2.4). Wolves consistently avoided coniferous-high, although in late summer this class was used to a large extent by 3 of 5 wolves. Wolves also tended to avoid coniferous-low vegetation class and the in-cutblock (inctbk) category across seasons, but because of the ubiquity of these vegetation classes across the study area, they are probably still important to wolves given they were used extensively. Vegetation quality was selected for during denning by 3 of 4 wolves, and wolves selected for west-facing slopes in 7 of 13 wolf-season models. Low slope angle was consistently selected for by wolves during late summer, as were mid elevations in winter and for 2 wolves in late summer (Table 2.4). Although no pattern is

Table 2.3 Top resource selection models by season for wolves in the Parsnip River Study Area, BC, 2007–2010. Presence of multiple models for one wolf indicate >1 competing top model, in which case all models with $\sum w_i \geq 0.95$ were averaged.

	Wolf								
Season	**Pack**	**Year**	**Model**	**K**[a]	n[b]	**LL**[c]	**AIC$_c$**[d]	w_i[e]	r_s[f]
Denning	Hominka	2007	Human Dominated-Topo	8	943	-298.14	612.41	1.000	0.769^*
	Arctic	2008	Vegetation-Prey-Topo	16	1558	-545.40	1123.11	0.857	0.897^*
	“	“	Habitat-Topo	13	1558	-550.24	1126.69	0.143	0.865^*
	Anzac	2008	Vegetation-Prey-Topo	17	2362	-879.48	1793.19	1.000	0.848^*
	Table	2008	Vegetation-Prey-Topo	13	1388	-621.17	1268.58	1.000	0.694^*
	Table	2009	Vegetation-Prey-Topo	17	4240	-1714.30	3462.73	1.000	0.942^*
Late	Hominka	2007	Vegetation-Prey-Topo	16	2854	-1079.70	2191.57	1.000	0.951^*
Summer	Anzac	2008	Vegetation-Prey-Topo	18	2616	-989.49	2015.21	1.000	0.699^*
	Wichcika	2009	Vegetation-Prey-Topo	17	5928	-2471.48	4977.06	0.997	0.942^*
	Anzac	2009	Vegetation-Prey-Topo	17	1401	-519.45	1073.28	0.981	0.842^*
	Table	2009	Vegetation-Prey-Topo	17	6305	-2519.98	5074.04	1.000	0.883^*
Winter	Hominka	2007	Vegetation-Prey-Topo-W	12	420	-249.31	523.27	0.794	0.590
	“	“	Vegetation-Prey-W	7	420	-255.89	525.98	0.205	0.428
	Wichcika	2010	Vegetation-Prey-Topo-W	16	9623	-4193.92	8419.90	1.000	0.683^*
	Table	2009	Vegetation-Prey-Topo-W	16	6041	-2336.06	4704.21	1.000	0.931^*

[a] Number of parameters in model.

[b] Number of points in model (animal GPS locations and randomly generated locations, see text).

[c] Log-Likelihood.

[d] Akaike's Information Criterian, corrected for small sample size (Burnham and Anderson 2002).

[e] Akaike Weight (Burnham and Anderson 2002).

[f] Spearman's rank correlation calculated using k-fold cross-validation (Boyce et al. 2002).

$^*p < 0.05$

Table 2.4 Beta-coefficients (SE in brackets) for variables in the top resource selection models for wolves by season in the Parsnip River Study Area, BC, 2007–2010. Top models were selected using AIC methods and all models with $\sum w_i \geq 0.95$ were averaged if no single top model. **Bold** indicates significance level $P < 0.05$.

	Wolf		**Vegetation Class**									
Season	**Pack**	**Year**	**Alpine**	**Conif_lo**	**Non_veg**	**Open_lo**	**Shr_dec_lo**	**Water**	**Wetland**	**Conif_hi**	**Open_hi**	**Shr_dec_hi**
Denning	Hominka[a]	2007										
	Arctic	2008		**-0.69(0.10)**		**0.88(0.11)**	**-0.43(0.13)**	**1.12(0.18)**	**-0.39(0.14)**	-0.04(0.13)	-0.22(0.18)	-0.23(0.16)
	Anzac	2008		**-0.78(0.18)**	0.44(0.54)	0.28(0.25)	0.28(0.22)	-0.33(0.34)	0.09(0.50)	**-0.92(0.31)**	0.45(0.64)	0.48(0.35)
	Table	2008		**-0.46(0.19)**		0.19(0.23)	-0.27(0.28)	**1.29(0.59)**	**-0.74(0.30)**			
	Table	2009		-0.33(0.18)	**0.8(0.39)**	**0.83(0.20)**	0.36(0.21)	**1.26(0.32)**	0.25(0.22)	**-1.48(0.29)**	-0.45(0.73)	**-1.25(0.54)**
Late	Hominka	2007		**-0.37(0.14)**		0.15(0.22)	-0.18(0.22)	**0.76(0.30)**	0.38(0.20)	**-0.58(0.22)**	0.32(0.35)	-0.49(0.36)
Summer	Anzac	2008	**2.24(0.51)**	**-1.44(0.17)**	0.45(0.39)	-0.33(0.24	**-0.64(0.25)**	0.14(0.32)	0.01(0.39)	**-0.47(0.21)**	0.59(0.31)	-0.55(0.36)
	Wichcika	2009		**-0.34(0.09)**	**0.61(0.24)**	0.07(0.12)	-0.08(0.16)	**-0.94(0.38)**	-0.27(0.17)	**-0.63(0.19)**	**0.48(0.20)**	**1.11(0.18)**
	Anzac	2009	0.43(0.49)	-0.4(0.23)		**1.16(0.39)**	-0.26(0.34)	0.99(0.65)	0.19(0.40)	**-0.69(0.25)**	-0.44(0.34)	**-0.98(0.46)**
	Table	2009		**-1.11(0.09)**	**1.14(0.26)**	**0.45(0.12)**	**-0.47(0.13)**	**1.24(0.23)**	**0.45(0.11)**	**-0.76(0.14)**	0.34(0.23)	**-1.28(0.21)**
Winter	Hominka[b]	2007		**-0.5(0.08)**		**1.15(0.09)**	-0.01(0.10)	0.07(0.12)	**-0.7(0.09)**			
	Table	2009		**-1.11(0.10)**	0.49(0.30)	0.12(0.12)	**-0.74(0.12)**	**0.98(0.16)**	0.09(0.12)	**-1.11(0.22)**	**1.18(0.25)**	0.1(0.19)
	Wichcika	2010		**-0.35(0.08)**	**1.37(0.18)**	**0.39(0.10)**	**0.23(0.08)**	**0.44(0.18)**	**0.33(0.13)**	**-0.65(0.11)**	**-0.96(0.22)**	**-0.81(0.15)**

Continued next page.

Table 2.4 continued

	Wolf		Variables[c]									
Season	**Pack**	**Year**	**Inctbk**	**D2rd**	**D2strm**	**Qual**	**Elev**	**Elev²**	**Slope**	**Northness**	**Eastness**	**Intercept**
Denning	Hominka	2007	**-0.48(0.21)**	**-0.46(0.17)**			**-14.83(4.46)**	**4.8(1.91)**	0.01(0.02)	-0.18(0.15)	**-0.85(0.17)**	**8.08(2.32)**
	Arctic	2008	**-0.31(0.08)**		-0.05(0.08)	0.01(0.02)	**32.27(1.34)**	**-18.35(0.85)**	**0.04(0.02)**	**-0.55(0.08)**	**-0.16(0.07)**	**-17.49(0.75)**
	Anzac	2008	**-0.49(0.13)**		**-1.08(0.25)**	**0.02(0.01)**	7.57(4.94)	-4.18(2.46)	**-0.06(0.01)**	-0.17(0.10)	-0.16(0.09)	**-6.57(2.61)**
	Table	2008	**0.19(0.09)**		0.14(0.17)	**0.04(0.01)**	-16.59(13.62)	6.87(7.71)	-0.02(0.01)	**0.33(0.11)**	**-0.58(0.12)**	2.00(6.06)
	Table	2009	**-0.31(0.06)**		-0.02(0.10)	**0.02(0.01)**	-4.36(3.08)	1.97(1.59)	**-0.05(0.01)**	0.12(0.07)	**-0.38(0.07)**	-2.2(1.58)
Late	Hominka	2007	0.07(0.11)		**-1.07(0.14)**	0.01(0.01)	**6.54(3.06)**	**-3.33(1.29)**	**-0.04(0.01)**	**-0.31(0.09)**	**-0.24(0.09)**	**-4.87(1.85)**
Summer	Anzac	2008	-0.13(0.11)		**-1.00(0.25)**	0.01(0.01)	4.90(3.56)	-2.49(1.47)	**-0.09(0.01)**	0.07(0.09)	-0.02(0.08)	-2.88(2.30)
	Wichcika	2009	0.09(0.05)		**-0.25(0.07)**	-0.01(0.01)	1.75(4.26)	-1.32(2.25)	**-0.1(0.01)**	-0.1(0.05)	**0.33(0.05)**	-0.23(2.08)
	Anzac	2009	**-0.77(0.21)**		-0.44(0.25)	-0.01(0.01)	-3.44(3.91)	2.01(1.62)	**-0.08(0.01)**	**0.29(0.14)**	**1.00(0.13)**	1.17(2.43)
	Table	2009	**-0.41(0.07)**		**0.28(0.08)**	**0.01(0.00)**	**9.75(2.42)**	**-4.48(1.23)**	**-0.08(0.01)**	**-0.13(0.05)**	-0.02(0.06/0	**-7.37(1.29)**
Winter	Hominka[b]	2007	**-0.54(0.07)**		**-0.99(0.10)**		**17.94(1.07)**	**-10.69(0.76)**	0.00(0.02)	**0.18(0.06)**	**-0.44(0.07)**	**-7.79(0.63)**
	Table	2009	**-0.28(0.06)**		**-0.65(0.09)**		**30.67(3.59)**	**-17.3(1.98)**	-0.01(0.01)	-0.04(0.06)	**-0.24(0.06)**	**-14.1(1.61)**
	Wichcika	2010	**-0.21(0.05)**		**0.18(0.05)**		**26.92(6.79)**	**-12.89(3.56)**	**0.02(0.01)**	-0.04(0.04)	0.03(0.04)	**-15.86(3.22)**

[a] Top model did not include vegetation class (see Table 1C). All other blanks indicate removal of vegetation class from the model due to complete separation or variable was not included in the top model.

[b] Top model did not validate using k-fold validation; beta-coefficients are shown only for comparative purposes.

[c] See Table 2.1 for explanation of variable names.

apparent in wolf selection for northness, wolves avoided eastness (and therefore selecting for west-facing slopes) during denning and winter.

Movements of wolves relative to moose, caribou and snow depth

We obtained approximately a full year of data for 3 wolves, which we used to examine wolf movements across the year. From these wolves, we documented 96 excursions by wolves above 1050 m. Using our definition of a hunting foray as when wolves could potentially be hunting caribou, we removed 21 of 96 excursions above 1050 m because wolves were either returning to fresh kills (*n* = 15) or the foray occurred during consumption of moose kills that were below 1050 m (*n* = 6). In those cases, wolves were not moving above 1050 m to hunt, but rather to feed or bed, respectively. Use of high elevations (>1050 m) was highest during snow-free months (July–October), decreased during early winter months, and then increased again during late winter months (Figure 2.4). Frequency of the 75 hunting forays on the other hand, was highest during late-winter and early-summer months (Figure 2.5).

We visited 20 of 51 identified clusters above 1050 m and 34 of 253 identified clusters below 1050 m (Table 2.5). Adult caribou kills were only found above 1050 m whereas moose kills were found in both elevational strata. Moose kills found above 1050 m, however, were below 1250 m, whereas both caribou kills found were above 1300 m.

Based on field investigation and the classification of the remaining clusters above 1050 m, 4 of 75 forays were moose kills at 1050–1250 m (3 were visited in the field); 8 forays led to likely caribou kills (2 were visited in the field); 3 led to possible caribou kill sites; 5 led solely to bed sites; and 55 were associated with non-kill-site clusters or no cluster at all. In total, these 3 collared wolves were involved in killing a maximum of 8–11 caribou (range based only on including likely caribou kills or both likely and possible caribou kills,

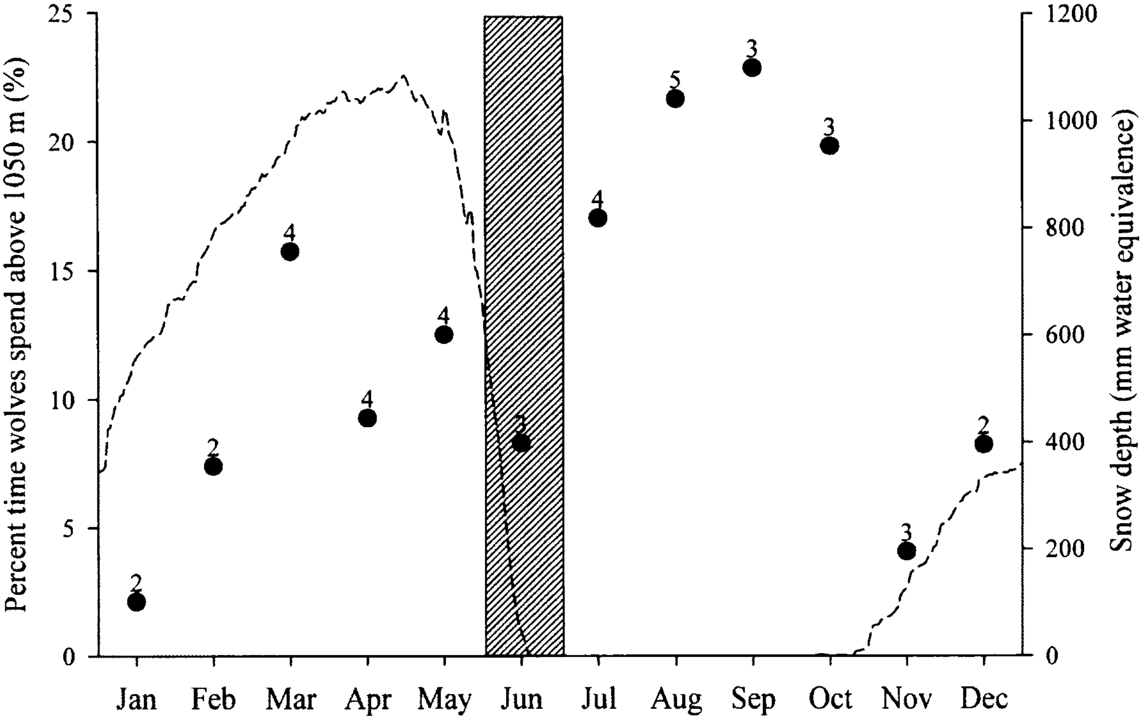

Figure 2.4 Average amount of time spent by wolves above 1050 m (●) relative to average daily snow depth (– – – –) in the Parsnip River Study Area, BC. Note: average snow depth was calculated only for full years of study (2007–2009). Labels indicate the number of wolves collared (could be >1 per pack given months were averaged across all years) in each month to calculate average percent time (i.e., percent of GPS locations). Shaded area approximates peak calving for caribou in northern BC (Bergerud et al. 1984, Bergerud and Page 1987, Gustine et al. 2006*a*).

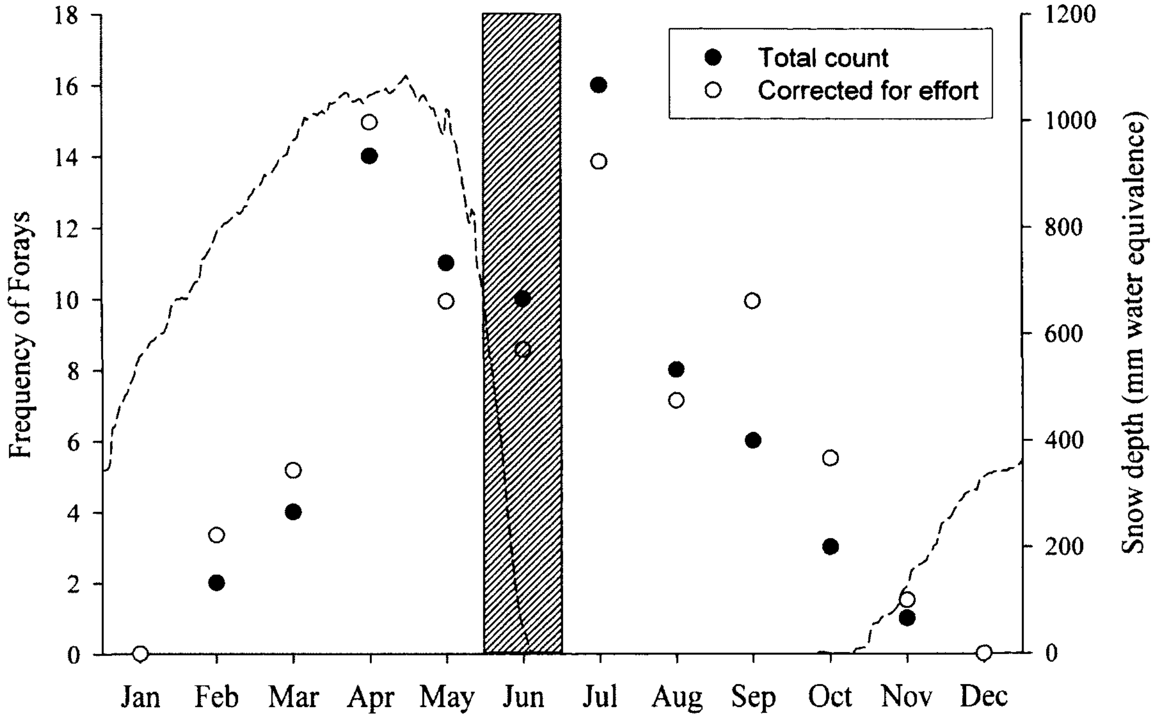

Figure 2.5 Frequency and timing of hunting forays by wolves ($n = 3$, packs: Hominka, Anzac and Table) above 1050 m relative to average (2007–2009) daily snow depth (– – – –) in the Parsnip River Study Area, BC. Filled circles indicate frequency of forays recorded from GPS data per month and open circles indicate number of forays after correcting for monitoring intensity using the total number of GPS locations collected for all 3 wolves during the month. Shaded area approximates peak calving for caribou in northern BC (Bergerud et al. 1984, Bergerud and Page 1987, Gustine et al. 2006*a*).

Table 2.5 Summary of field investigations of clusters from GPS-collared wolves (*n* = 4, packs: Anzac, Table, and Anzac across 2 years) during June–August 2008–2009 in the Parsnip River Study Area, BC (total wolf-collar months = 8). Totals include total number of clusters visited of the total number of clusters identified (in brackets).

	<1050 m	**>1050 m**
Caribou kill	0	2
Moose kill	5	3
No large kill	29	15
Total (identified)	34(253)	20(51)

see methods for details), or 2–5 caribou/pack, annually. Relative success rate remained similar across seasons (Table 2.6).

DISCUSSION

Previous studies suggest that resource selection by wolves is well described by vegetation communities, prey densities and road densities (Oakleaf et al. 2006, Milakovic2008, Mladenoff et al. 1995, Milakovic et al. 2011). Where sites for denning are limiting, such as in arctic eskers (McLoughlin et al. 2004), or where human settlement is dense (Jedrzejewski et al. 2005), selection for denning sites or avoidance of human settlements can become most important. Collared wolves in the PRSA selected for landscape characteristics consistent with areas where moose are typically found and avoided areas where caribou are most commonly found. Landscape characteristics associated with moose that wolves selected for were: open-vegetated areas, open water, proximity to streams, lower elevations, and valley bottoms (low slope angle). Previous work in the PRSA has shown that caribou select for fir and fir-leading stands at high elevation during all seasons and almost completely avoid all other vegetation types (Jones et al. 2007, Jones 2007). In this study, collared wolves were largely absent from alpine areas and consistently avoided high-elevation coniferous areas where caribou are likely to occur.

The relative availability of moose and caribou in the PRSA was different. Moose densities across most of the study area were ~1.18 moose / km^2 in 2005 and ~0.47 moose / km^2 in 2009; caribou densities remained at ~0.048 caribou / km^2. Wolf-diet analysis in the PRSA showed that moose and beaver comprised 88–98% of their summer diet, whereas caribou comprised only 0.4–12% of summer diet (see Chapter 3). Wolves, however, remain

Table 2.6 Hunting forays above 1050 m by wolves (*n* = 3, packs: Hominka, Anzac and Table) and relative kill success rates by season in the Parsnip River Study Area, BC, 2007–2009. Success was classified according to field investigations and through visual assessment of GPS-collared wolf movements during forays likely leading to caribou or moose kills (see text for details).

Wolf Season	Total # Hunting Forays	# Hunting Forays Leading to Moose kill	# Hunting Forays Leading to Caribou kill	Moose + Caribou Kill Success Rate (Caribou only)
Denning	30	4	1	0.17 (0.13)
Late Summer	38	6	3	0.24 (0.16)
Winter	7	1	0	0.14 (0.14)

the most frequent predator of collared adult female caribou across BC's mountain caribou range (Wittmer et al. 2005a), including in the PRSA (D. C. Heard, unpublished data) and an important predator of caribou calves (Gustine et al. 2006*a*) despite their apparent avoidance of areas selected by caribou. Avoidance of landscape features associated with caribou may be explained by the potential for a functional response in resource selection, driven by the relative availability of moose and caribou (Mysterud and Ins 1998). For example, in areas of low human activity in Banff National Park, wolves were non-selective for proximity to human activity, but when human activity increased, wolves avoided proximity to humans (Hebblewhite and Merrill 2008). Therefore, although influential on wolf selection, human activity remained unimportant (i.e., non-selected) until a certain threshold was surpassed. In the PRSA, the relative prey densities may be affecting the selection coefficients for landscape variables associated with caribou. If caribou density was higher, there might have been a shift away from avoiding caribou habitat to non-selection, or even to selection, for caribou habitat (see Mysterud and Ims 1998). There is evidence that when both moose and caribou are abundant, wolves select for caribou (Dale et al. 1995). Consequently, means other than selection models may be necessarily to understand wolf interactions with caribou at low densities. Although wolves did not select for caribou, they still can have a large impact on survival rates. Examining seasonal elevation use by wolves and prey, as well as wolf movements, allowed an understanding of these interactions in more detail.

Overall, use of elevation by moose in the PRSA was different from caribou. Moose select for areas of high shrub stem counts, as their diet is composed mainly of shrubs (Eastman 1977), which are more common at lower elevations. Use of elevation by wolves is similar to their main food source, moose, whereas caribou consistently use high elevations (Figure 2.3). Use of elevation by caribou changes little throughout the year, but moose and wolves clearly show more use of higher elevations in late summer. This characterization of spatial separation of caribou from moose and wolves among seasons is also consistent with previous work involving wolves, moose, and caribou in other mountainous areas of BC (Bergerud and Page 1987, Seip 1992, Stotyn 2008).

Our sample of moose VHF locations could be biased, because moose were collared at low elevations in winter and, therefore, moose that have an affinity for higher elevations may not have been represented in our collared sample. Consequently, the overlap between caribou and moose may be greater than our results suggest. Furthermore, this change in elevational use by moose during late summer may encourage wolves to spend more time in areas that would have lower overall prey density if moose were not present, and this could potentially be drawing wolves into caribou refugia (Robinson et al. 2010).

Both the use of elevation by VHF-collared caribou and the cluster investigations of locations from GPS-collared wolves supported our use of 1050 m as the threshold elevation to understand wolf movements when they are potentially hunting for caribou. No clusters associated with adult caribou kills were found below 1300 m. There is some evidence, however, that caribou in the PRSA occasionally go to low elevations. For example, uncollared caribou were seen twice on roads during summer field work. Caribou, however, clearly spend most of their time at higher elevations (Figure 2.3). Jones (2007) observed that, of 1764 telemetry locations on 6 collared female caribou in the PRSA, only 10 locations were located below 1100 m. During this study we located 28 collared caribou 9 out of 251 times below 1100 m, but more error is inherent in locating our VHF collars than would be associated with Jones' (2007) GPS-collar locations. Most importantly, the only 2 caribou telemetry locations below 1000 m during this study were of confirmed mortalities. A better understanding of why some caribou wander to low valley bottoms is clearly needed, including the addition of collaring male caribou to understand how their movements may differ from adult females collared in this and Jones' (2007) studies.

Wolves spent twice as much time, on average, at high elevations during snow-free months as in winter, spending 17–23% of their time from July–October above 1050 m (Figure 2.4). When considering the frequency of hunting forays (after removing returns to kill sites, which would inflate this frequency when wolves regularly return to homesites), the relationship with snow depth is similar, but shifts to earlier in the year (Figure 2.5). The difference between the total time spent by wolves above 1050 m (Figure 2.4) and the frequency of forays above 1050 m (Figure 2.5) is likely because wolves are more nomadic later in the summer, no longer needing to return regularly to the homesite because pups are old enough to follow the pack on hunts and they could spend more time at high elevations during each foray. In later snow-free months, hunting forays by wolves were less frequent, but wolves spent more time at high elevations during each foray.

Wolves started going more frequently to higher elevations before snow depths decreased, and the frequency of forays decreased before any snow started accumulating again in the fall (Figures 2.4); the same is true for time spent above 1050 m (Figure 2.5). Snow depth, therefore, does not fully explain this aspect of wolf hunting behaviour; snow hardness and the availability of caribou calves may be influential.

Snow conditions affect vulnerability of prey to wolves, because of changes in the relative abilities of wolves and their prey to move in snow (Mech and Peterson 2003). Differences in foot morphologies allow caribou to have a lighter foot loading than wolves on snow (Telfer and Kelsall 1984). This advantage, however, may deteriorate with snow-crust layers, giving wolves the ability to hunt in the snow unhindered (Peterson 1977). In this study, we compared the average amount of time that wolves spent above 1050 m and average snow depth across the 3 complete years of data collection (2007–2009). The relationship in March seems to deviate from the general trend in this relationship (Figure 2.4), but this deviation was driven by one wolf collared during March of 2010, which spent 41% of its time at high elevations (much more than the other 3 wolves that comprise this average). Snow depth, and likely snow hardness, differed significantly during the *el Nino* year of 2010. Snow depth reached a maximum of only 775 mm (of water equivalence) during this year and a maximum of 1140, 1076 and 1101 mm in the 3 preceding years, respectively. Although no data were collected on snow crusting, it is likely to have been more common and with an earlier onset in 2010 compared to other years. Despite this extreme case, there is a trend towards an early increase in forays before snow depth decreases which may be indicative of snow hardening in late winter due to solar radiation and rain-on-snow events aiding wolf movement. Had there been snowmobile activity in the study area, wolf movement to high elevation may have been facilitated even more. Snow crusting, however, does not explain the decreased presence of wolves at high elevation during later snow-free months, before snow depth started increasing. Snow depth, therefore, provides at best, a partial refuge for caribou from wolves during the height of winter, but is not exclusively driving whether or not wolves hunt in areas where caribou are present.

When present, wolves often prey on caribou calves at high rates (Bergerud and Page 1987, Adams et al. 1995, Gustine et al. 2006*a*). Further, when wolves were removed from a system, caribou calf survivorship improved substantially (Gasaway et al. 1983, Hayes et al. 2003). In general, wolf predation on calves is much lower during winter than in summer (Ballard et al. 1987, Mech et al. 1995, Ballard et al. 1997). Given that caribou in the PRSA calve in late May to early June (Jones 2007), that recruitment levels for caribou were low in summer, and that winter calf survival was high (Gillingham et al. 2010), wolves may be cueing in on this early summer seasonal food source when going to high elevations. A depletion in the availability of caribou calves may explain why wolves cease to go to high elevations long before the snow begins to accumulate.

On using a non-automated approach for cluster analysis

Most kill-rate studies have been performed in winter because kill sites are easier to locate than during summer. During summer, kills of juveniles difficult to identify in the field; whereas during winter, there are proportionally fewer kills of juvenile ungulates and juveniles are larger in size, making them easier to identify than they would be during summer (Mech and Peterson 2003, Sand et al. 2008). We used an automated procedure to guide field efforts for cluster investigation similar to other studies (Webb et al. 2008). When determining success rates of wolf forays, however, we used minimum criteria from field investigations in combination with a more subjective, visual method to classify clusters into kill sites and non-kill sites. When comparing models to discern between large-bodied kill sites and non-kill sites, Webb et al. (2008) found that the number of locations within 100 m of the cluster center and the number of non-consecutive days within 100 m of the cluster, were variables present in all top models for distinguishing among kill sites and non-kill sites. Similarly, we determined the maximum diameter of clusters and the total non-consecutive hours at clusters that were visited and not visited in the field.

One advantage of using this visual approach to cluster analysis is avoiding the need to test multiple definitions of what is considered a cluster of GPS locations (e.g., GPS locations within 100 m, 200 m, and 1 km, etc. of each other), Instead it allows for a more subjective, but dynamic, definition during the analysis of what constitutes a cluster, which varies in size from one to the next. Another problem with summer kill rates in particular is the changing dimensions of meta-clusters. We considered a meta-cluster to be a potential kill-site cluster along with surrounding bed sites associated with a kill site during feeding and digestion. At large distances meta-clusters become difficult to discern. For example, we observed a GPS-collared wolf bedding for 4 h at locations up to 20 km away from a kill, and then returning to the kill site. The presence of meta-clusters has not been addressed in the literature, but spatial data of GPS-collared wolves on large-bodied prey contain many of them. During the denning period, wolves also frequently return to den sites to feed pups and then return to kill sites, further complicating the definition of a cluster. Although not practical for large data sets, when researchers are examining only a subset of the data, for example, visual analysis of movements may help correctly discern between kills and non-kill clusters. This assertion, however, should be tested with field investigations of clusters identified beforehand as kill sites and non-kill-sites.

Hunting success by wolves varies from 10–49% across studies (Mech and Peterson 2003). Defining and identifying success is inherently imprecise because of complicating factors such as multiple kills during a single hunting bout, multiple tests of prey before making a kill, and the fact that the size of prey for wolves ranges from voles to moose (see Chapter 3). In this study, we considered only kill sites above 1050 m that likely corresponded to the size of a 13-month-old caribou or larger. Our kill-rate estimates are inflated because of our inability to visit all clusters at high elevation and the reliance on visual GPS-cluster analysis for the remainder of the clusters. However, we measured the proportion of forays leading to probable kills to give a relative success rate across seasons. Wolves spent much more time in areas where they were likely to encounter caribou during denning and late summer seasons than during winter (Figure 2.4), but the caribou-kill-success rate was similar across seasons (Table 2.6). We believe this consistency across seasons is being driven by a single caribou kill during the 5 months of winter. This implies that wolves could be varying their *effort* according to snow conditions, to maintain a sufficient kill-success rate. VHF-collared moose showed less fidelity for lower elevations during late summer, and this is when the overall kill-success rate of wolves increased (from 0.24 kills / foray to 0.14 and 0.17 for denning and winter, respectively). Again, we note that caribou calf-kill rates would be very imprecise using this technique (or others), but calves could certainly constitute an incentive for wolves to hunt at higher elevations. Dale et al. (1995) did not find any effect of snow depth on wolf kill rate and this may be true for wolves at higher elevations in the PRSA as well, but wolves may also put less effort into hunting caribou when snow depths are at their maximum.

The overall kill rate on caribou, however, may change across seasons. During summer, wolves are more likely to hunt alone or in smaller groups and thus, a larger number of killing groups could be present on the landscape than during winter. This behaviour would cause our summer estimates to be biases and be under-representing kill rates and the number of forays during summer.

In summary, caribou appear to be spatially separated from moose and wolves. Infrequent movements by wolves, which are not highlighted by large-scale RSF methodologies, however, imply that wolves still spend some time hunting for caribou, although this effort is substantially lower during winter. Snow may provide at least a partial refuge for caribou from wolves and from the primary prey of wolves during early winter, which is consistent with conclusions of other researchers (Bergerud and Page 1987, Seip 1992). Snow hardness may remove this mechanism of refuge in late winter. To fully understand the seasonality of this spatial separation, more research is needed on the effects of changes in snow conditions, such as snow crusting (which could increase with climate warming) and how this influences wolf movements. Additionally, more research is needed on wolf kill rates on caribou calves to understand the potential for cuing wolf movements to higher elevations.

MANAGEMENT IMPLICATIONS

The dynamics among wolves, moose, and caribou have been highly modified by the increase in moose numbers, due to anthropogenic changes to the landscape. The densities of wolves and moose are likely linked based on diet analysis (see Chapter 3) and other studies. Reducing moose could be an integral part of caribou recovery. Understanding the predator response to declining prey densities in systems characterized by apparent competition requires knowledge of how predators move in relation to their prey (Holt and Lawton 1994). At a coarse scale of elevational use, movements of wolves were similar to moose. Furthermore, wolves did not frequently foray into areas where caribou were more common. Wolves in the PRSA were monitored during a period of sharp decline in primary-prey density. Because prey switching is a possible outcome of such an experiment (Seip 2008), this study period represented the most likely time when wolves would increase hunting pressure on caribou. This was a period of relative food shortage for wolves but kill rates of adult caribou remained relatively low, with approximately 2–5 caribou/pack/year (~10% of the population, Gillingham et al. 2010). Although any level of predation may still have important implications for a low-density species with low recruitment, the 10-fold difference between moose and caribou densities does not make prey switching a viable option for wolves at current prey densities in the long term. This kill rate remains, however, conservative because it assumes that collared wolves are representative of the entire pack and does not account for predation on calves. In summer, for example, wolves could be hunting in many smaller groups and thus, this estimate of kill rate would be biased too low and actual kill rates could be higher. More research is needed on pack splitting and calf predation within caribou ranges.

This study showed that wolves avoid caribou-associated habitat characteristics and that the spatial overlap between wolf and caribou is lowest during winter months. Spatial separation may be critical for the persistence of a secondary prey species with lower fitness (Sinclair et al. 1998), but the benefits to wolves of going to higher elevations may change as the density of moose decreases. The low frequency of forays during the height of winter relative to other seasons implies that caribou may, at best, be temporarily inaccessible to wolves.

CHAPTER 3: WOLF DIET AND THE IMPLICATIONS FOR CARIBOU RECOVERY DURING A MOOSE POPULATION DECLINE[2]

INTRODUCTION

Understanding what an animal eats is fundamental to understanding the relationship between an animal and its environment (Litvaitis 2000). Interest in the diet of wolves (*Canis lupus*) arises due to their predation on livestock (Meriggi and Lovari 1996), predation on game species (Murie 1944, Skogland 1991), and the need to describe their general ecology as a threatened or endangered species in some portions of their range. Recently, there has been growing interest in understanding wolves as a predator on endangered prey species, such as on reindeer (*Rangifer tarandus fennicus*) in Finland (Kojola et al. 2009), Przewalski's gazelle (*Procapra przewalskii*) in China (Jiang et al. 2000) and Vancouver Island marmot (*Marmota vancouverensis*) in Canada (Bryant and Page 2005).

Woodland caribou (*R. tarandus caribou*) are threatened across Canada (COSEWIC 2002) and wolf predation has been identified as the major proximate cause of their decline (Bergerud 1974, Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005*a*). Caribou and moose (*Alces alces*) exist in a multi-predator / multi-prey system characterized by apparent competition – a form of indirect competition where an increase in one prey species leads to a decrease in another, but only because of an increase in a shared predator (Holt 1977). Across much of woodland caribou range, moose numbers have increased in the last century and a half, due mainly to human forestry practices (Peterson 1955, Spalding 1990, Rempel et al. 1997), which has led to an increase in wolf numbers (Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005*b*). As a result, predation on caribou also has increased, but the numerical

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response of wolves remains coupled to the abundance of their primary prey, moose, and not to caribou (Hebblewhite et al. 2007). Thus, even as caribou numbers decline, there is no feedback to wolf numbers. This asymmetric relationship has led to the endangerment of many woodland caribou populations throughout their range (DeCesare et al. 2010).

One management approach to dealing with the effects of apparent competition on caribou is to decrease the moose population in order to decrease wolf density and reduce predation pressure on caribou (Seip 2008). Among study areas, there is a strong correlation between wolf density and total ungulate biomass (Keith 1983, Fuller 1989, Fuller et al. 2003). Theoretically, decreasing moose numbers should reduce wolf numbers proportionally. Understanding wolf diet is an important first step towards predicting how wolves would respond to this reduction in primary prey.

There are 4 main methods to quantifying wolf diet: scat analysis, stomach content analysis, direct cataloguing of wolf kills, and stable isotope analysis (Peterson and Ciucci 2003). Scat analysis was pioneered by Murie (1944) and remains the most widely used method to quantify wolf diet (see Appendix C). It is non-invasive and samples are often abundant in predictable locations, even for rare or endangered wolves (Marucco et al. 2008). In contrast, stomach content analysis requires collecting wolf carcases. Direct cataloguing of wolf kills is very diverse in its methodology and can involve back-tracking animals (Murie 1944), aerial kill-site observation (Burkholder 1959), snow tracking with radio collars (Hebblewhite et al. 2003), or Global Positioning System (GPS) cluster analysis (Sand et al. 2005, Webb et al. 2008).

The most recently developed methodology to understanding wolf diet is through stable-isotope analysis. Inert tissues such as hair, feathers and claws retain the isotope signature they accrued from the diet during their period of growth (Hobson 1999). Wolves go through an annual molt in late spring and new hairs grow during warmer months (Young and Goldman 1944). Therefore, guard hairs should represent the summer-fall diet of wolves (Darimont and Reimchen 2002). Because metabolic processes discriminate between isotopes differently, isotopes are routed differently to different tissue types (Tieszen et al. 1983). Experimentally derived discrimination factors quantify the difference between consumer diet (mainly prey muscle tissue) and specific consumer tissues (Roth and Hobson 2000). Diet-mixing models, which account for this discrimination, quantify wolf diet using the isotope signatures from both wolf hair and bone collagen relative to the isotope signatures of common prey species (Szepanski et al. 1999, Darimont and Reimchen 2002, Urton and Hobson 2005).

It is difficult to discern between calves and adult prey in direct cataloguing and isotope-analysis methods. Despite much progress, analysis of clusters of Global Positioning System (GPS) locations for wolf kill sites has yet to accurately predict kill sites of medium or small-bodied prey without extensive field investigation (Merrill et al. 2010) and there is little sign of ungulates <6 months old at wolf kill-sites in the field (Mech and Peterson 2003). Isotope analysis too is unlikely to be able to discern between calves and adult ungulates if isotope signatures are similar (Jenkins et al. 2001). Scat analysis, on the other hand, does allow for the quantification of the proportion of wolf diet composed of calves versus adults (Thompson 1952, Jedrzejewski et al. 1992, Theberge and Theberge 2004).

Previous work within mountain caribou range has implied that wolves are more likely to be eating caribou during snow-free months when movement is easier and there is access to juveniles (Steenweg et al. 2009, Chapter 2). Capitalizing on the seasonality and lower costs of scat and hair isotope analysis, we used these 2 methods to address the diet composition of wolves and their reliance on moose and caribou during summer. In the Parsnip River Study

Area (PRSA), of north-central BC, we hypothesized that the summer diet would be composed mainly of moose, caribou and beaver (*Castor canadensis*), based on knowledge of available prey species in the area. Specifically, we expected it to be dominated by moose and beaver and to contain little caribou. We also hypothesized that calves would constitute a considerable portion of wolves' diets because wolves in general tend to focus on young when they are available (Mech and Peterson 2003) and wolves have been shown to be a common predator of caribou calves during the first 3–5 weeks after birth (Gustine et al. 2006*a*).

STUDY AREA

The PRSA is located 100 km NE of Prince George, BC (see Chapter 2 for more details on local topography and vegetation). Moose densities were previously very high in the PRSA, with an approximate density of 1.18 moose / km^2 in 2005 (Walker et al. 2006). Following the call by the Mountain Caribou Recovery Plan for the reduction of primary prey consumed by caribou predators in the PRSA (Seip 2005, Wilson 2009), moose-hunting quotas were increased starting in 2006. This resulted in an approximate halving of the moose population by 2009 (Gillingham et al. 2010). Therefore, during this study (2008–2009), moose densities were in sharp decline and reaching very low densities for the area. Beaver were abundant (F. Booker, local trapper, personal communication), which is expected given the ubiquity of ox bows and riparian areas in the study area. Moose and beaver mainly occupy lower elevations, in contrast to caribou, which remain at high elevations in the central Rocky Mountains in the eastern portion of the study area (Jones 2007). During the study, caribou densities were low, ~0.048 caribou / km^2 (Steenweg et al. 2009, updated as per D.C. Heard, unpublished data) and relatively stable (Gillingham et al. 2010).

METHODS

Homesites are comprised of dens and rendezvous sites where wolves frequently return to feed pups in summer (Joslin 1967). We sampled wolf scats from homesites and roads, which are common protocols for wolf-scat studies (see Appendix C). We compared these results to isotope analysis in order to describe wolf diet from early summer to early fall (hereafter referred to simply as summer). As a result, there is a predictably high density of scats and the time of deposition is constrained to the period when wolves occupy the homesites.

Scat analysis

Scats were collected from homesites and from 210 km of logging roads, which are present only at lower elevations. Homesites were located by visually analyzing GPS-collared wolf movements (Spatial Viewer, unpublished program, M.P. Gillingham) and were visited in summers 2008 and 2009, a minimum of 2 weeks after wolves had vacated the area (see Chapter 2 for collaring methods). Roads are commonly used as travel corridors by wolves because they increase their travel efficiency (Trombulak and Frissell 2000, James et al. 2004) and roads also provide access to a large number of scats that are easily sampled, but this potentially introduces sampling bias (see Appendix C). In June 2009, all major forest roads in the study area were driven to clear roads of old scats, which were not analyzed. This required 2 observers to drive at ≤25 km/h and visually locate and remove all scats from the roadbed. In early to mid-October, roads were again driven with the same protocol in order to collect scats for analysis.

Based on wolf-telemetry data from 2008, we mapped 100% Minimum Convex Polygon (MCP) home ranges of wolf packs (Steenweg et al. 2009) using Hawth tools (Hawth's Analysis Tools for ArcGIS, available at http://www.spatialecology.com/htools) in

ArcMap (Environmental Systems Research Institute, v9.3, Redlands, California, USA). Because of the different amount of roads within each pack's home range (~20-35 km), we randomly selected 40 scats from all scats found on roads for each pack; if fewer than 40 scats were collected for a pack, we analyzed all scats for that pack. During preliminary analyses, a sample size of 40 scats was sufficient to identify all prey species, including those that were rare (see Appendix B).

Incorrectly identifying coyote scats as wolf scats is a common concern during wolf scat analysis (Weaver and Fritts 1979), but coyotes are exceedingly rare in the study area. Only once during 3 years of intensive flights did we observe coyotes in the study area where scats were collected. We, therefore, assume this concern to be negligible. Very small diameter scats were not collected on roads because foxes are present in the study area. Small scats at homesites, on the other hand, were assumed to be from wolf pups and were included in the scat analysis. Scats that were close to one another on roads (<5 m apart) and looked of similar age were also discarded to reduce double-sampling from the same individual and the same meal (Huggard 1993).

All scats were frozen until lab analysis. They were autoclaved at 131°C for 25 min to eliminate possibly viable pathogen eggs (Kennedy and Carbyn 1981), washed and loosened with water and a drop of detergent, and then air dried. Each scat sample was manually spread out in a glass bowl and the presence of any large items that could help identify prey items was noted (hooves, claws, feathers, teeth, etc.). We created a reference-slide collection of known wolf prey species from hairs collected in the field, from local trappers and from museum specimens (from the Royal British Columbia Museum, Victoria, BC). Ten hairs were randomly selected from each scat and viewed under a microscope to determine prey type using medullar and cuticle patterns compared to our reference collection and to keys

(Adorjan and Kolenosky 1969, Kennedy and Carbyn 1981). Results are presented as percent frequency occurrence of prey items in wolf scat from homesites and from roads.

To approximate the importance of prey-species biomass to wolf diet, we converted the frequency occurrence to a measure of biomass consumed. We used the average weights of prey species in the study area and the equation relating number of collectable scats per kill (y) to the mass of each prey species (x) such that $y = 0.008x + 0.439$ (Weaver 1993). Because this conversion was only developed for prey species from the size of a snowshoe hare (*Lepus americanus*) to an adult moose, we omitted prey species smaller than hares from this analysis, as well as unknown prey items. We bootstrapped the frequency occurrence results 2000 times using STATA (Stata Corporation, College Station, TX) in order to estimate the 95% confidence intervals (Marucco et al. 2008).

Isotope analysis

We collected guard hairs from wolves during radio collaring. Samples were analyzed to determine the ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ isotopes (UBC Okanagan Laboratory, Kelowna, BC). Isotope signatures are expressed in delta notation ($\delta^{15}N$, $\delta^{13}C$) comparing the ratio in the sample to the ratio in a standard (atmospheric N_2 and PeeDee belemnite; DeNiro and Epstein 1978, 1981).

Isotope signatures of prey species were provided by the Mountain Caribou Recovery Project, which had collected samples as part of a larger mountain caribou study. Although local samples would have been more appropriate, these were the only samples available. Only species comprising >5% of wolf diet (from scat analysis) were included in the isotope analysis. An important assumption of stable-isotope analysis of predator diet, is that prey signatures are significantly different from one another (Ben-David et al. 1997*a*,*b*). To test the difference among prey signatures, we used a randomization test based on a K nearest-neighbour statistic (Rosing et al. 1998, program available from authors). We used a Bayesian-mixing model, MixSIR (Moore and Semmens 2008, program available from http://conserver.iugo-cafe.org/) to estimate the contributions of each prey to wolf diet. This program uses a sampling-importance-resampling algorithm to develop posteriori distributions of the proportional prey contributions to the mix (i.e., wolf diet) and allows for the incorporation of uncertainty in the discrimination values and prey signatures, as well as any prior knowledge (informed priors) if available.

Results from scat analysis can be used as informed priors, and the parameterization of the MixSIR model requires a measure of variation in these priors (Moore and Semmens 2008). We used the biomass consumed from the 2 scat sampling approaches (homesites and roads) as 2 separate and equally valid measures of the proportion of each prey species in wolf diet. A dirichlet distribution (a common continuous multivariate probability space used in Bayesian statistics) was parameterized using a maximum likelihood fitting process in STATA (Maarten et al. 2006). The dirichlet distribution coefficient for the proportion of caribou in wolf diet, however, was not significant ($P = 0.75$) because of the high variation in the relative proportion of caribou in wolf diet calculated from homesites and roads (7% and 1% of diet, respectively, after removing all prey species comprising <5% of diet from scat analysis). Poorly defined prior distributions cause the MixSIR model to function poorly (Semmens and Moore 2008). Therefore, we were unable to run the model with informed priors and used a uniform distribution of prior prey contributions instead. A potential advantage of isotope analysis is that results are individual-wolf-based, which allows for a decomposition of variation in isotope signatures among individuals and packs (Semmens et al. 2009).

Previous work has shown that differences in discrimination factors are usually negligible in ungulates (Tieszen and Boutton 1988), and we, therefore, assumed isotope values for ungulate muscle and hair to be equivalent. Because no studies have investigated the isotope-specific fractionation values for wolves, we used discrimination values of +3.4‰ and +2.6‰ for changes in $\delta^{15}N$ and $\delta^{13}C$, respectively, from a study on captive foxes (Roth and Hobson 2000). This is a common assumption used in isotope analysis of wolf diet (Darimont and Reimchen 2002, Urton and Hobson 2005, Darimont et al. 2009, Adams et al. 2010, Derbridge 2010, Milakovic and Parker 2011). Variation around these discrimination values was obtained from Roth and Hobson (2000) and expressed as standard deviations of 0.20‰ and 0.26‰ for changes in $\delta^{15}N$ and $\delta^{13}C$, respectively.

RESULTS

Scat analysis

We collected and analyzed 191 scats that contained the remains of 216 prey items. Eighty-five scats were analyzed from the homesites of 2 wolf packs (Table and Anzac), and 106 scats were analyzed from roads for 5 packs (Table, Anzac, Arctic, Hominka, Upper Table). Eighty-seven percent of all scats had only one prey item present, 13% had 2 prey items, and none had >2. Differences in prey composition were apparent between scats collected from homesites and roads (Figure 3.1). When summing frequencies from both sampling approaches (Figure 3.1), moose was the most common prey in wolf scat, present in 65% of all scats (roads and homesites) collected (27% moose calves and 38% adult moose). Beaver was also common, present in 14% of scats, while caribou was found in 5% of scats (3% calf, 2% adults). The remaining 16% of scats by frequency occurrence consisted of the following: 6% muridae (various vole and mouse species); 3% sciuridae (red squirrels (*Tamiasciurus hudsonicus*) and ground squirrels (*Spermophilus* spp.); 2% unknown ungulate

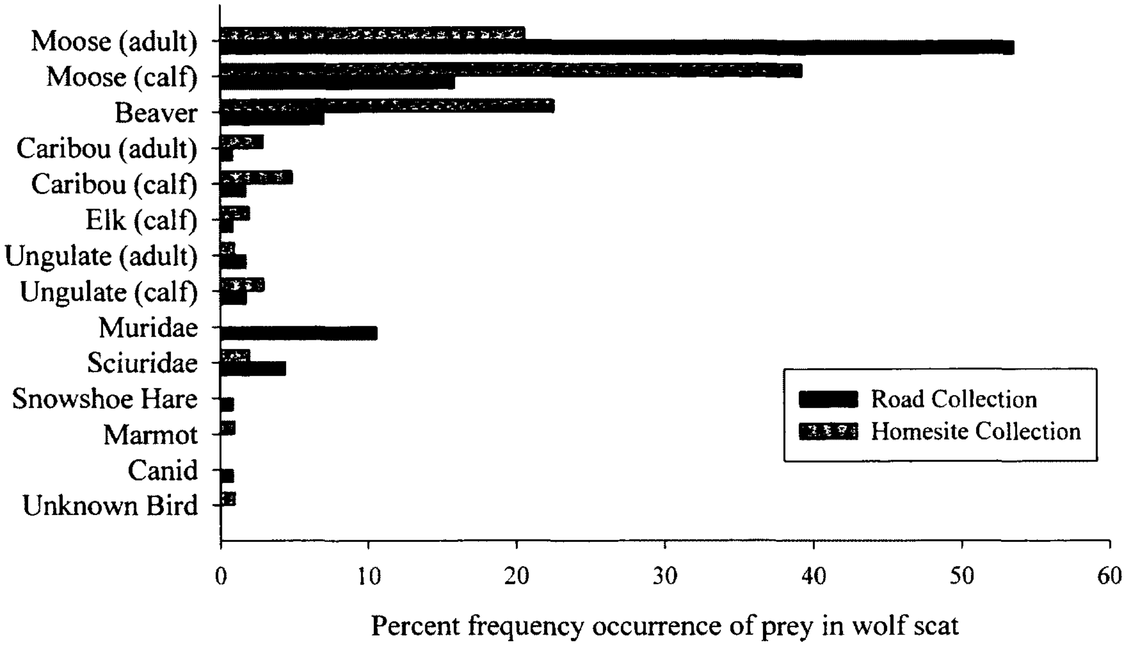

Figure 3.1 Percent frequency of occurrence of prey found in wolf scat (*n* = 191) in the Parsnip River Study Area, BC. Percent frequency occurrence is calculated separately for scat collection from roads and homesites (see text for definition of homesite). Ungulates categories (adult and calf) refer to prey items that could not be identified to species.

calves; 1% unknown ungulate adults; and < 1% for each of the other prey items (hoary marmot (*Marmota caligata*), snowshoe hare, unknown canidae (*Canis* spp.), and unknown bird).

Both scat-sampling approaches indicated that adult moose constituted the majority of the total biomass consumed (Table 3.1). The order of importance was also the same between scat-sampling approaches, with adult moose (53.8%, 88.8% for homesite and road collection, respectively) followed by moose calf (28.6%, 7.3%), beaver (10.2%, 2.0%), caribou (4.0%, 0.8%) and caribou calf (2.0%, 0.6%). Together, moose, beaver and caribou comprised 98.6% or 99.5% of wolf diet in summer, depending on the sampling approach. Large overlap of wolf-pack ranges across roads (see Steenweg et al. 2009) and the few pack homesites visited (2 packs, 7 homesites total) precluded an analysis of scats at the pack scale.

Isotope analysis

We collected 24 hair samples from wolves in 7 packs (Table, Anzac, Arctic, Hominka, Upper Table, Tacheeda, Wichcika). Prey signatures obtained from the Mountain Caribou Recovery Project consisted of 26 hair samples from moose and 14 from beaver, both from various locations across mountain caribou range in BC. Caribou-hair samples were restricted to the Omenica region, BC ($n = 34$). By plotting isotope signatures from wolves and prey, after taking into account discrimination between prey tissue and wolf hair (i.e., adding the discrimination factor), it is clear that wolf signatures did not coincide with the signature of the dominant prey, moose (Figure 3.2). Four wolves were re-sampled while re-collaring, or following mortality, and showed little difference in isotope signature in different years, implying that diet changed little between years (unpublished data). The randomization test based on the K nearest-neighbour statistic indicated that isotope signatures for moose

Table 3.1 Percent biomass of prey species consumed by wolves as determined by wolf scat analysis using 2 sampling approaches (homesite and road collection) in the Parsnip River Study Area, BC, 2008–2009. Means and 95% confidence intervals are reported.

				Homesite			**Road**	
Prey Species	**Mass (kg)**	**kg/scat**[a]	$\bar{X}$	**95 C.I.**	*n*	$\bar{X}$	**95 C.I.**	*n*
Moose	375[b]	3.44	53.5%	(42–62)%	21	88.8%	(87–90)%	61
Moose Calf	65[c]	0.96	28.4%	(24–33)%	40	7.3%	(4–10)%	18
Beaver	19.2[d]	0.59	10.1%	(7–13)%	23	2.0%	(1–3)%	8
Caribou	170[b]	1.80	4.0%	(0–8)%	3	0.8%	(0–2)%	1
Caribou Calf	30[e]	0.68	2.5%	(0–4)%	5	0.6%	(0–1)%	2
Elk Calf	38[f]	0.74	1.1%	(0–3)%	2	0.3%	(0–1)%	1
Snowshoe Hare	1.34[d]	0.45	0.0%	-	0	0.2%	(0–1)%	1
Marmot	4.59[d]	0.48	0.4%	(0–1)%	1	0.0%	-	0

[a] Calculated as 0.008 * prey mass + 0.439 (Weaver 1993)

[b] From Shackleton 1999

[c] From Franzmann and Schwartz 1997

[d] From Nagorsen 2005

[e] From Lavigueur and Barrette 1992

[f] From Cook et al. 1996

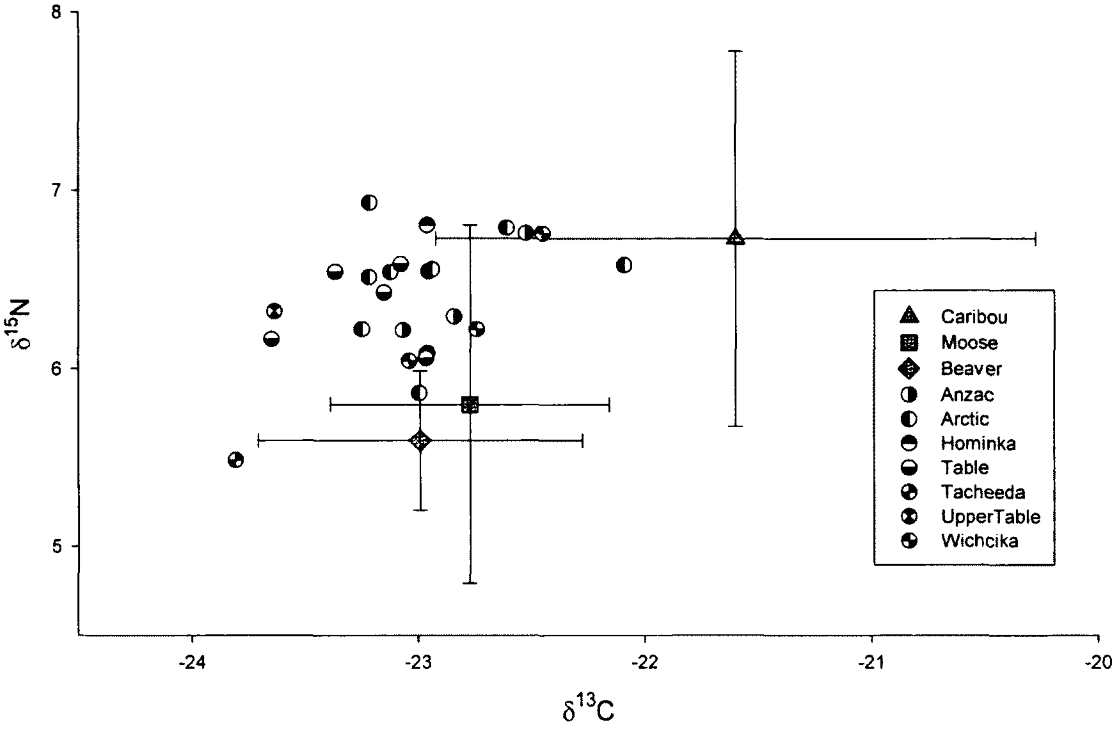

Figure 3.2 Stable-isotope signatures of individual wolf (pack membership denoted by shading of circles) and common prey species (gray shapes) in the Parsnip River Study Area, BC, 2007–2010. Error bars indicate standard deviation for prey species. Different circle symbols denote different pack membership. Note that for presentation, prey signatures include discrimination values (see text).

(δ^{15}N: 2.4 ± 1.0; δ^{13}C: -25.4 ± 0.6; $\bar{X}$ ± SD) and beaver (δ^{15}N: 2.2 ± 0.4; δ^{13}C: -25.6 ± 0.7) were not significantly different from one another ($P = 0.464$). Therefore, we dropped beaver from the mixing-model analysis because it constituted a small portion of the diet compared to moose, nonetheless 'moose' signature does contain some unknown proportion of beaver. Caribou (δ^{15}N: 3.3 ± 1.1; δ^{13}C: -24.2 ± 1.3) and moose were significantly different from one another ($P < 0.001$).

Isotope analysis indicated that moose were the more predominant prey of wolves, but credible intervals were wide (Table 3.2). Isotope analysis for the diet of all wolves pooled together indicated that moose comprised 88% (credible interval: 73–98%) and caribou comprised 12% (3–27%) of wolf summer diet. Within a pack, the proportional contribution of caribou to the diet was always higher, but more variable. The mean contribution varied from 15–42% among packs, but the width of the credible interval was inversely proportional to the sample size. Packs with very low sample sizes ($n \leq 3$) had credible intervals wider than 50%.

DISCUSSION

Different diet-analysis methods have different advantages, with varying seasonalities, costs, and levels of detail, but confidence in estimates of diets naturally increases when results are consistent across methods. Isotope analysis assesses an integrated diet during the period of hair growth, but provides little information about the diversity of wolf diet, or the differential importance of calves and adult ungulates. Scats, on the other hand, are a collection of single meals that allow for a more detailed description of wolf diet but can be biased by collection method (see Appendix C).

Both scat analyses and isotope analysis supported our hypothesis that the diet of wolves in summer in the PRSA was composed mostly of moose, caribou and beaver.

Table 3.2. Proportions of caribou and moose in the diet of wolves in the Parsnip River Study Area, BC estimated from results of stable isotope analysis of wolf hairs. Mean and 95% credible intervals were calculated from posterior distributions from the MixSIR isotope mixing model (Semmens and Moore 2008).

		Caribou		**Moose**	
Pack	***n***	$\overline{X}$	**95% Credible Interval**	$\overline{X}$	**95% Credible Interval**
All Wolves	24	0.12	0.03–0.27	0.88	0.73–0.98
Anzac	3	0.29	0.04–0.70	0.71	0.30–0.96
Arctic	9	0.21	0.04–0.50	0.79	0.50–0.96
Hominka	2	0.30	0.03–0.81	0.70	0.19–0.97
Table	5	0.15	0.04–0.50	0.85	0.42–0.99
Tacheeda	1	0.30	0.02–0.92	0.70	0.08–0.98
Upper Table	1	0.42	0.03–0.93	0.58	0.19–0.97
Wacheeda	3	0.29	0.05–0.69	0.71	0.31–0.95

Furthermore, as hypothesized, wolves relied primarily on moose, which comprised a minimum of 66% of wolf summer diet and more likely >80% of the diet (Tables 3.1, 3.2). Scat analysis estimated the contribution of moose to wolf diet at 82.4% (66–95%) and 96.1% (91–100%) depending on homesite versus road sampling, and the estimate from isotope analysis lies in the middle, at 88% (73–98%). The proportion of caribou in the diet was low, with results differing slightly between analysis methods. Results from scat analysis ranged from 1.4% (0–3%) to 6% (0–12%), whereas the proportion was 12% (3–27%) based on isotope analysis at the population level. Because beaver and moose isotope signatures were not significantly different, isotope analysis could not discern between isotope signatures of moose and beaver, and thus, the proportion of moose from isotope analysis also included beaver. Relative to moose, however, the contribution of beaver to the diet was little. Estimates from scat analysis indicated that beaver constituted between 2% (1–3%) and 10.2% (7–13%).

The proportions of moose and caribou were relatively consistent with what was expected based on analysis of movements of wolves (see Chapter 2). During summer, wolves denned and spent most of their time in valley bottoms where moose and beavers are most commonly found, occasionally making forays to higher elevations where caribou are present. Wolves spent ~20% of their time at mid to high elevations during summer, frequently killing moose at mid elevations (Chapter 2). Furthermore, wolves spent more time in early summer than in late summer at high elevations, which is consistent with when caribou were identified in wolf scat. There were more remains of caribou calves and adults found in homesite scats (6.5%) than roads (1.4%). Homesite scats had an earlier sampling window (May–July). Homesite scats also included the only scat with marmot, another high-elevation species. Furthermore, road scats were collected from logging roads which are absent from high elevations where caribou are present, and thus collecting scats from roads may bias the results and underestimate the contribution of caribou to wolf summer diet (see Appendix C for more on this discussion).

Wolf diet in the PRSA is similar to previous studies on wolf diet within mountain caribou range (Seip 1992, Allison 1998, Stotyn 2008). Around Quesnel Lake, BC (250 km south of the PRSA) wolf diet comprised of moose (~70%), caribou (20%), deer (5%) and other occasional species (5%) from summer scat analysis (Seip 1992). Furthermore, the combined summer scat analysis from 3 different study areas within mountain caribou range in BC resulted in the following percentages: moose (47.4%), caribou (18.9%), beaver (21.8%), and other (11.6%) (Allison 1998). Although the higher proportion of caribou in the diet relative to our study could be the result of higher caribou densities, rather, these 44 scats were combined from collections from dens, roads and some kill sites, the latter of which are often biased towards the prey species at the kill site (see appendix C for more on this topic). In Revelstoke, BC (450 km SE of the PRSA), isotope analysis resulted in estimates of biomass consumed by wolves for moose (95.4%), deer (2.6%), caribou (1.3%), and beaver (0.7%) (Stotyn 2008). The isotope signature for beaver, however, was based on a single sample and later dropped from their analysis along with deer, in order to test a binomial model such as ours, resulting in moose and caribou comprising 97.1% and 2.8% of summer diet, respectively.

Results from scat and isotope analyses for wolf diets have been shown to be similar in other studies (Darimont et al. 2008, Milakovic and Parker 2011). In this study, the proportion of moose in wolf diet was similar across diet-analysis methods at the population level. Caribou, on the other hand, was in different proportions in scat versus isotope analyses (Table 3.2, 3.3), similar to Milakovic and Parker (2011) who found elk, moose and sheep in similar proportions across methods, but not caribou. One possible explanation for this discrepancy is that, unlike other prey, caribou inhabit high-elevation areas away from low-elevation wolf dens. The fact that caribou are killed and consumed at high elevation may make them less likely to be in scats at lower elevation dens and roads (see discussion on the diffusion of scat samples in Appendix C). Therefore, scats could be under-representing caribou in the diet, causing this discrepancy between isotope and scat analysis results.

Isotope signatures may differ among packs due to differences in prey availability, differences in hunting strategies, or isotope analysis error. Here, credibility intervals are too wide to compare packs accurately (Table 3.2). Given that the level of management action in the study area is at the population scale, however, analyses were more informative when including all wolves in order to make inferences at the population level, rather than splitting among packs or individuals.

There are several possible explanations for the wide credible intervals in the prey proportions from isotope analysis. Some criticisms of the assumptions required for isotope analysis of wolf summer diet from hair are: the uncertainty in the timing of wolf hair growth and the applicability of using discrimination factors from a captive fox experiment for a wolf diet analysis (Derbridge 2010). Stotyn (2008) noted that the captive fox experiment (Roth and Hobson 2000) used a diet of 50% carbohydrates, which could lead to different discrimination values than for a wolf diet composed almost exclusively of protein and fat.

Given the importance of moose and beaver in scat analysis, we would expect the wolf signature to fall near the moose isotope signature after accounting for discrimination. Comparing isotope signatures of wolves and prey (Figure 3.2), a mismatch between wolf isotope signature and the signature of their primary prey, moose, is evident. The discrimination value modifies the relationship between prey and predator signature, by moving prey signatures across the predator isotope signature landscape (by simply adding the discrimination value to prey signatures) and similarly affects the mixing model analysis. Isotope analysis, however, has been used in at least 5 recent wolf studies using these same assumptions (Urton and Hobson 2005, Darimont et al. 2008, Darimont et al. 2009, Adams et al. 2010, Milakovic and Parker 2011). Some of these studies were able to capitalize on the larger differences among prey-isotope signatures when wolf diet includes marine mammals (e.g., Darimont et al. 2009) or fish (e.g., Adams et al. 2010). In contrast, Milakovic and Parker (2011) successfully analyzed the diet of wolves that rely exclusively on ungulate prey, which have similar isotope signatures, but their credible intervals were also wide. Wolf-specific discrimination values could help eliminate this concern and benefit these types of analyses.

Another explanation for the disparity between wolf and prey isotope signatures could be a missing prey species in the isotope analysis. Although scat analysis discounts the likelihood that another species could constitute a large portion of the diet, one could hypothesize that the prevalence of calves in wolf summer diet may cause a shift in isotope signature of wolves. Research has shown that calves of caribou, but not of moose, have enriched isotope signature from their mothers (Jenkins et al. 2001). Until 100 days of age, caribou calves have significantly higher $\delta^{15}N$ signatures than their mothers due to the enriched milk received while nursing. If caribou calves with higher $\delta^{15}N$ values were a common food source for wolves during the summer, this could account for the apparent shift towards higher $\delta^{15}N$ values relative to moose isotope signatures (see Figure 3.2).

Finally, much of the uncertainty in the proportions of prey in wolf diet from isotope analysis (i.e., wide credible intervals) is likely due to high variation in prey signatures in the model (see Figure 3.2). Prey-isotope signatures were estimated from across the entire range of mountain caribou, often far from the PRSA. More local prey samples may improve this estimate by reducing variation in prey signatures.

MANAGEMENT IMPLICATIONS

Despite the discrepancies among results from different scat-collection approaches and isotope analysis, they suggest similar food habits. This supports the benefit of using multiple techniques to analyze diet in order to account for different biases and assumptions associated with different methods.

The summer wolf-diet composition in the PRSA supports the theoretical framework for a system characterized by apparent competition that could lead to a species' extinction. Wolves appear to rely heavily on a single primary-prey, moose, and therefore, wolf densities are likely coupled to moose densities. Caribou on the other hand, are a low-density, secondary-prey species for wolves and their densities are not likely linked. Multi-prey systems can lead to apparent competition and wolves could potentially hunt caribou to extinction if it were not for some degree of spatial refuge provided by snow and elevation (Sinclair et al. 1998).

The broader management experiment in the PRSA of reducing moose densities through increased hunting quotas to recover caribou is based on the premise of a strong positive correlation between wolf and moose densities (Keith 1983, Fuller 1989, Fuller et al. 2003). In the PRSA, wolf summer diet is relatively simple (~99% moose, beaver and caribou) and is mostly composed of moose. Because of the low density of caribou and small size of beaver, switching prey is, at best, an ephemeral option for wolves. We, therefore, expect that a decline in moose density will result in a decline in wolf density. Furthermore, our results confirm that wolves do consume some caribou during summer months, and, therefore, it is appropriate to assume that the caribou population should respond positively to projected lower wolf densities in the long run (Lessard 2005).

CHAPTER 4: INDIRECT PREDATOR REDUCTION THROUGH PRIMARY-PREY MANAGEMENT[3]

INTRODUCTION

Strong numerical coupling between predator and prey populations through trophic interactions is one of the cornerstones of ecology. For example, predator and prey numbers fluctuate predictably over time, each as a function of the other's density (Lotka 1925, Volterra 1926). Such simple density-dependant feedback mechanisms that regulate predator-prey dynamics can be complicated by the presence of apparent competition (Holt 1977). In such systems, prey species appear to be in competition because the increase in one species results in the decline in another, but the mechanism is not of direct competition, but rather of a shared predator. Predation can, therefore, decrease the numbers of multiple prey species, while predator numbers are regulated by the numbers of only a subset of those prey species. This asymmetric relationship between apparently competing species can eventually lead to the endangerment of one species (DeCesare et al. 2010) and can make conservation efforts complex.

Many woodland caribou (*Rangifer tarandus*) populations across North America are in decline, and apparent competition with other ungulates, through increases in predator populations, has been identified as a leading cause (Bergerud 1974, Seip 1992, Rettie and Messier 1998, Wittmer et al. 2005*b*). Mountain caribou (*R. t. caribou*) of southern British Columbia are federally listed as threatened (COSEWIC 2002) and red-listed provincially (BC Conservation Data Centre 2010). Most sub-populations of mountain caribou are at >50% risk of extirpation within 20 years (Hatter 2006). Their decline is related to increases in the

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populations of other ungulates, mainly moose (*Alces alces*), but also elk (*Cervis elaphus*) or deer (*Odocoileus* spp.) in the southern part of their range (Kinley and Apps 2001), which have increased in the last half-century through the conversion of forests to early-seral growth stands by logging (Spalding 1990). This abundance of moose has in turn increased populations of predators, increasing predation pressure on caribou (Bergerud 1974, Bergerud and Elliot 1986, Seip 1992, Wittmer et al. 2005*b*). In the northern portion of mountain-caribou range, wolves (*Canis lupus*) are the most common predators of collared caribou (Wittmer et al. 2005*a*) and are a focus of caribou recovery initiatives (Wilson 2009). The need for wolf reduction has been suggested as critical for mountain caribou persistence (Wittmer et al. 2005a, Bergerud 2007) and the large-scale reduction in wolf numbers is being considered as one management action for mountain-caribou recovery (Seip 2008, Wilson 2009).

In Alaska, Yukon and northern BC, there is a long history of large-scale wolf reductions that have successfully improved adult survival, recruitment, or both, in ungulate populations (Gasaway et al. 1983, Bergerud and Elliot 1986, Bergerud and Ballard 1988, Boertje et al. 1996, Bergerud and Elliot 1998, Hayes and Harestad 2000, Hayes et al. 2003). Since the mid–late 20th century, however, attitudes towards wolves have been changing globally (Boitani 2003) and the same is true in BC (Hoffos 1987). Public opposition to the direct reduction of wolves in BC remains strong (Pynn 2010) despite the recommendations of the Mountain Caribou Recovery Science Team to help recover endangered caribou (Seip 2005, Wilson 2009). To balance the need for wolf management and the reluctance of the public to accept large-scale wolf killing, other approaches to reducing wolf densities have been proposed (Seip 2008). Reducing the abundances of prey species consumed by wolves to indirectly reduce wolf densities is one strategy that may meet this challenge head on and help recover caribou populations (Messier et al. 2004, Wittmer et al. 2005*a*, Seip 2008). If hunting quotas were increased enough to reduce the numbers of the primary-prey species of wolves, wolf numbers should decline and potentially alleviate predation pressure on caribou, although pack density and kill rates should also be considered (Hayes et al. 2000). The time scale of such an approach to wolf reduction, however, will be longer than directly reducing wolves.

Many studies have looked at the relationship between wolf population dynamics and food supply, and wolf density is ultimately limited by food availability (Mech 1970, Van Ballenberghe et al. 1975, Keith 1983, Peterson and Page 1988). Wolf density and available ungulate biomass are highly correlated across studies (Keith 1983, Fuller 1989, Fuller et al. 2003) and wolf densities follow the trends in prey densities (Mech 1977, Peterson and Page 1988, Mech et al. 1998). A decrease in the density of primary prey should, therefore, result in a decrease in wolf density.

Food supply ultimately regulates wolf densities, but social behaviour is the proximate cause of wolves' numerical response to changes in food supply (Peterson and Page 1988). For example, breeding wolves can use their social status to restrict food from other pack members by feeding first and maintaining their own condition. This can lead to increases in malnutrition, and therefore decreases in survival probability, or can lead to increases in dispersal rates of younger wolves (Mech 1977, Packard 2003). Wolves also may be forced to "trespass" into other packs' territories in search of food, increasing the chance of confrontation and leading to increased intra-specific mortality. We predicted that a human-induced reduction in food supply for wolves should either increase mortality rates, increase dispersal rates, or both.

In fall 2006, with the support of local First Nations, guide outfitters and the hunting community, moose hunting quotas were increased in the Parsnip River Study Area (PRSA), BC, as recommended by the caribou-recovery-implementation plan (Seip 2005, Wilson 2009) with the expectation that moose density would decline. Diet analysis indicated that moose comprised ~80–90% of wolf summer diet by mass (see Chapter 3). We expected, therefore, that wolf density would be highly correlated with moose density. Our overall objective was to test the reduction in primary prey as a means of indirectly reducing wolf density, to ultimately increase mountain caribou survival in the area. We hypothesized that annual wolf mortality rate, annual dispersal rate, or both, would increase in the short term (within 2-5 years) following a reduction in moose densities. A change in either of these vital rates might provide evidence of a numerical response by wolves, because neither wolf, nor pack, densities could be monitored.

STUDY AREA

Moose in the PRSA were abundant and near carrying capacity before the increase in moose hunting quota (Walker et al. 2006). In 2005, the population was estimated at 3000 ± 440 individuals ($\overline{X}$ ± SE) with a density of 1.18 moose / km^2 and had changed little since the 1998 estimate (2600 ± 600 individuals and 1.1 moose / km^2; Heard et al. 1999). Changes in hunting quota were made in 2006 and the moose density declined considerably. By winter 2008–2009, total moose abundance and density were estimated at 1818 ± 297 individuals and 0.73 moose / km^2 (Steenweg et al. 2009). By 2009–2010, they were estimated at 1181 ± 151 individuals and 0.47 moose / km^2 (Gillingham et al. 2010). Although moose dominated wolf diet, beavers (*Castor canadensis*) are abundant in the valley bottoms of the study area and also comprised 2–10% of wolf summer diet (Chapter 3). Mountain caribou, on the other hand, are at low density in the study area, at ~0.048 / km^2 (CI: 0.042–0.064, 184 total;

Steenweg et al. 2009, updated as per D. C. Heard, unpublished data) and comprised 0.4–12% of wolf summer diet (see Chapter 3). Currently, caribou density is stable in the PRSA (Gillingham et al. 2010).

METHODS

Starting in 2006, wolves in the PRSA were caught by net gunning from a Bell 206 helicopter in winter (Altoft Helicopters, Prince George, BC) and by modified padded leg-hold trapping in summer (Braun Wolf Traps, Wayne's Tool Innovations Inc., Campbell River, BC). We immobilized wolves with Telezol and then fitted them with very high frequency (VHF) and Global Positioning System (GPS) radio collars (LRMT-3 and 4400S, respectively, Lotek Wireless Inc., Newmarket, ON) in accordance with the guidelines of the Canadian Council on Animal Care (2003). Wolves were monitored for mortality signals approximately once a month from fixed-wing aircraft (Guardian Aerospace, Vanderhoof, BC). When possible, mortalities were investigated in the field.

Survival rates were calculated using the staggered-entry, Kaplan-Meier procedure (Pollock et al. 1989) where survival $S(t)$ is calculated from the product of the survival rate estimate for all i intervals such that:

$$S(t) = \prod (r_i - d_i)/r_i$$

We estimated the annual survival as the product of all survival rates across months (i). The survival rate for each month (i) was calculated as the difference between the number of radio collars known to be active in the study area during each month (r_i) and the number of known radio-collar deaths during each month (d_i), as a proportion of r_i. This is essentially the proportion of collars that survived for each month i. Wolf radio collars that ceased to be heard during flights were right censored (i.e., no longer included in the analysis) as of the half-way date between the telemetry flights flanking when the collar signal changed (Hayes and Harestad 2000). The date of wolf mortality was similarly delimited.

We used Greenwood's (1926) formula to calculate the variance as suggested by Cox and Oates (1984), such that:

$$\mathrm{Var}[S(t)] = [S(t)]^2 \sum[d_i / (r_i (r_i - d_i))]$$

In order to estimate the 95% confidence intervals, we followed the suggestion of Pollock et al. (1989) and used:

$$S(t) \pm 1.96\ \mathrm{Var}[S(t)]$$

Resulting upper confidence intervals that were >1 were rounded to 1 because real survival rates cannot be >1. All survival rates were then converted to, and presented as, mortality rates (1 minus survival rate).

Dispersal rates can be calculated in largely the same manner as survival rates (Kenward 2001); we modified the staggered-entry, Kaplan-Meier procedure to estimate dispersal rates. Just as mortality rate equals 1 minus the rate at which tagged animals did not die (i.e., 1 minus survival rate), we calculated the dispersal rate as 1 minus the rate at which tagged animals did not disperse (i.e., 1 minus retention rate). In avian survival studies, radio-tagged animals with unknown fates (resulting from loss of the radio signal) are treated in 2 different ways to obtain 2 estimates of survival (Kenward 2001). A known survival rate only considers radio tags with known fates, such that radios with unknown fates are removed from analysis as of the date of their last signal (just as in the survival analysis above). In contrast, a minimum survival rate assumes all unknown fates are mortalities. This assumption is made because when a bird dies, the radio tag is often consumed along with the bird and is never recovered (Kenward 2001). Accordingly, we calculated a known dispersal rate as 1 minus the known retention rate while considering only radio collars with known fates. Unlike in avian studies, however, we did not assume that a missing collar indicated wolf mortality. With wolves, the loss of a radio signal is seldom associated with the death of the animal because radio collars are not destroyed when the wolf dies. Therefore, we considered the loss of a signal to be indicative of wolf dispersal for the minimum retention rate. We calculated a maximum dispersal rate as 1 minus the minimum retention rate, assuming any loss of signal was actually a dispersed wolf.

We compared wolf dispersal and mortality rates from our study area to data from a concurrent study in the South Peace Study Area (SPSA) located 60 km to the north-east of the PRSA (Dale Seip, BC Ministry of Forests, unpublished data). Wolf collaring in the SPSA (using the same VHF and GPS collar models) began in 2007 and the monitoring schedule of that project was very similar to the PRSA project. Monthly searches recorded mortality signals. Both studies used the same fixed-wing company and flights often coincided. In the SPSA study area, however, no changes were made to hunting quotas, thus allowing for this area to be a control, helping us understand normal rates of wolf dispersal and mortality.

Left censoring of each wolf's contribution to the staggered-entry, Kaplan-Meier analysis was marked at the first full calendar month of collaring (Figure 4.1), such that if the wolf was collared in the first half of the month, that month was included. If the wolf was collared in the second half of the month, the following calendar month was considered the first month collared. The right-hand limit of each timeline represents the calendar month in which the status of the collar changed (right censoring). If the exact date was unknown we used the date half way between the telemetry flights of when the wolf was last heard alive and when we received the first indication of a change in status.

Fates of collared wolves were categorized as one of the following: dispersal, unknown, mortality or alive. Dispersal was conclusive when collars with unknown fates were

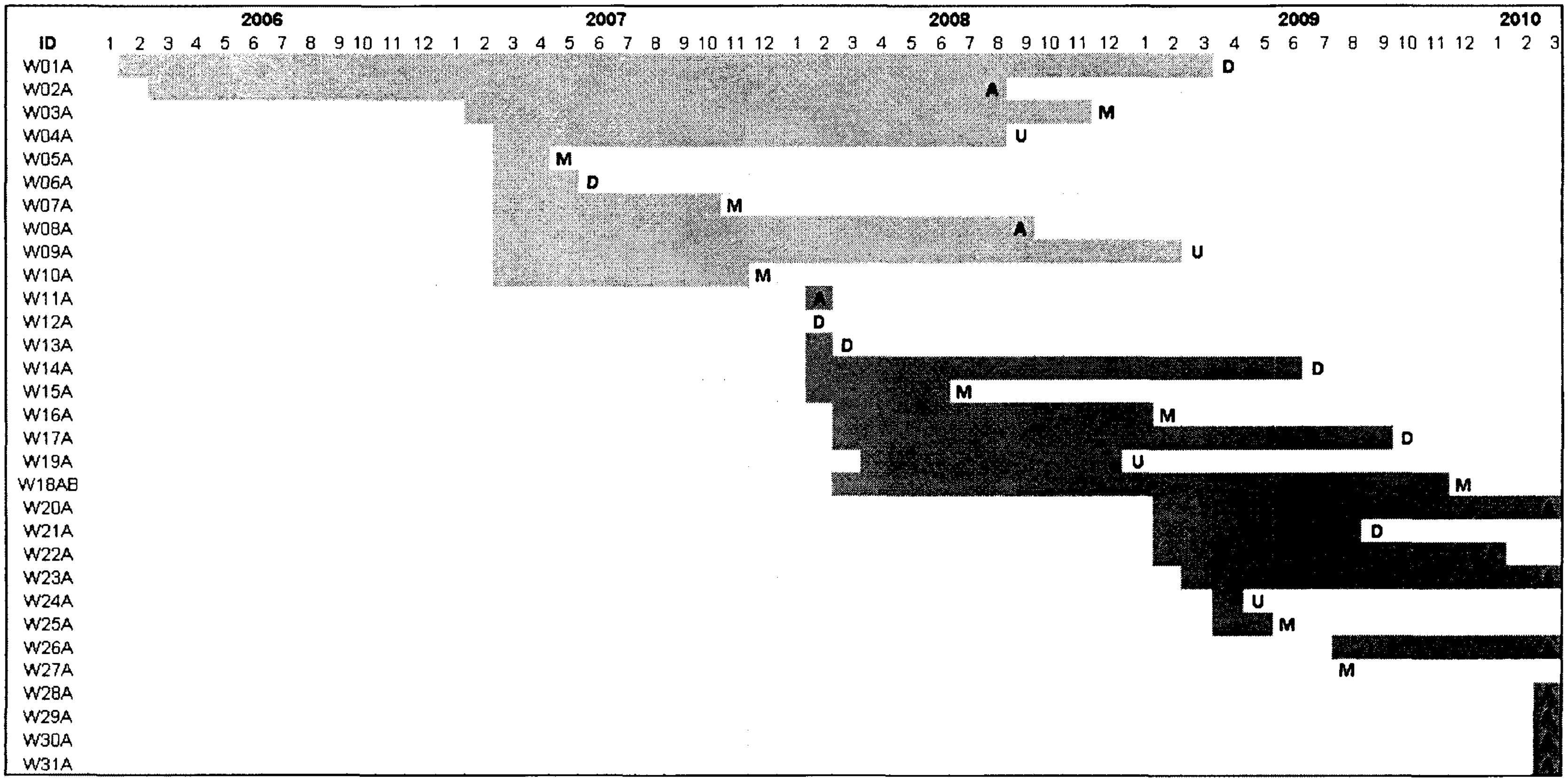

Figure 4.1 Collared durations for wolves captured in the Parsnip River Study Area, BC. Top heading consists of years and months by number. Beginning of shading represents collaring and shading continues until the collar fate changes or monitoring is discontinued. Letters at end of each timeline represents ultimate fate of collar; categories are: dispersal (D), unknown (U), mortality (M), or alive (A) when monitoring discontinued. See text for definitions of categories. All monitoring ceased 31 Mar 2010. Age at collar fate is presented in Appendix E.

recovered or heard outside the study area by another wildlife project in the area, or when the collar was returned by a trapper or hunter from a minimum of 50 km outside the PRSA. This definition of dispersal ensured that a wolf left the area impacted by the lower moose, rather than moving to, or establishing, an adjacent pack within the experimental area. Unknown fates were collars with a loss of signal and no subsequent recovery of the collar. Mortality was defined as wolf mortality within the study area following field investigation. The alive fate consisted of wolves that were alive when monitoring was discontinued for one of the following reasons: the collar was removed from the wolf, the collar battery failed on schedule, the wolf dropped the collar (from young wolves with small necks) or monitoring was terminated as the March 2010 end of study approached. Although data are presented until March 2010, annual mortality and dispersal rates were only analyzed for full years of wolf monitoring (2006–2009).

RESULTS

Thirty-one wolves were collared in each of the treatment (PRSA) and control (SPSA) study areas. Breeding status of wolves collared in both areas was not known but the average age of collaring was similar. In the treatment area, average age of collaring was 3 (SD: 1.6, range: 1–5.5) and in the control the average age at collaring was 3.4 (SD: 1.4, range: 1–5.5). Both study areas had similar tallies for mortality, unknown fates and alive at the end of the study, but more wolves dispersed from the treatment area (Table 4.1). Ten wolves died in each area from a variety of causes. In the treatment area, causes of mortality were: legally shot/trapped (4), kicked by moose (1), starvation (1), truck collision (1), recapture mortality (1), and unknown cause (2). In the control area (SPSA) causes of mortality were: legally shot/trapped (5), kicked by moose (1), killed by other wolves (1) and unknown cause (3).

Table 4.1 Summary of the fates of collared wolves in the Parsnip River Study Area, BC, 2007–2010 where moose numbers were reduced through an increase in hunting quotas (treatment), relative to concurrent study of collared wolves in the South Peace Study Area, BC, where no changes to hunting quotas were made (control). See text for definitions of fate categories and see Appendices D and E for ages of wolves.

Fate	**Treatment**	**Control**
Dispersal	7	2
Unknown	4	6
Mortality	9	10
Alive	11	13
Total	31	31

In the treatment area, 7 wolves dispersed with a mean age of 2.8 (SD: 1.5, range: 1–5.5), while in the control, 2 wolves dispersed with a mean age of 4.8 (SD: 1.1, range: 4–5.5). When wolves with unknown fates were included as dispersers, 11 wolves potentially dispersed from the treatment area ($\bar{X}$ age: 3, SD: 1.4, range: 1–5.5) and 8 potentially dispersed from the control ($\bar{X}$ age: 4, SD: 0.9, range: 2.5–5.5). Dispersal distances from the treatment area for known dispersers were approximately 50, 60, 120, 160, 220, 220, and 300 km, spanning all cardinal directions (see Appendix D). The dispersal distances from the control area were 250 and 320 km to the SE and SW, respectively. Of the 9 known dispersed wolves, 2 were heard alive by wildlife researchers in adjacent study areas, 5 wolves were shot or trapped legally, and 2 wolves have unclear histories. All 9 animals had fully functioning VHF-transmitters upon recovery. Dispersed wolves that were shot or trapped, lived for an average of 9 months (range 2–17) outside the study area before being killed (see Appendix D). The month of dispersal (and when the status of unknown collar-fates changed) was spread throughout the year, such that there was no seasonal trend in dispersal or collars going missing (Figure 4.1). The same was true for the control area.

Annual mortality and dispersal rates were also calculated for the first year of study in each area (Tables 4.2 and 4.3), but sample sizes were exceedingly low. Only 2 wolves were collared in each area during the first study year, leading to no confidence in these rate estimates. In the control area, both collared wolves in the first year went missing after a single month of monitoring. For all subsequent years, n was ≥ 10 wolves.

Annual mortality rates varied between 0.20 and 0.46 in the treatment area across years and remained at 0.43 in the control area during both years of study (Table 4.2). Known dispersal rates in the treatment area were between 0.11 and 0.45 and the maximum dispersal

Table 4.2 Annual mortality rates (95% confidence intervals in parentheses) for wolves in the treatment Parsnip River Study Area, BC, where moose numbers were reduced by about 50% between 2007–2009 and for wolves in the control South Peace Study Area, BC, where no changes to moose hunting quotas were made and moose densities were assumed to be unchanged.

Study Area		**Year**			
		2006	**2007**[a]	**2008**	**2009**
Treatment	Mortality rate	0	0.32 (0.02–0.63)	0.20 (0.00–0.45)	0.41 (0.10–0.73)
	n	2	10	12	10
Control	Mortality rate		0	0.43 (0.15–0.71)	0.43 (0.11–0.75)
	n		2	17	13

n = number of collared wolves within the study area during the year.

[a] Year following increased hunting quota in treatment study area.

Table 4.3 Annual dispersal rates (95% confidence intervals in parentheses) for wolves in the treatment Parsnip River Study Area, BC, where moose numbers were reduced by about 50% between 2007–2009 and for wolves in the control South Peace Study Area, BC, where no changes to moose hunting quotas were made and moose densities are assumed to be unchanged. Known dispersal rates only consist of known dispersed wolves for analysis and exclude collared wolves with unknown fates. Maximum (Max) dispersal rates assume collared wolves with unknown fates have dispersed.

Study Area	**Rates**	**Year**			
		2006	**2007**[a]	**2008**	**2009**
Treatment	Known Dispersal	0	0.11 (0.00–0.32)	0.17 (0.00–0.38)	0.45 (0.12–0.78)
	Max Dispersal	0	0.11 (0.00–0.32)	0.25 (0.00–0.49)	0.63 (0.35–0.90)*
	n	2	10	12	10
Control	Known Dispersal		0.5	0.00 (0.00–0.00)	0.08 (0.00–0.24)
	Max Dispersal		1	0.35 (0.11–0.59)	0.08 (0.00–0.27)
	n		2	17	13

n = number of collared wolves with in the study area during the year.

[a] Year following increased hunting quota in treatment area.

* indicates significant difference from 2007 treatment maximum dispersal rate and from 2009 control known and maximum dispersal rates (see text).

rates ranged from 0.11 to 0.63 (Table 4.3). In the control area, dispersal rates were lower, ranging from 0.00 to 0.08 and 0.08 to 0.35 for known and maximum dispersal rates, respectively.

Based on overlapping 95% confidence intervals, there was no statistical difference among mortality rates or known dispersal rates in treatment or control areas (Table 4.3). When n is less than 20 during any interval, i, used to calculate a final rate for time t, the staggered-entry, Kaplan-Meier survival rate estimate has poor precision (Pollock et al. 1989). Despite this lack of power, however, the 2009 maximum dispersal rate in the treatment area (0.63) was significantly different from both the 2007 maximum dispersal rate in the treatment area (0.11), and from the 2009 dispersal rate in the control area (0.08) based on non-overlapping confidence intervals (Table 4.3).

Of the 31 wolves captured in the PRSA, all except 4 were in good health at capture. Furthermore, 2 of the 4 unhealthy (i.e., very thin) wolves captured during winter 2007, survived 9 months each with collars on, and eventually succumbed independently to a vehicle collision and an unknown cause. Their unhealthy state at capture, therefore, did not seem to contribute to their eventual mortality. Another unhealthy wolf at capture was a skinny wolf pup collared in 2008; it dispersed after less than a week in the study area and survived a minimum of 2 more months. The final unhealthy wolf at capture was an emaciated female in summer 2009. She was at least 5 years old, had not produced pups that year, although she had in the past, and she died within a month of collaring due to starvation.

DISCUSSION

The staggered-entry, Kaplan-Meier survival analysis is common in wildlife radio-telemetry studies (Murray 2006). It allows for the inclusion of newly collared animals and animals with unknown or other non-mortality fates, up until the time the collared animal changes status (Pollock et al. 1989). The nature of dispersal data is similar to survival data, such that they are both time-to-event data (Kenward 2001) and, therefore, the advantages of using the Kaplan-Meier approach for survival analysis should be transferable to dispersal analysis. One obvious but important distinction, however, is that not all collared animals will at one point disperse, whereas they will all eventually die.

Through a meta-analysis of 19 published studies of hunted wolf populations with growth and mortality rates, Fuller et al. (2003) showed that growth rates of wolf populations were zero when annual mortality rates were around 0.36 ± 0.06. Although the mortality rates presented in our 2 study areas are based on small sample sizes and, therefore, have wide confidence intervals, they appear to be close to this normal level of mortality rates for hunted populations (Table 4.2).

In this study, we have no evidence for a change in mortality rate, but neither is there any evidence for any mechanism for an increase in mortality rate. Decreases in food availability can lead to increases in wolf mortality through either malnutrition or increased intra-specific strife (Mech 1977, Peterson and Page 1988). Neither of these scenarios seem likely in our treatment area. Of the 31 wolves captured in the PRSA, all except 4 were in good health at capture and 2 of these 4 did not likely die due to their condition (see results). As further evidence of the good health experienced by most wolves, 3 wolves whose bodies were intact upon mortality investigation in mid winter 2008 and 2009 were necropsied and all had fat reserves. Therefore, there is little evidence of a high propensity of malnutrition and even less evidence of an increase in malnutrition resulting from the declining moose density. In addition, although we have little on which to judge this evaluator, there is no evidence of an increase in inter-pack aggression. Mortality of one wolf in the SPSA was thought to be due to inter-pack aggression, but none of the known mortalities in the PRSA were associated with such behaviour. We conclude, therefore, that mortality rate probably has not changed following the increase in hunting quotas of moose.

Collars with unknown fates can be indicative of outcomes other than dispersal. As mentioned above, the destruction of the collar along with a wolf is unlikely, but collars do malfunction. In this study, different collar types (VHF and GPS) performed quite differently. For example, 2 wolves were spotted with GPS-collars one year after being collared, but with no radio signal (one in each study area). In addition, another GPS collar with no radio signal was located serendipitously in the PRSA on a frozen wolf lying in the snow 10 m away from the rest of the pack that was feeding on an adult moose. Necropsy later confirmed that this wolf succumbed to cranial wounds, likely inflicted by a moose kick days earlier. Clearly, these 3 wolf collars malfunctioned and their recorded fates were changed accordingly. All 3 collars were GPS collars, and all had varying degrees of damage to the battery cases that led to water corrosion. Despite these 3 collars that malfunctioned, it was much more common that wolves with unknown collar status were later confirmed to have dispersed. Nine of the 13 wolves initially with unknown fates were eventually confirmed to have dispersed, up to 320 km away from the study area. When recovered, all of these collars were functioning VHF collars, which are known to be typically hardier and longer lasting than GPS collars. Based on the observation that more wolf collars of unknown status were found to have dispersed than to have malfunctioned, and because 7 of the 10 remaining collars with unknown fates were VHF and not GPS collars, we believe our assumption that missing wolf collars are likely dispersed wolves, is reasonable.

Annual sample sizes (range 10–17) contributed to wide confidence intervals for both mortality and dispersal rates. Despite these wide confidence intervals, however, the 2009 maximum dispersal rate in the treatment area was higher than both the 2007 maximum dispersal rate in the treatment area, and the 2009 dispersal rates in the control area. Therefore, the dispersal rate in the treatment area seems to have increased in 2009 to a higher level than in previously years in the treatment area and higher than the control area. Furthermore, although not statistically significant, there is a trend for increasing dispersal rates over time in the treatment area.

Along with increased dispersal or mortality, decreased reproduction could also drive a numerical response by wolves, but this seems unlikely in this study area. Mech (1977) examined causes of wolf mortality following a decline in deer in Superior National Forest in Minnesota. Under food availability stress, wolf numerical response was caused by a progression of responses. First, pups showed signs of malnutrition, then breeders decreased reproduction and finally, increased intra-specific strife was documented as wolves entered territories of other packs in search of food. Mech (1977) concluded that breeding wolves prioritize their own health and reproductive ability over the nutrition of other pack members. Moreover, the relationship between reproductive output of wolves and available ungulate biomass is weak. A decline of 83% of the available ungulate biomass in central Alaska decreased the litter size of wolves by only 31% (Boertje and Stephenson 1992, Fuller et al. 2003). Although we have no data on reproductive rates, with only a 50–60% reduction in moose density in the PRSA, a large reproductive response would not be expected.

Dispersal, like mortality, is a natural process in wolf populations; Mech and Boitani (2003) even described wolf packs as "dispersal pumps". Dispersal is essentially the outcome of a successful litter being reared by a breeding pair, and results from the requirement of younger wolves to leave the pack. In this study, more younger wolves dispersed, but wolves of all ages dispersed from both control and treatment areas, and the average age of dispersal was similar when including collars with unknown fates.

Dispersal helps fulfill the need to find a mate and reproduce and can be triggered by food shortage, social aggression or social disruption. In the PRSA, there is evidence that one pack disbanded after the male breeder was killed in a truck collision. Subsequently, the only remaining collared wolf in that pack then dispersed within 3 months and there was no evidence of a pack occupying that territory for the following 2 years. We have no information on the movements of wolves following dispersal, or whether or not wolves that dispersed were successful in finding a mate and territory. For example, one wolf, for which the collar battery had already died on schedule, was eventually shot in the study area 20 months with after having dispersed. Information on movements after dispersal is needed to understand the ultimate successes of dispersing wolves.

Previous work suggests that dispersal is the main mechanism for how wolf density is regulated by food supply (Fuller 1989, Bergerud and Elliot 1998, Hayes and Harestad 2000). Normal rates of dispersal across wolf populations range between 10–40% per year (Fuller et al. 2003). Not only is the 2009 maximum dispersal rate in the PRSA treatment area significantly higher than estimates made in earlier years and from the control area, this dispersal rate is also the only rate that is higher (0.63) than what is common for wolves (see Table 4.3). This implies that following the decrease in moose density, the wolf response was a strong increase in dispersal rate. Although a better understanding of wolf and pack densities in the study area would have been able to confirm the implications of such an increase in dispersal rate, it is likely that such an increase will lead to a numerical response.

Increased moose-hunting quotas, and, therefore, the start of the decline in moose numbers, began in fall 2006. The increased dispersal rate of wolves in 2009 represents the response of wolves 2–3 years following this change in quota. A lag time of 2–3 years in the numerical response of wolves to declining prey populations is common in studies of naturally declining prey densities, although a lag as long as 5–7 years has also been documented (Gasaway et al. 1983). For example, following declines in deer in Minnesota initiated by a severe winter in 1968–1969, wolf densities began to decline only in winter of 1970–1971 (Mech 1977). In Denali National Park, Alaska, a 2-year lag was apparent between the decline in wolf density and the preceding decline in caribou density caused by a severe winter that increased vulnerability of caribou to wolf predation (Mech et al. 1998). On Isle Royale, Michigan, wolf numbers also were shown to lag behind a declining moose population by 2 years in a more or less cyclical manner (Peterson and Page 1988). Therefore, this 2–3 year lag in dispersal rate of wolves following moose reduction in the PRSA, further supports that an increased dispersal rate may indicate a numerical response by wolves.

MANAGEMENT IMPLICATIONS

The original objective of our research was to document a numerical response in wolves more directly, by tracking average winter pack size and number of packs with the aid of collared wolves. With every collar that disappeared, however, it became more difficult to track packs and more important to understand rates of wolf dispersal from the study area. With every collar that was recovered, it became more possible to track dispersal. Collars were often recovered 100s of km away and up to 31 months following loss of the radio signal. Future research on the biological mechanisms of wolf numerical response would benefit from the use of GPS collars with satellite uploads of GPS locations that could help rule out the malfunctioning of collars when collar signal is lost and would allow for a more effective method of tracking wolf dispersal.

A numerical response seems likely with this increased dispersal rate. Increasing the moose-hunting quota, therefore, seems to be an effective approach to reducing overall wolf density. Although the killing of wolves in the short term may be politically acceptable in this area (Seip 2005, Wilson 2009), indirect wolf reduction appears to be a good alternative to direct culling of wolves and would better conform to current values in the rest of BC. Reducing the amount of early-stage forests that support high moose densities is required for any long-term reduction in wolf numbers (Seip 2008), but a reduction in moose density may help reduce wolf predation on caribou in the medium term.

Aiding caribou recovery is the ultimate motivation for reducing wolf density in the PRSA. The effect of this manipulation on caribou survival may, however, not only depend on wolf density, but also on pack density and on kill rates of packs. In other words, a wolf numerical response does not guarantee a response in kill rate on caribou. Although this study was not able to estimate pack density or kill rates of packs, the experimental approach being used here to evaluate the implications for caribou recovery will eventually allow for an account of the total effect that a reduced moose population will have on the caribou population. Therefore, in order to fully evaluate this management strategy, monitoring of caribou densities (which are currently stable in the PRSA) needs to continue.

CHAPTER 5: CONCLUSION

Throughout different aspects of this study, I examined some of the biological considerations of trying to manage an endangered species in a system characterized by apparent competition. Understanding wolf movements, diet, and numerical response is critical to assessing the feasibility of promoting caribou recovery through increased moose-hunting quotas.

Refuges may be necessary to allow the persistence of secondary prey species (Sinclair et al. 1998). Here, I looked at fine spatial and temporal movements to build upon previous work studying when wolves select for habitat that caribou select for, in order to understand when wolves are potentially hunting for caribou. I provided evidence in Chapter 2 that mountain caribou are spatially separated from moose and wolves to some extent, but overlap does occur, especially during snow-free months. The use of elevation by wolves largely mirrors that of moose (Chapter 2), and this may cause wolves to move into caribou-inhabited areas more frequently during summer, decreasing the effectiveness of elevational separation. Wolf diet is predominantly moose (see Chapter 3); wolf densities, therefore, are more likely to be coupled with moose density than with caribou density. Given the spatial overlap between wolves and caribou, and that wolf and moose densities are coupled with only weak feedback from caribou densities, an asymmetric relationship, characterized by apparent competition between moose and caribou, has likely led to the endangerment of caribou in this population, like in many others (DeCesare et al. 2010).

Although caribou are of low importance to wolf diet, wolves are common predators of caribou. In the PRSA, the caribou population is small, ~180 in total (Gillingham et al. 2010). Low levels of predation, therefore, could still be critical to the viability of the caribou population. Cluster analysis indicated that the number of caribou killed by wolves in the PRSA could range as high as 2–5 caribou / pack / year not including calves. With 4–5 packs in the study area with home ranges that overlap caribou range (Gillingham et al. 2010) ~8–25 caribou could be expected to be killed per year. This estimate is similar to wolf kill rates on VHF-collared caribou reported by Gillingham et al. (2010). If the survival rates of VHF-collared adult female caribou are representative of the total population, then the mortality rate of caribou would range from 0–30 caribou killed by wolves per year, also similar to estimates from the wolf movement analysis above. Given the low rates of recruitment, this level of mortality could cause declines in this caribou population.

Although not conclusive, forays into caribou habitat and the remains of caribou in wolf scat were both rare during this period of declining moose, suggesting that a shift by wolves to killing more caribou did not occur. Furthermore, because of the low density of caribou and small size of other prey in wolf diet, it would be difficult for wolves to shift their diets to make up for the lost biomass as moose decline. This simple, moose-dominated diet, therefore, makes the PRSA an ideal location to test decreasing moose densities as a viable method for caribou recovery.

I observed that wolves eat mostly moose, even while moose densities were in decline. According to many studies on moose-wolf dynamics, a decrease in moose led to a numerical decline in wolf numbers (Peterson et al. 1984, Messier and Crete 1985, Fuller 1989, Mech et al. 1998). I showed evidence for dispersal as a mechanism for such a numerical response by wolves although breeding animals were not likely the dispersers. To confirm this, however, additional information would be required regarding changes in the number of packs, in the size of packs, or in the over-all wolf density in the PRSA. What I did see was that wolf dispersal rate seems to have increased in the study area. Dispersal is the mechanism through which wolves are thought to be regulated by food supply (Fuller 1989, Bergerud and Elliot 1998, Hayes and Harestad 2000). A confirmation of increased wolf dispersal, however, would benefit from the use of GPS collars with satellite uploads of GPS locations, which would avoid any bias associated with losing track of collars that leave the study area.

If wolves are declining, their simple diet may make it possible to predict wolf response to the decrease in moose, through the known relationship between wolf and ungulate biomass (Keith 1983, Fuller 1989, Fuller et al. 2003). Moose in the PRSA declined from 1.18 to 0.47 moose / km^2 and caribou densities remained relatively stable at about 0.048 / km^2 (Steenweg et al. 2009, updated as per D. C. Heard unpublished data). Using the linear equation ($y = 3.3x + 3.5$) where y is the ungulate biomass index and x is wolf density, I would expect a decline in the ungulate index from 7.2 to 2.9 (see Fuller et al. 2003 for conversions). This would then translate to a halving of the wolf density.

The decreased moose density may have been initiated by increased hunting quotas, but hunter kill rate does not account for the magnitude of the changes observed in moose densities (D.C. Heard, unpublished data). It is more likely that the lag in the numerical response of wolves (see Chapter 4) caused moose density to decline further; such lag responses are common in wolf-prey systems (Mech 1977, Peterson and Page 1988, Mech et al. 1998). To maintain low wolf densities, it is important to retain low moose densities (Gasaway et al. 1983, Boertje et al. 1996, Bergerud and Elliot 1998, Hayes et al. 2003). This may become difficult, however, if hunters continue to perceive that their success rates are too low (R.W. Steenweg, personal observation). The ultimate success of this approach to caribou recovery may depend on such social factors, if the PRSA loses its reputation as a good moose-hunting area, although this should not yet be the case, as moose densities remain relatively high (~0.47 / km^2).

In the PRSA, as in the current literature on mountain caribou, little is known about caribou calf mortality and caribou recruitment remains low (Gillingham et al. 2008, Steenweg et al. 2009, Gillingham et al. 2010). In some systems, wolves are common predators of caribou calves (Adams et al. 1995, Gustine et al. 2006*a*) and when wolves are reduced, caribou recruitment increases 2–5 fold (Bergerud and Elliot 1998). Currently, understanding predation on calves remains difficult. Unlike in ranges of the northern ecotype of caribou, which calve in more open areas (Gustine 2005), mountain caribou calve in subalpine treed areas, making the capture or observation of caribou calves impossible. Increased fix rates for wolf GPS-collars when caribou are calving might be one approach for further investigation. Currently, kill sites for small prey remain difficult to discern from GPS-cluster data to determine causes of neonatal mortality (Merrill et al. 2010). The addition of caribou calves to isotope diet analysis may shed some light on summer predation of calves by wolves, but in general, calf mortality remains a challenge for mountain caribou research.

Even if an increase in the dispersal rate of wolves leads to a wolf numerical response, both pack density and kill rates of packs may be more important for total kill rates on caribou than overall density of wolves (Hayes et al. 2000). The experimental approach being used here to evaluate the implications for caribou recovery will eventually allow for an account of the total effect that a reduced moose population will have on the caribou population. The ultimate evaluator for the success of using increased moose-hunting quotas to recover caribou, therefore, will be an increase in caribou abundance. Caribou vital rates have responded positively to decreases in wolf density in other areas (Bergerud and Elliot 1998, Hayes et al. 2003). Currently, the PRSA caribou herd remains stable (Gillingham et al. 2010), while other mountain caribou herds continue to decline. To confirm that this is a viable approach to caribou recovery continued monitoring of caribou abundance and survival is needed.

In summary, my findings suggest that increasing moose harvest may be a viable approach to caribou recovery, but a full evaluation of this strategy will require the implementation of the following recommendations. Firstly, the moose population needs to be maintained at a low density in order for this experiment to run for a sufficient amount of time to test this approach to caribou recovery. Secondly, although I have shown some evidence of a numerical response by wolves, wolf dispersal would be better monitored using GPS collars with satellite uploads of GPS locations. Finally, a numerical response by wolves may allow the caribou population to persist, but continue monitoring of caribou survival and abundance is critical, because the ultimate goal of this experiment is a positive effect on the caribou population.

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APPENDICES

APPENDIX A: Characterization of vegetation classes

Table A.1 Abundance and description of the vegetation classes created to classify the landscape for resource selection models of wolves in the Parsnip River Study Area, BC.

Vegetation Class	% of Study area	Description
Alpine	1%	High-elevation areas with no vegetation (i.e., rock, snow, ice)
Coniferous-high	20%	Higher elevation conifer stands (>1050 m), mostly dominated by sub-alpine fir (*Abies lasiocarpa*), also spruce hybrid (*Picea englemanni x glauca*)
Coniferous-low	40%	Lower elevation conifer stands(≤1050 m), mostly hybrid white spruce (*P. englemanni x glauca*) and sub-alpine fir (*A. lasiocarpa*), some lodge-pole pine (*Pinus contorta*)
Non-vegetated	1%	Areas with little-to-no vegetation such as shore edges and roads (but not rock and ice)
Open-vegetated-high	4%	Alpine meadows dominated by herbs and evergreen shrubs (e.g., *Empetrum nigrum, Cassiope spp.)*
Open-vegetated-low	9%	Herb-domintated areas such as recent cutblocks and low-elevation meadows
Shrub-deciduous-high	5%	Avalanche chutes (*Alnus spp., Salix spp.*) and sub-alpine shrubby areas (mainly *Arctostaphylos sp, Salix spp., Vaccinium spp.*)
Shrub-deciduous-low	13%	Shrub-dominated riparian areas and medium-aged cutblocks (*Alnus spp., Salix spp.*), and deciduous stands (*Betula papyrifera, Populus tremuloides, P. balsamifera*)
Water	2%	Open water areas such as large rivers and lakes
Wetland	5%	Moss-dominated areas such as bogs

APPENDIX B: Preliminary scat analysis results

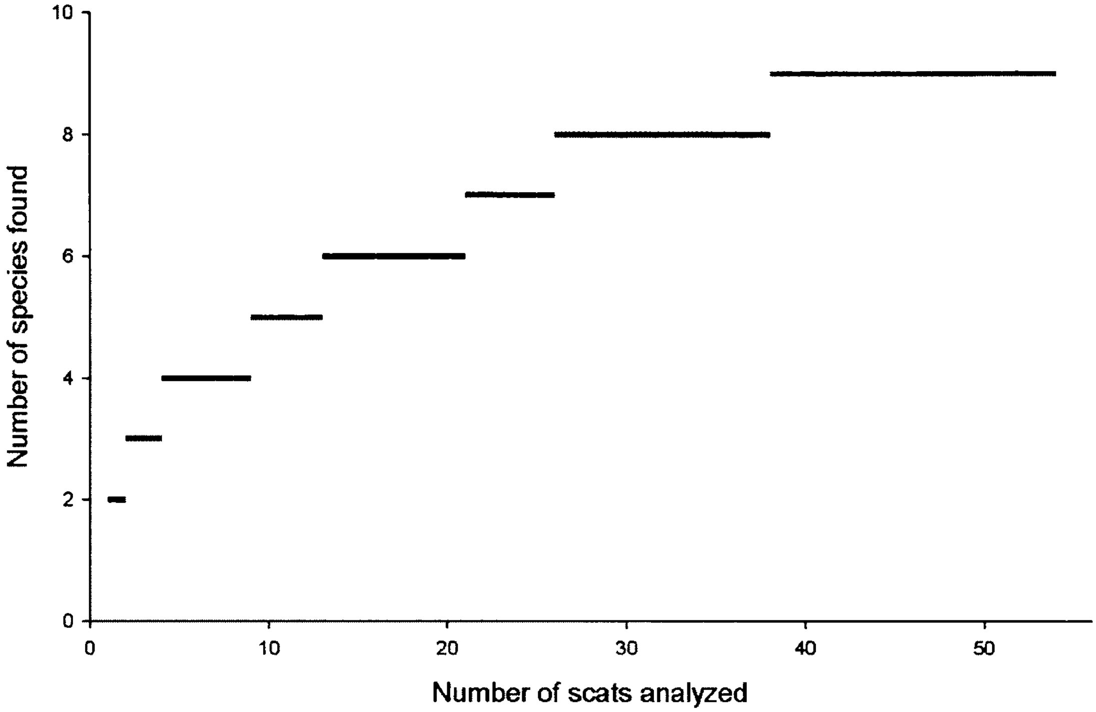

Figure B.1 Cumulative number of species identified in wolf scats during preliminary analysis of scats collected in the Parsnip River Study Area, BC 2008–2009. Note that after 30–40 scats, the number of new species starts to plateau as per a typical species-effort curve (Fisher et al. 1943).

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APPENDIX C: Where do wolf scats come from? On differences among approaches to scat collection

Through our work on wolf diet (see Chapter 3), it became apparent that a broader discussion is needed regarding scat collection protocols. Scat analysis was pioneered in Alaska by Murie (1944) and remains the most widely used method to quantify wolf diet. As a result, wolf diet has been quantified in every corner of their range, from Arizona to Greenland, Spain to Mongolia, and back to north-western Alaska (e.g., Merkle et al. 2009, Marquard-Peterson 1998, Barja 2009, Van Duyne et al. 2009, Stephenson and James 1982, respectively). Many accuracy issues and biases have been addressed throughout the wide application and long history of scat analysis, but no research has addressed how results may differ, depending on where scats are sampled.

One of the first biases associated with scat analysis addressed in the literature, is the over representation of small prey items and under representation of large prey items in wolf scats, which occurs because of the surface to volume ratio. This ratio is proportional to the amount of a prey that is indigestible and digestible (i.e., hair/bone and flesh) (Mech 1966, Carbyn 1974). Large prey, for example, produce a large number of scats that have little observable remains (hair, bones, etc.) because of the large number of meals that constitute only flesh (muscle, viscera, etc). This bias has arguably been resolved by converting the results of scat analysis from frequency occurrence to biomass consumed, which is more ecologically relevant (Klare et al. 2011). The conversion is possible by using linear relationships calculated from feeding trials with captive wolves (Floyd et al. 1978, Weaver 1993, Ruehe et al. 2003). Another concern with scat analysis is discerning among scats of canid species. In areas where wolf ranges overlap with other canids, researchers have developed protocols to distinguish between wolf and coyote scats (Weaver and Fritts 1979) and between wolf and fox scats (Marucco et al. 2008). In addition, the reliability of observers' abilities to distinguish among species during microscope analysis has been questioned (Fritts and Mech 1981, Ciucci et al. 1996, Spaulding et al. 2000).

Scats are distributed non-randomly on the landscape and random samples can be difficult to collect. Walking transects is one method of random collection (e.g, Darimont et al. 2008). Convenient sample methods include collecting scats from dens (e.g., Meriggi and Lovari 1996) or on roads (e.g., Barja 2009). We reviewed 58 articles, books, reports and theses (hereafter, simply referred to as articles), which used scat analysis to characterize wolf diet to determine the methods that were most commonly used (Table C.1). These articles were collected using Web of Science searches and from Peterson and Ciucci (2003:130).

Through our review of 58 articles that report the results of scat analysis to characterize wolf diet, it became apparent that we used the 2 most common methods for scat collection: from homesites and roads. What also became apparent is a prevalence of poor, or simply a lack of, sampling methods about the analysis of wolf scat. In 16% (9/58) of articles, the methodology of how scats were collected was either opaque or completely absent. When sampling method was described, scats were collected from homesites in 55% (27/49) of articles and collected from roads in 63% (31/49) of articles.

Ideally, scat should be collected using a random-sampling regime, such as walking transects, which was used in 8% (4/49) of articles that described their methodology. This method, however, is time-intensive, and therefore it is often desirable for scat collection to be directed to areas of higher scat concentration such as dens (Meriggi and Lovari 1996), on roads (Barja 2009), or where wolves are known to have been recently (e.g., through back-tracking in snow).

Table C.1 List of 58 reviewed articles, books, reports and theses that reported results of scat analysis to characterize wolf diet and the methods provided to collect scat.

Scat collection method used (total count)
[1]Homesite (27)
[2]Road/trail (31)
[3]Transects (4)
[4]Tracking (12)
[5]Carcass/kill site/GPS cluster (5)
[6]Opportunistic (10)
[7]Unclear (9)

Allison 1998[1,2,4,5]
Andersone and Ozolins 2004[7]
Ansorge et al. 2006[7]
Ballard et al. 1987[1]
Barja 2009[2]
Bergerud et al. 1984[3]
Bjorge and Gunson 1983[7]
Carbyn 1974[1,2,4]
Carbyn 1980[1,2,4]
Ciucci et al. 2004[2]
Darimont et al. 2004[2,6]
Darimont et al. 2008[3]
Derbridge 2010[1,2,6]
Frenzel 1974[2]
Fritts and Mech 1981[1,2]
Fuller 1989[1,2]
Fuller and Keith 1980[1,2]
Gade-Jorgensen and Stagegaard 2000[2,4,6]
Gazzola et al. 2005[7]
Heard and Williams 1992[1]
Huggard 1993[1,2,4,6]
Huitu 2000[2,4]
James et al. 2004[1,2,6]
Jedrzejewski et al. 1992[7]
Jedrzejewski et al. 2002[4]
Jhala and Giles 1991[7]
Kelsall 1957 (as cited by Pimlott 1967)[1]
Kuyt 1972[1]
Latham 2009[1,4,5]
Liu and Jiang 2003[4]
Marquard-Peterson 1998[1,6]
Marucco et al. 2008[4]
Mattioli et al. 1995[3]
Merkle et al. 2009[1,2,6]
Meriggi et al. 1996[3]
Messier and Crête 1985[2]
Milakovic 2008[1]
Müller 2006[1,2,5]
Murie 1944[1,2,6]
Nores et al. 2008[7]
Olsson et al. 1997[2]
Peterson et al. 1984[1,6]
Potvin et al. 1988[2,4,5]
Reed et al. 2006[1,2,4,5]
Salvador and Abad 1987[2]
Scott and Shackleton 1980[1,2]
Shelton 1966[2]
Sidorovich et al. 2003[2]
Spaulding et al. 2000[1]
Stephenson and James 1982[1]
Theberge and Cotrell 1977[1]
Theberge and Theberge 2004[1,2]
Thompson 1952[2]
Thurber and Peterson 1993[2,7]
Tremblay et al. 2001[2]
Van Ballenberghe et al. 1975[1,2]
Van Duyne et al. 2009[6]
Voigt et al. 1976[7]

To test if there was a difference in the results from different scat-sampling methods used in our study (homesite versus road collection, see Chapter 3), we used the G-test (Sokal and Rohlf 1994) in STATA (Stata Corporation, v9.2, College Station, TX). To meet assumptions of group-expected frequencies, we dropped 3 uncommon items from the analysis (marmot, unknown canid and unknown bird) and grouped prey items into 4 categories (adult ungulate, calf ungulate, beaver, and small mammal).

Comparing results from the 2 scat-sampling techniques, some important differences were evident. All classes of ungulates calves (moose, caribou, elk and unknown) were more common in homesite scat samples, as was beaver (Figure 3.1). Adult ungulates (moose and unknown ungulates, but not caribou) were more common in road scats. Sciuridae and muridae were also more common in road scats. After grouping the scats into 4 broader categories of adult ungulate, calf ungulate, beaver, and small mammals (Table C.2), the results from homesite and road sampling were significantly different ($\chi^2_3 = 49.4116$, $P < 0.001$).

The difference in results between homesite and road scat-collection approaches is likely due to a combination of local prey availability, the temporal window of the sampling method, and movement ecology of wolves in different areas. Researchers in Algonquin Park, Ontario, reported a significantly higher frequency of beaver in scats at homesites than in other areas of a pack's home range (Theberge et al. 1978). This difference was also present in the data from wolves in Minnesota (Van Ballenberghe et al. 1975, extrapolated from Tables 3 and 6). Theberge et al. (1978) attributed this difference to high densities of beaver lodges near wolf dens, and this situation may be analogous in the PRSA, where wolf homesites are located in valley bottoms and riparian areas are wide with many ox bows, creating lots of habitat for beavers. Local availability would not in itself constitute a bias because wolves

Table C.2. Frequency occurrence of prey groups found in wolf scat, as a function of sampling technique in the Parsnip River Study Area, BC, 2008–2009.

	Sampling method		
Group	**Homesite**	**Road**	**Total**
Adult ungulate	25	64	89
Calf ungulate	50	23	73
Beaver	23	8	31
Small mammals	2	18	20
Total	100	113	213

may be focusing on this species due to its local availability, but the following simplified consideration of diffusion may help explain this bias.

When examining data from Global Positioning System (GPS) collared wolves (see Chapter 2), it became clear that wolves spend a lot of their time far from homesites and, therefore, are not simply consuming prey that is locally available. Large prey are often fed upon in multiple bouts, with wolves resting or returning to homesites between feeding bouts (Peterson and Ciucci 2003). Many scats from kills far from homesites are likely to be deposited while resting near those kill sites or while traveling back and forth to the homesite and are thus not being deposited at the homesites. On the other hand, prey killed near a homesite will likely have most of the scats produced from that kill deposited at the homesite because of the reduced travel time and possible choice of the homesite for resting. Therefore, scats from homesites could be biased towards kills made closer to homesites and against kills made far away that require long travel distances and result in increased chances that wolves rest between eating bouts before returning to the homesite.

Researchers in Greenland also reported a significant difference between scats collected from dens and elsewhere in the home range, and attributed this to the seasonal availability of a vulnerable prey species (Marquard-Peterson 1998). Geese (*Branta leucopsis* and *Anser brachyrhynchus*) were frequently identified in scats at dens of one wolf pack during 2 years of sampling (40% frequency occurrence). The authors emphasized that the denning season corresponded to when these geese were undergoing an annual molt that rendered them flightless and more vulnerable to predation for 3–4 weeks.

Similarly in the PRSA, as in all other areas where wolves prey heavily on ungulates, calves that are born in late-spring to early-summer comprise a new flush of available food for wolves (Mech and Peterson 2003). In Alaska, wolves largely switch from adults of moose and caribou to calves, starting in May, and calves remain a large proportion of the diet until August (Mech et al. 1995). Likewise, Theberge and Theberge (2004) found that the presence of deer fawns in wolf diet peeked in June and decreased thereafter. Wolves may consume calves in proportion to their availability and the declining presence in diet is due to lower availability (Ballard et al. 1987).

In the PRSA, calves of moose, elk, caribou, and unknown ungulate were all more common in scats from homesites than from roads, whereas adults of moose and unknown ungulate were more common in road scats. Based on GPS-collar data, we know homesite scats represent a May-July diet, and based on sampling protocol, road scats represent June to early-October diet. Therefore, the seasonal flush of calves available to wolves may be captured differently, depending on the temporal window of the sampling method used, such that the later sampling window of the road scats represents a later proportion of this seasonal abundance.

Another important concern regarding the sampling window is how our ability to discern between hairs of calf and adult ungulate changes seasonally. The time period during which researchers feel comfortable distinguishing between the 2 age groups for North American ungulates varies across species, regions and studies. Some authors report calves present in scats until the end of August (Thompson 1952, Messier and Crete 1985, Theberge and Theberge 2004), others until the end of September (Pimlot 1967, Scott and Shackleton 1980), while others still, report proportions of calves in diet until the end of October (Peterson et al. 1984, Ballard et al. 1987). Following Bubenik's (1998) claim that most moose calves should have completed their summer molt from calf hairs to a winter coat of guard hairs and under-fur by mid-September, the last month of our 4.5-month sampling window for road scat (June to Mid-October, see Chapter 3 methods) may include scats with calf hair that is no longer distinguishable from adult hairs.

Another source of bias to consider when comparing homesite and road scat collection methods involves speculation on wolf movement and hunting ecology. Scats collected on roads contained a much higher proportion of scats from small mammals like hares, sciuridae and muridae (Figure 3.1). Small mammals may constitute prey items that are not necessarily hunted in great numbers given their small size, low percent digestibility, and therefore, little reward for effort. Rather, they are likely opportunistically consumed when encountered while traveling and hunting, and are not large enough to return to the homesite to feed to pups. We speculate, therefore, that roads scats, which are deposited where wolves tend to travel, contain more small mammals than scats from homesites because they are opportunistic meals. If small mammals were available in high numbers and a common food source for wolves during summer, we would expect homesites scats to contain more remains of small mammals (Figure 3.1).

Some authors have noted a difference between the results obtained from scats collected in different areas of wolf home ranges (Theberge et al. 1978, Scott and Shackleton 1980, Marquard-Peterson 1998), but there is seldom recognition by researchers of the biases associated with the chosen collection method. We have shown here that the 2 most common collection approaches can have associated biases and can give different results. Therefore, when scats are collected by numerous methods and clumped together to present a single estimation of wolf diet, a practice prevalent in 37% (18/49) of the articles reviewed, this bias may be weighted towards different methods. Furthermore, the term "opportunistic" was used in 20% of the articles (10/49) as the primary or additional scat sampling method and this convenience sampling could similarly bias results.

We also note that 10% (5/49) of articles included scats from kill sites, GPS clusters or carcasses. From the earliest study on wolf-scat analysis, Murie (1944:52) alluded to the potential biases associated with how scats are collected. In 1939, Murie followed wolves in Alaska for the entire summer, and stated that "[I] spent much time in search for remains for sheep carcasses and skulls, so covered a great deal of territory where wolves had fed on sheep. As a result, I found many scats at and near the carcasses and these naturally contained sheep remains". It seems necessary to reiterate these concerns and to extend them to biases in other scat collection methods. We conclude that as a minimum, a more clear description of sampling method should be presented and that an acknowledgement of potential biases associated with various sampling regimes should be included in any discussion of wolf-diet analysis based on scats.

Diet analysis is the most common form of wolf research (Peterson and Ciucci 2003). This discussion highlights some of the potential biases associated with different scat-sampling methods. Bayesian isotope analysis with local prey samples may provide one method for dealing with these biases by integrating the results from multiple scat sampling methods and considering them all equally valid samples of wolf diet (see Chapter 3 methods). This approach also could potentially incorporate results of scat analysis with more current isotope techniques and provide a synthesis of various methodologies into a single estimate of diet proportions (Semmens et al. 2009).

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APPENDIX D: Characteristics of dispersed wolves

Table D.1 Characteristics of collared wolves known to have dispersed from the Parsnip River Study Area, BC (treatment) and the South Peace Study Area, BC (control) during a reduction in moose densities following an increase in moose hunting quota in the treatment area. Mort = mortality.

Study Area	**Wolf**	**Distance (~km) and direction**	**Area recovered**	**Last known fate**	**Est. date of dispersal**	**Died/ Last heard alive**	**Difference (months)**	**Age at dispersal**[a]
Treatment	W06A	160 SE	McBride	Mort - trapped	2007-06-28	2008-02-04	7	2
	W12A	60 NW	North of MacKenzie	Alive	2008-02-08	2009-07-01	17	1
	W13A	300 S	Spahats Falls	Unclear[b]	2008-03-01	2010-10-01	31	2
	W01A	220 NW	NW of Germansen Landing	Mort - shot	2009-04-29	2009-11-15	7	5+
	W14A	120 SE	Goat River	Mort - trapped	2009-07-02	2010-12-02	17	4
	W21A	220 SE	Tete Jaune	Mort - shot	2009-09-11	2009-11-22	2	2
	W17A	50 SW	Alfred Lake	Mort - shot	2009-10-10	2010-10-03	12	3
Control	W001	250 SE	Jasper Park North Boundary	Unclear[c]	2007-04-01	2009-09-01	29	4
	W013	320 SW	Houston	Mort - shot	2009-05-01	2009-11-01	6	5+

[a] Age is in years; based on estimate of age at collaring (see Appendix E), plus additional time collared during study; 5+ refers to 5 or greater.

[b] Collar returned with location but no history of the fate of the wolf.

[c] Collar heard on mortality but never retreived.

APPENDIX E: Characteristics of all collared wolves

Table E.1 Characteristics of all collared wolves in the Parsnip River Study Area, BC

ID	Collar type	Date activated	Sex	Age at collaring	Color	Pack	Fate	Age at Fate
W01A	VHF	27-Jan-06	M	5+	Black	Reynolds	Dispersed, shot	5+
W02A	VHF	13-Mar-06	F	N/A	Black	Tacheeda	Collar Dropped	N/A
W03A	VHF	9-Feb-07	M	N/A	Black	Tacheeda	Mort, Shot	N/A
W04A	VHF	26-Feb-07	M	N/A	Grey	Reynolds	Unknown Fate	N/A
W05A	VHF	12-Mar-07	F	N/A	Black	Arctic	Mort, Shot	N/A
W06A	VHF	12-Mar-07	M	2	Grey	Arctic	Dispersed, Trapped	2
W07A	VHF	12-Mar-07	F	1	Black	Hominka	Mort, Unkn Natural	1.5
W08A	VHF	12-Mar-07	M	5	White	Anzac	Collar Dropped	5+
W09A	VHF	12-Mar-07	M	1	Black	Anzac	Unknown Fate	4.5
W10A	GPS	13-Mar-07	M	5+	Blue	Hominka	Mort, Veh. Collision	5+
W11A	GPS	22-Jan-08	F	2	Black	Arctic	Collar Dropped	1.5
W12A	GPS	22-Jan-08	M	1	Black	Hominka	Dispersed	1
W13A	VHF	13-Feb-08	F	2	Black	Arctic	Dispersed	2
W14A	VHF	13-Feb-08	F	2	Black	Arctic	Dispersed, Trapped	4
W15A	VHF	13-Feb-08	F	3	Grey	Anzac	Mort, Unkn Natural	3
W16A	GPS	26-Feb-08	M	4	Light Brown	Arctic	Mort, Moose Kick	5
W17A	VHF	26-Feb-08	F	1	Grey	Table	Dispersed, Shot	3
W18A	GPS	26-Feb-08	M	5+	Grey-Brown	Table	Recollared	5+
W18B	GPS	17-Jan-09	M	5+	Grey-Brown	Table	Mort, Capture-related	5+
W19A	GPS	28-Mar-08	M	1	Black	Anzac	Unknown Fate	2
W20A	VHF	21-Jan-09	M	2	Grey-Brown	Arctic	Mort, Shot	3
W21A	VHF	6-Feb-09	M	1.5	Dark Grey	Arctic	Dispersed, Shot	2
W22A	VHF	6-Feb-09	M	3	Light Grey	Table	Collar Dropped	4
W23A	VHF	19-Feb-09	F	1	Gray	Arctic	Alive at Study End	2
W24A	GPS pod	10-Mar-09	F	3.5	Black	Arctic	Unknown Fate	4
W25A	GPS pod	10-Mar-09	F	4	Light Grey	UpperTable	Mort, Shot	4
W26A	GPS	23-Jul-09	M	4	Grey	Wichcika	Alive at Study End	5
W27A	GPS	31-Jul-09	F	5+	White-Grey	Anzac	Mort, Natural Starvd	5+
W28A	GPS	26-Feb-10	F	2	Grey	Wichcika	Alive at Study End	2
W29A	GPS pod	8-Mar-10	F	5+	Black	Table	Alive at Study End	5+
W30A	VHF	8-Mar-10	F	2	N/A	Table	Alive at Study End	2
W31A	VHF	12-Mar-10	F	1	N/A	Wichcika	Alive at Study End	1

APPENDIX F: Wolf home ranges

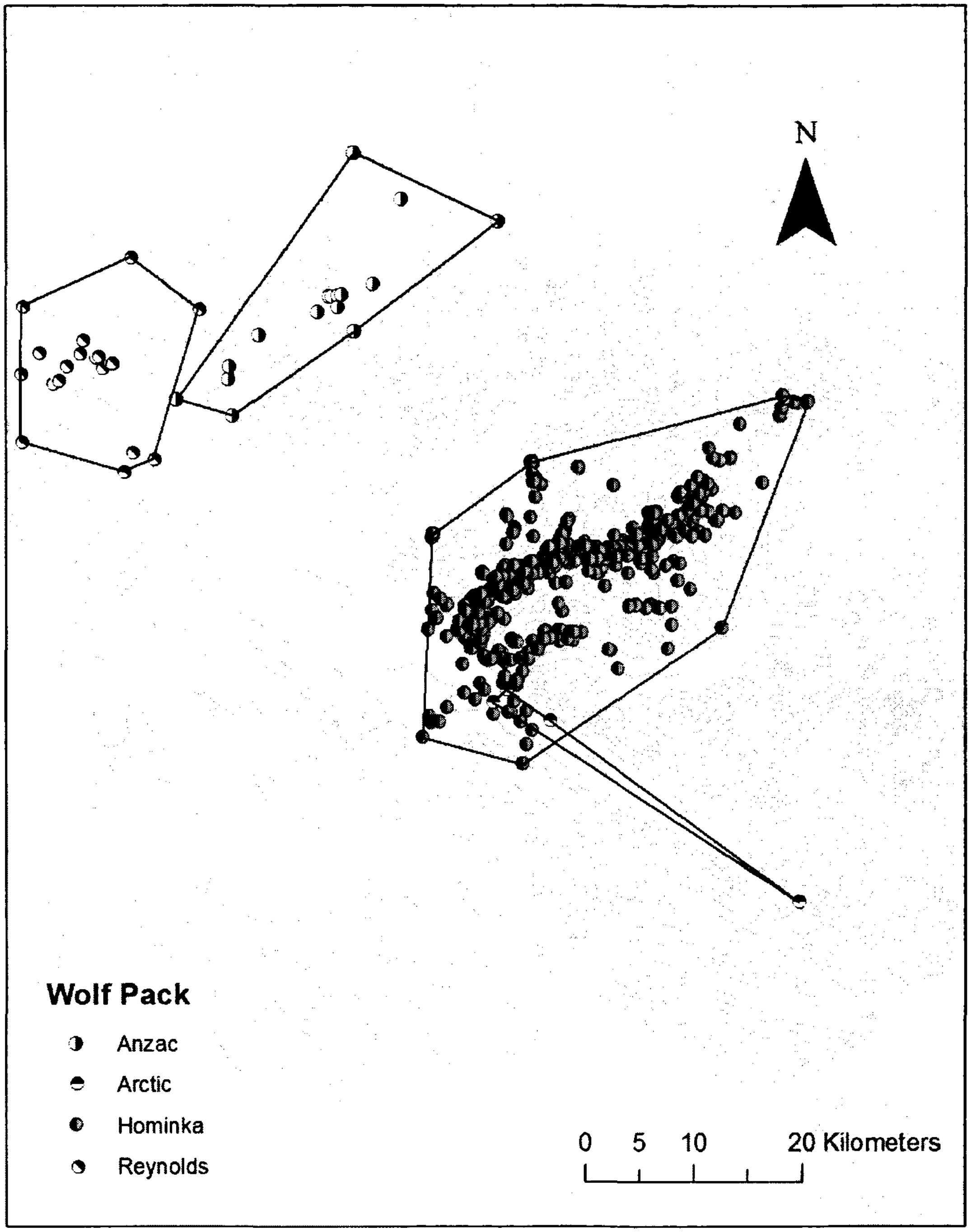

Figure F.1 2007 locations of VHF- and GPS-collared wolves and 100% MCP pack home ranges for wolves in the Parsnip River Study Area, BC. MCP created using Hawth Tools for ArcMap.

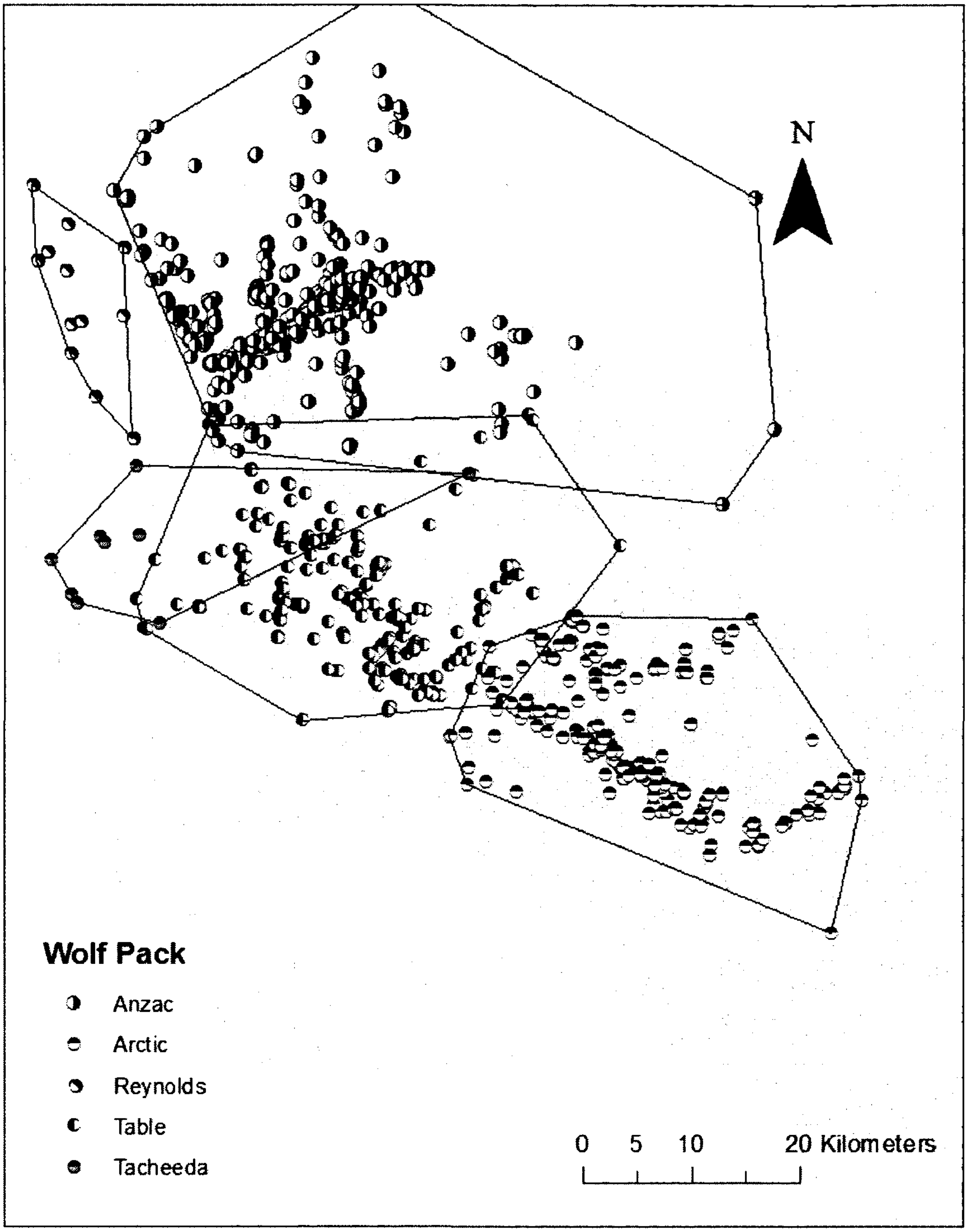

Figure F.2 2008 locations of VHF- and GPS-collared wolves and 100% MCP pack home ranges for wolves in the Parsnip River Study Area, BC. MCP created using Hawth Tools for ArcMap.

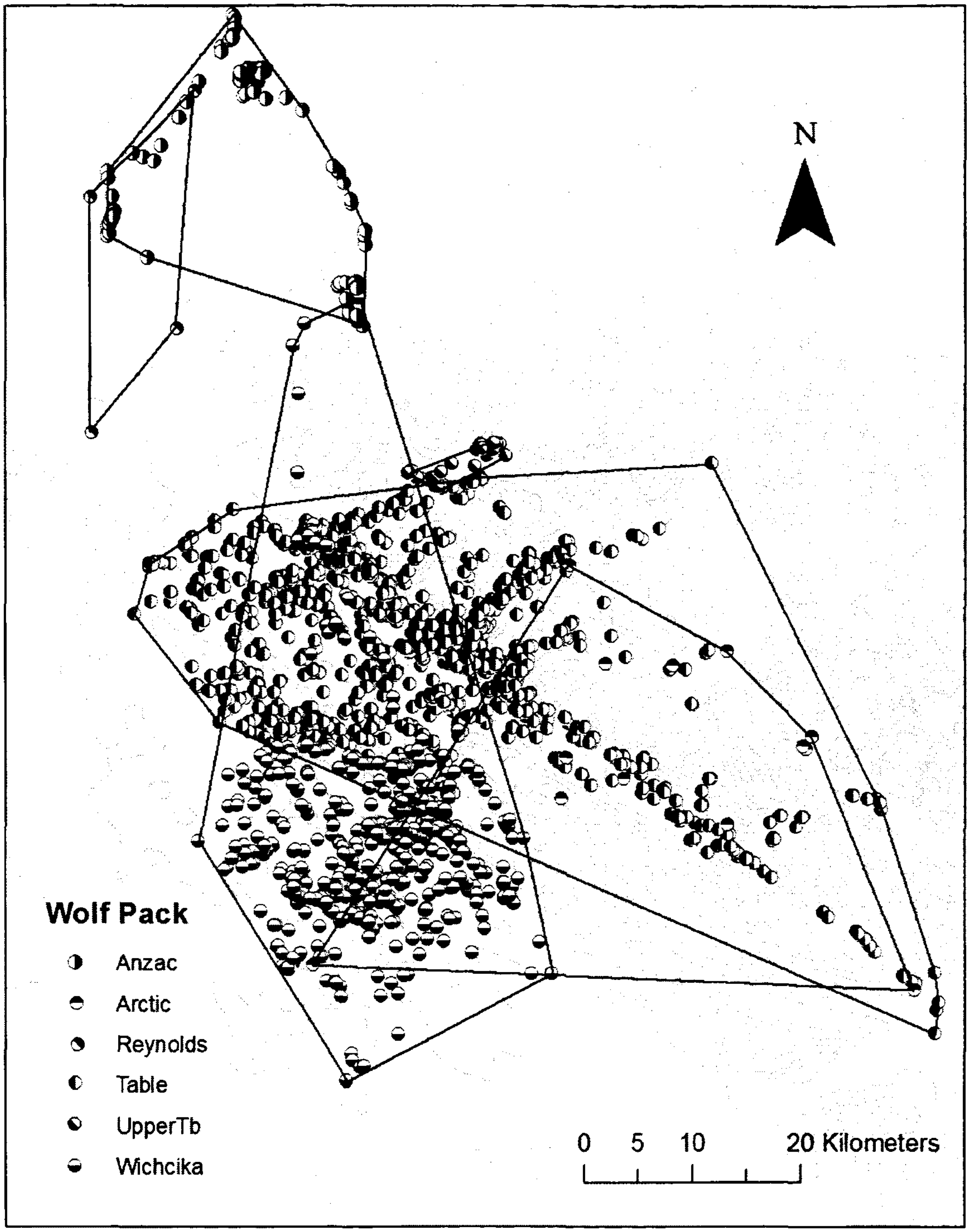

Figure F.3 2009 locations of VHF- and GPS-collared wolves and 100% MCP pack home ranges for wolves in the Parsnip River Study Area, BC. MCP created using Hawth Tools for ArcMap.

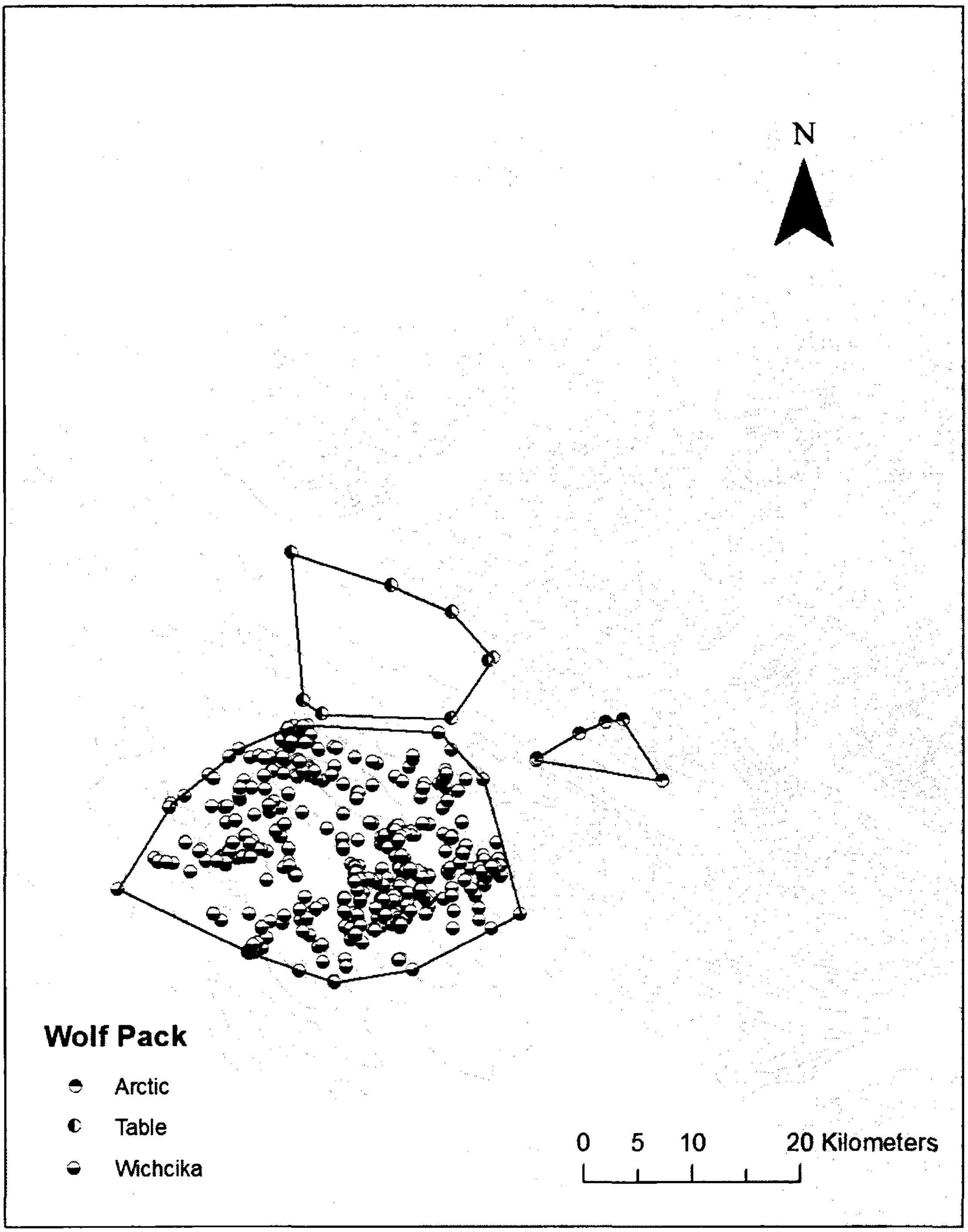

Figure F.4 2010 locations of VHF- and GPS-collared wolves and 100% MCP pack home ranges for wolves in the Parsnip River Study Area, BC. MCP created using Hawth Tools for ArcMap.