“Animals know more than anybody. That’s why they survive up there.”

−Woodie Elias, Gwich’in Elder (2008)

University of Alberta

Dall sheep (*Ovis dalli dalli*), grizzly bear (*Ursus arctos*) and wolf (*Canis lupus*) interactions in the Northern Richardson Mountains, Canada

by

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To Dall sheep, grizzly bears and wolves of the Northern Richardson Mountains

May you forever roam freely and wildly

&

À Yuki et Sola, merveilleuses sources d'inspiration

ABSTRACT

Assessing the impact of predators on a prey population is inherently challenging, *a fortiori* in remote ecosystems. With this thesis, I studied the interactions between a recently declining Dall sheep (*Ovis dalli dalli*) population and two predators: grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*), in the secluded Northern Richardson Mountains, Canada. After reviewing the status of this Dall sheep population, I investigated its interactions with grizzly bears and wolves –mostly the indirect effects of predation; using satellite telemetry, habitat utilization analyses, δ^{13}C and δ^{15}N stable isotopes, behavioural observations, and the documentation of Gwich'in and Inuvialuit Traditional Ecological Knowledge (TEK).

At the spatial level, Dall sheep were in close association with grizzly bears in intensively used areas, although wolves were more likely to be encountered elsewhere. Individual predators also showed various levels of spatial associations with Dall sheep. Based on stable isotope analyses, both predators have a remarkably diverse diet and consume Dall sheep, albeit not predominantly. Animal sources composed most of the grizzly bear diet, with vegetation and aquatic browsers (beavers and moose) constituting the two most important consumed groups. Aquatic browsers constituted the wolves' principal food, followed closely by mountain mammals (arctic ground squirrels, caribou and Dall sheep). At the behavioural level, the habitat utilization patterns of rams appeared to be guided by foraging needs, whereas ewes were predominantly influenced by

predator avoidance. In early summer, ewes foraged longer, were more vigilant, rested less, and exhibited less dominance behaviour than rams, which were exposed to higher predation risk and stayed in smaller groups. TEK complemented and enriched this research, notably regarding historical population trends, habitat utilization, and predator-prey relationships.

Ultimately, this thesis highlights the complexity and plurality of factors affecting Dall sheep behaviour and their interactions with grizzly bears and wolves. It also emphasizes the individual variability within each species and the several predator avoidance strategies used by Dall sheep to reduce their vulnerability. Although my research was not designed to assess the role of predation in driving this population, historical data stress the imminent contribution of harvest to past abundance fluctuations. More frequent monitoring would help disentangling the effects of various factors on this population.

PREFACE

I blessedly discovered the Northern Richardson Mountains while working as a Wildlife Biologist for the Gwich'in Renewable Resources Board, in Inuvik, Northwest Territories, between 2005 and 2008. One of my first duties in this position was the recovery of satellite collars previously worn by Dall sheep (*Ovis dalli dalli*) rams. Accompanied by Jari Heikkilä, Executive Director at the time, I hiked down steep canyons, dug for collars buried in snow, while witnessing in awe the astonishing landscapes surrounding us. The Dall sheep carcasses we found were almost always paired with eminent signs of wolves (*Canis lupus*) or grizzly bears (*Ursus arctos*). Although these signs suggested previous predation or scavenging activity, the remains had been lying there for too long and we could only guess what happened to those rams.

Returning in the Northern Richardson Mountains the following summer for a habitat investigation, I kept gathering similar observations and continued wondering about the relationships between these three species. Local harvesters also reported anecdotes of Dall sheep predation during routine meetings with the Gwich'in Renewable Resource Councils. Those observations, combined with a shared interest within communities of the Gwich'in Settlement Area to elucidate the recent decline in this Dall sheep population, triggered the start of my doctoral research on Dall sheep, grizzly bear, and wolf interactions. This is how I engaged into the greatest journey…

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To All: Hai cho! Quyanainni! Merci! ありがとう! Thank you!

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1. Introduction

1.1. Dall sheep, grizzly bears and wolves

Important stochastic fluctuations have been reported in ungulate populations around the world (Sæther 1997). Long-term monitoring studies, notably on mountain ungulates like Soay sheep (*Ovis aries*) and bighorn sheep (*Ovis canadensis*), have helped elucidate how limiting factors –on their own or synergistically, may influence population fluctuations. Density dependence (Portier *et al.* 1998, Milner *et al.* 1999, Hone and Clutton-Brock 2007), especially in combination with climatic conditions (Coulson *et al.* 2001, Hone and Clutton-Brock 2007) and diseases or parasites (Gulland 1992, Bunch *et al.* 1999, Monello *et al.* 2001), have been recurrently linked to variations in abundance and demographic rates. However, when human harvest (Simmons 1973) occurs or predators (Ross *et al.* 1997) are present, those can also have significant effects on mountain ungulates and weaken density-dependent feedbacks. This relationship appears to be particularly pronounced in northern ecosystems (Wang *et al.* 2009).

Dall sheep (*Ovis dalli dalli*) in the Northern Richardson Mountains are isolated at the northeastern limit of the species distribution range (Nichols 1978, Bowyer and Leslie 1992). Estimates from aerial monitoring did reveal important abundance fluctuations since the 1970s, with variations of tenfold magnitude recorded through the years. The population peaked at an estimated 1730 animals in the late 1990s (Nagy and Carey 2006) and plummeted down to the 700s in

2003 and afterwards (Nagy *et al.* 2006, Davison and Cooley 2006, K. Russell, Fish and Wildlife Branch, Yukon Department of Environment, unpub.).

Previous research on this population has questioned the adverse effects of overharvest (Simmons 1973), investigated its population dynamics as well as the home ranges and movements of rams (Barichello *et al.* 1987, Barichello and Carey 1989), reported instances of golden eagle (*Aquila chrysaetos*) predation (Barichello *et al.* 1991), and examined the prevalence of certain diseases and parasites (Hoberg *et al.* 2002, Kutz *et al.* 2004). Despite the presence of seemingly healthy populations of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) in the Northern Richardson Mountains, very little attention had however been devoted to the interactions of Dall sheep with these predators. Nevertheless, during consultations with local communities –key to the co-management framework prevailing in the Canadian Arctic (Moller *et al.* 2004, Berkes 2009), predators have recurrently been identified as potential culprits of the population decline. Moreover, local knowledge cited both grizzly bears and wolves as the most frequent Dall sheep predators in this area (Shaw *et al.* 2005).

Research in Alaska identified grizzly bears as the main predator of caribou (*Rangifer tarandus*) calves (Adams *et al.* 1995) and their potent role as an ungulate predator seems to culminate when prey are only few weeks old (Zager and Beecham 2006). Likewise, grizzly bears could prey on Dall sheep in the Northern Richardson Mountains, particularly on lambs –although this remained unverified. Following records of heavy harvest in the 1990s (The Joint Secretariat 2003, GRRB 2009), a grizzly bear management plan was adopted in 2000, limiting harvest through a quota system locally administered by renewable resource councils within the Gwich'in Settlement Area (GRRB 2000). A similar plan was also adopted in the bordering Inuvialuit Settlement Region. Overall, little had been documented regarding the grizzly bears' habitat use, nutritional ecology, and impact on Dall sheep, if any, in the Northern Richardson Mountains.

As for wolves, they can notably limit Dall sheep populations (Murie 1944, Sawyer *et al.* 2002, Mech *et al.* 2003). Arctic wolves mostly rely on ungulates, such as caribou and moose (*Alces alces*), and some packs follow barren-ground caribou herds in their migratory paths (Walton *et al.* 2001). Although wolves in the Northern Richardson Mountains were found to depend on moose and, seasonally, on the Porcupine Caribou herd (*Rangifer tarandus granti*) (Hayes *et al.* 1997, Hayes *et al.* 2000), they may also benefit from Dall sheep, muskoxen (*Ovibos moschatus*), and a variety of small mammals. Little is known on these wolves' habitat use, nutritional ecology, and impact on Dall sheep. Wolves are commonly harvested in the area, although there is no management plan in place.

In addition to predation and other limiting factors mentioned before, Dall sheep in the Northern Richardson Mountains may be subject to increasing stress in the future. In addition to a confirmed interest in establishing commercial hunting (Gwich'in Land Use Planning Board 2003), this mountain range and surrounding areas are threatened by natural resources exploitation (mining, oil and gas) (Holroyd and Retzer 2005) and climate change, which is particularly pronounced in the Arctic (Hinzman *et al.* 2005, Post *et al.* 2009). By examining the interactions between Dall sheep, grizzly bears, and wolves, my thesis not only addresses specific ecological questions as described next, but also provides important baseline information, which may become essential in the advent of development to assist the sound management of these three populations.

1.2. Indirect investigation of predation

Predation can have profound effects on a prey, directly and indirectly. The mechanism of predation may be decomposed in two stages: the encounter itself, and a successful attack given an encounter (Holling 1959, Hebblewhite *et al.* 2005). Predation success depends on several factors (e.g., body condition and proximity between prey and predator, landscape features, footing stability...) and is inherentely a stochastic event. Succesful attacks lead to prey mortality, a direct effect, and are challenging to monitor in the field, particularly in remote areas. However, indirect effects related to the prey's avoidance of predators –the first stage of predation, are ubiquitous and more easily investigated (Peckarsky *et al.* 2008). Studying those indirect effects, also called non-consumptive or trait-mediated, is a promising approach to obtain new insights about predator-prey relationships.

The indirect effects related to predation risk include vigilance behaviour (Lima 2002, Childress and Lung 2003), reduced feeding (Fortin *et al.* 2004), altered activity budget (Kie 1999), and habitat shift of prey species (Edwards 1983). In ungulates, predation risk has also been frequently related to sexual segregation (Main *et al.* 1996, Corti and Shackleton 2002), contrasting with other potential causes of sexual segregation (Main *et al.* 1996, Ruckstuhl and Neuhaus 2002, Singh *et al.* 2010).

1.3. Thesis outline

In this doctoral thesis, I aimed to provide updated knowledge on Dall sheep in the Northern Richardson Mountains, examine factors driving their habitat selection and sexual segregation, and characterize their interactions with two potential predators: grizzly bears and wolves. Partly due to the remoteness of the area and inherent logistical constraints, I concentrated my investigation on the indirect effects of predation, gathering insights through a series of complementary approaches: global positioning satellite (GPS) telemetry, stable isotopes signatures, behavioural observations, strengthened by appropriate statistical and modelling tools. Moreover, because Gwich'in and Inuvialuit people have traveled and inhabited the study area for countless generations, likely spanning several hundred years, I documented their knowledge acquired locally and through oral tradition with a series of interviews. My thesis is organized into the following chapters:

Chapter 2: Status of Dall sheep (*Ovis dalli dalli*) in the Northern Richardson Mountains

Notwithstanding aerial surveys conducted every two to six years, the most recent comprehensive investigation of Dall sheep population dynamics and habitat use in the Northern Richardson Mountains dated back more than 20 years (Barichello *et al.* 1987). To help make informed management decisions, a status report summarizing all known information regarding this population, both from scientific sources and aboriginal traditional knowledge, was ordered in the 2008-2013 recommended management plan for Dall sheep in the Northern Richardson Mountains[1]. This chapter fulfills this need, using the same headings as the management plan to increase its ease of use for reviewers of the plan. It describes the species, lays out the management context, summarizes population monitoring, reviews its limiting factors, describes its habitat and potential impacts of future development and climate change, and highlights the importance of education and information exchange to ensure the long-term conservation of this population.

Chapter 3: Spatial overlap of Dall sheep, grizzly bears and wolves in the Northern Richardson Mountains

The breadth of home range overlap is a useful measure of spatial associations between individuals or populations and can help examine several

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[1] Available online at: http://www.env.gov.yk.ca/mapspublications/documents/N-Richardson_Sheep_Mgmt_Plan_DRAFT_2008.pdf <Accessed 15 November 2011>

types of interactions such as: mating associations (Doncaster 1990), sexual segregation (Gehrt and Fritzell 1998), home range drift (Edwards *et al.* 2009), and predation risk (Hammond *et al.* 2007, Robinson *et al.* 2010). In this chapter, I measured home range overlap between Dall sheep, grizzly bears and wolves, based on GPS locations of individuals belonging to each species, monitored between 2004 and 2008. I present estimates from two methods: the two-dimensional overlap based on fixed-kernel density contour lines (Doncaster 1990), and the three-dimensional overlap based on the species combined utilization distributions (Fieberg and Kochanny 2005). This chapter reveals spatial patterns of associations between Dall sheep, grizzly bears and wolves.

Chapter 4: Assessing predation risk of grizzly bears and wolves on Dall sheep

To evalute the effect of grizzly bear and wolf predation risk on Dall sheep, I started by assessing the variability in risk posed by individual predators from the overlap between the utilization distribution of the monitored individuals (Fieberg and Kochanny 2005), assuming that spatial associations between predators and prey are a proper index of predation risk. I then analyzed the seasonal habitat utilization patterns of Dall sheep ewes and rams with models including topographical features, land cover, and predation risk variables (Marzluff *et al.* 2004, Millspaugh *et al.* 2006). I also measured the carbon and nitrogen stable isotope signatures from tissues of grizzly bears and wolves as well as various food sources, and estimated the proportion of Dall sheep in their diet using a Bayesian mixing model (Parnell *et al.* 2010). This chapter reveals distinctive patterns of seasonal habitat utilization for rams and ewes, outlines the individual variability in predation risk among grizzly bears and wolves, and characterize the diet of these predators.

Chapter 5: Dall sheep behaviour and sexual segregation under wolf and grizzly bear predation risk

Predation risk can lead to several effects on prey behaviour, including increased vigilance, decreased foraging, and potentially sexual segregation (Main and Coblentz 1996, Corti and Shackleton 2002). Other hypotheses have been proposed to explain sexual segregation in ungulates, notably related to differential activity budgets of males and females (Ruckstuhl and Neuhaus 2000). Based on one month of field observations and the simultaneous monitoring of wolves and grizzly bears, this chapter investigates Dall sheep behaviour and sexual segregation in relation with predation risk, here interpreted in terms of spatial associations with predators, vigilance behaviour, and whether predators had been observed nearby. Particularly, I assessed the prevalence of Dall sheep sexual segregation during early summer and tested for differences between activity budgets of rams, ewes, yearlings and lambs. I then examined the vigilance and foraging behaviours of rams and ewes through a series of linear models including prey organization, environment, and predation variables. This chapter provides an overview of Dall sheep behaviour shortly after lambs are born, contributes to the debate on sexual segregation, and highlights the plurality of factors affecting vigilance and foraging behaviours in the presence of predators.

Chapter 6: Traditional ecological knowledge of Dall sheep, grizzly bears and wolves, and their interactions, in the Richardson Mountains

Traditional ecological knowledge (TEK) is the knowledge acquired through extensive observation of an area or a species, either passed down in an oral tradition or shared among users of a resource (Huntington 2000). TEK can be a useful tool to gain additional insights on ecological systems, address management problems, and fill the bridge between local communities, resource users, and managers (Berkes *et al.* 2000). In the Richardson Mountains, typical scientific investigations have started to be undertaken only recently (early 1970s) –contrasting with many generations of accumulated knowledge of the Gwich'in and Inuvialuit people, who have lived in and traveled the area extensively. To document their knowledge, I conducted a series of semi-directed interviews with Gwich'in and Inuvialuit elders and active land users. Interview questions concerned the users' experience in the Richardson Mountains; Dall sheep, grizzly bear and wolf ecology, including issues like population trends, habitat use and diet, and limiting factors for each species; interactions between Dall sheep, grizzly bears and wolves; as well as climate change, development, and management recommendations.

1.4. Thesis format

The following chapters were formatted for individual publications in peer-reviewed scientific journals. Chapter 2 is currently "In Press" as a *Yukon Fish and Wildlife Branch Report*, but was modified in this thesis to include the latest 2010 aerial survey estimates. Chapter 3 has also been published in a special issue of *Galemys* devoted to mountain ungulates. A general conclusion is presented in Chapter 7, which discusses the factors driving this Dall sheep population and reviews my main research contributions.

Regarding the nomenclature used in this thesis, I would like to note that another small Dall sheep population inhabits the southern portion of the Richardson Mountains. Unless otherwise specified, my research focuses on the larger population located in the northern portion of the range, commonly referred to as the "Northern Richardson Mountains". In some situations, for instance when referring to traditional ecological knowledge (Chapter 6), I use the term "Richardson Mountains" to concisely refer to the whole area, including the southern and northern portions.

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2. Status of Dall Sheep (*Ovis dalli dalli*) in the Northern Richardson Mountains[1]

2.1. Introduction

2.1.1. Classification and distribution

Mountain sheep are ungulate members of the order Artiodactyla, sub-order Ruminantia, Bovidae family, and genus *Ovis*. There are two species of mountain sheep in North America: bighorn sheep (*Ovis canadensis*), found mainly in the Canadian and American Rockies, extending from central Alberta and British Columbia to areas of the southern United States and northern Mexico; and thinhorn sheep (*Ovis dalli*), found in mountainous regions of northern British Columbia (BC), Yukon Territory (YT), Northwest Territories (NT), and Alaska. Thinhorn sheep can be further divided into two subspecies: Dall sheep (interchangeably written Dall's sheep, *Ovis dalli dalli* Nelson 1884), present on the northern portion of the species range, and Stone sheep (or Stone's sheep, *Ovis dalli stonei* J. A. Allen 1897), found in the southern portion. Two additional subspecies, *O. d. kenaiensis* and *O. d. fannini*, were also defined in earlier literature (Cowan 1940), but their use is now questionable and current taxonomy

[1] A modified version of this chapter has been published as: Lambert Koizumi, C., J. Carey, M. Branigan, and K. Callaghan (2011). *Status of Dall's sheep (Ovis dalli dalli) in the Northern Richardson Mountains.* Yukon Fish and Wildlife Branch Report TRC-11-01, Whitehorse YT, Canada.

is generally limited to *O. d. dalli and O. d. stonei*. The Gwich'in name for Dall sheep is *divii* (Gwich'in Elders 1997) and the Inuvialuit name for sheep is *imnaiq* (Lowe 2001). The name Dall sheep originates from William Healy Dall (1845–1927), an American Naturalist who described observations of mountain sheep during his travels in Alaska and in the Yukon.

The Dall sheep population of the Northern Richardson Mountains is isolated at the northeastern limit of the species distribution (Figure 2.1). As such, exchanges with other populations are limited and this population may be particularly sensitive to habitat or population disturbances. The nearest population is located in the Southern Richardson Mountains, approximately 75 km south. The population in the Southern Richardson Mountains was divided into two groups and its abundance was estimated around 60 to 140 individuals (Hoefs 1978, Barichello *et al.* 1987). Despite the relatively short distance between the populations in the Southern and Northern Richardson Mountains, the exchange rate between them is unknown. These populations have therefore been considered distinct and managed as such.

2.1.2. Physical description and natural history traits

Dall sheep is an animal of the alpine, found in the most rugged and mountainous environments of northern North America. Males and females are sexually dimorphic, as rams are heavier and bear larger horns than ewes (Cowan 1940, Bowyer and Leslie 1992). Each winter, except during their first, the cessation of horn growth creates an annual segment on the horn, which can be counted to accurately estimate the age of the individuals. Based on a bighorn sheep study, this aging technique is reliable for rams, but may only provide a minimal age for ewes (Geist 1966). Horn growth is related to age and body condition, which in turn is influenced by resource availability. As such, northern sheep tend to have smaller horns than southern populations (Hoefs 1984a). Measured males' height at the shoulder ranges from 916 to 1090 mm (Bowyer *et al.* 2000). Body weight is generally at its peak in late summer, averaging 74 kg for adult rams and 56 kg for adult ewes (Nichols and Bunnell 1999).

Dall sheep have evolved in remarkably cold environments, and their coat (along with that of Arctic fox (*Vulpes lagopus*)) was found to have the best insulating properties when compared to other northern mammals, including ringed seal (*Phoca hispida*), wolf (*Canis lupus*) and polar bear (*Ursus maritimus*) (Scholander *et al.* 1950). The pelage of Dall sheep is creamy white and their thick winter coat, which is shed in the spring (Cowan 1940), tends to be whiter than their slightly tan summer coat (Gwich'in Elders 1997) –perhaps because of the dirtier environment in the summer time. Individuals at the southern part of the subspecies range exhibit a darker grayish variation (Cowan 1940).

Dall sheep are primarily grazers of a variety of plants composed mostly of grasses and sedges (Nichols and Bunnell 1999). No formal investigation has been done on the diet of Northern Richardson Mountains sheep but it is likely similar to other thinhorn sheep populations. In Alaska, Dall sheep diet was estimated at 66% grasses and sedges, 17% browse and forbs, 10% lichens, and 7% moss. Lichen consumption appears to increase during the winter (Nichols 1978b).

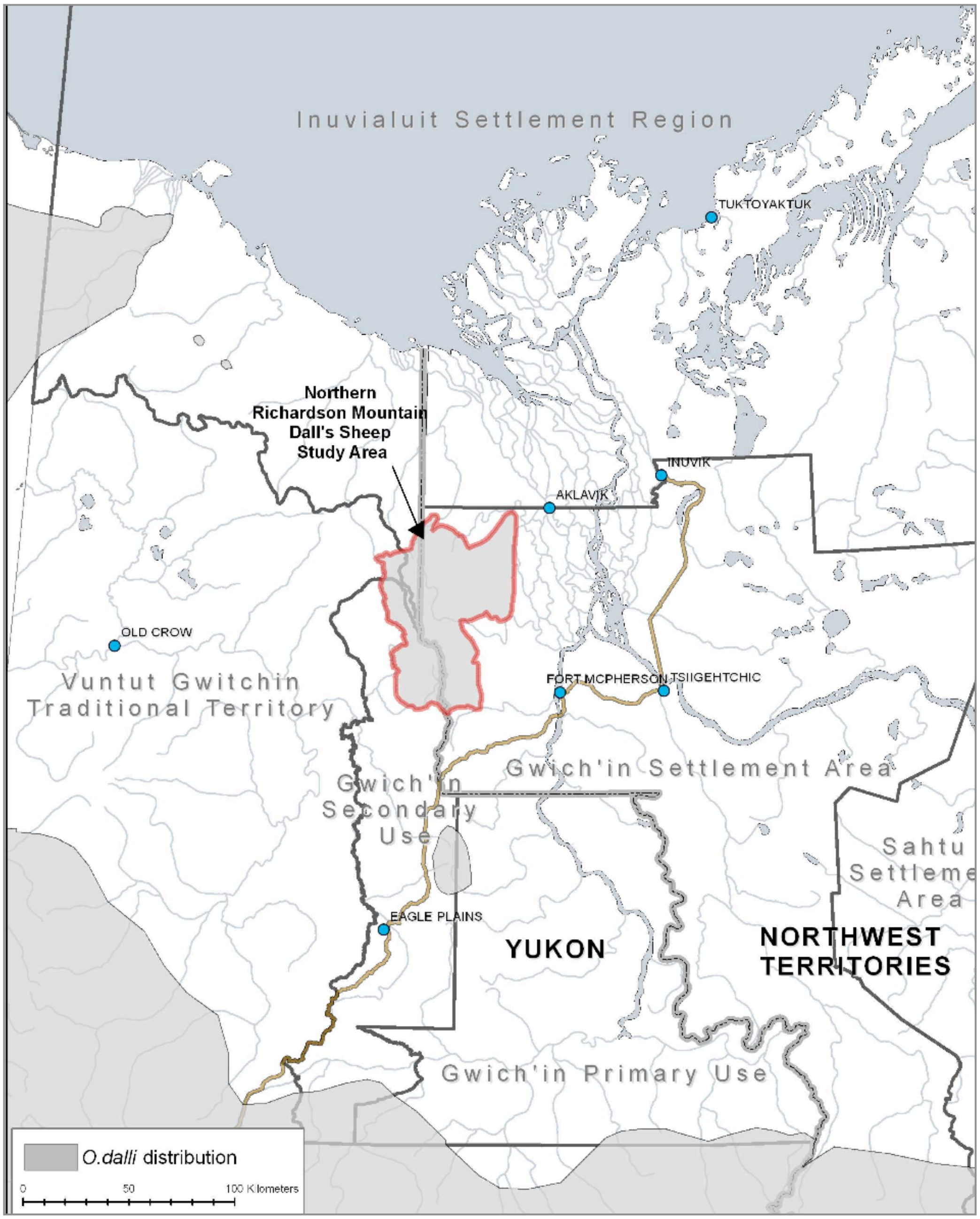

Figure 2.1. Delimited range of Dall sheep in the Northern Richardson Mountains (in red), showing the species distribution and its geopolitical environment (map source: Management Plan for Dall's Sheep in the Northern Richardson Mountains, *page v*).

2.2. Cooperation

2.2.1. Management context

The Northern Richardson Mountain Dall sheep range straddles the NT-YT border and overlaps the Gwich'in Settlement Area, the Gwich'in Secondary Use Area, the Inuvialuit Settlement Region, and the Vuntut Gwitchin First Nation Traditional Territory (Figure 2.2). The nearest human settlements are Aklavik and Fort McPherson, respectively located about 20 km east and 50 km southeast from the margin of the Northern Richardson Mountains. The next closest settlements are Inuvik and Tsiigehtchic (NT) to the east, and Old Crow (YT) to the west. As such, management of this population involves multiple parties and is subject to various legislation: the Northwest Territories Wildlife Act, the Yukon Wildlife Act, the Inuvialuit Final Agreement (adopted in 1984), the Gwich'in Comprehensive Land Claim Agreement (adopted in 1992), and the Vuntut Gwitchin First Nation Final Agreement (adopted in 1993).

The need for a management plan for this Dall sheep population first emerged after early studies on this population. There were concerns regarding overharvest (Simmons 1973), gas pipeline proposals (Hoffman 1974), and the construction of the Dempster Highway (which concerned mostly the Southern Richardson Mountains population) (Hoefs 1978). After a series of population surveys (Males 1980, Latour 1984b) and the completion of a three-year study on the dynamics, habitat use, and movements of this population (Barichello *et al.* 1987), a management plan was drafted in 1989 by the NT and YT governments.

However, the document was never adopted and the initiative laid dormant for several years. Coincident with the population surveys in 1991, 1997, 2001, and 2003 (Davison and Cooley 2006, Nagy and Carey 2006a, 2006b, Nagy *et al.* 2006a, Nagy *et al.* 2006b), local communities and wildlife authorities repeatedly recognized the need for a plan (Shaw *et al.* 2005). Finally, in 2005, interested parties met in Dawson City and, in the spirit of co-management, the group reaffirmed the need for a management plan for Dall sheep in the Northern Richardson Mountains.

2.2.2. Stakeholders and planning process

Partners involved in the management and conservation of the Dall sheep population in the Northern Richardson Mountains include the following governments, co-management boards, and councils:

- Vuntut Gwitchin Government
- Gwich'in Tribal Council
- Inuvialuit Game Council
- North Yukon Renewable Resources Council
- Gwich'in Renewable Resources Board
- Wildlife Management Advisory Council (North Slope)
- Ehdiitat Gwich’in Renewable Resources Council
- Tetlit Gwich’in Renewable Resources Council
- Gwichya Gwich’in Renewable Resources Council
- Nihtat Gwich’in Renewable Resources Council

- Inuvik Hunters and Trappers Committee
- Aklavik Hunters and Trappers Committee
- Yukon Fish and Wildlife Management Board
- Yukon Government
- Government of Northwest Territories

The goal of the planning process for this population is to secure its long-term conservation and habitat preservation in the Northern Richardson Mountains, as well as to provide for traditional and other uses that benefit all people.

2.3. Population monitoring

2.3.1. Evolution and genetics

It is believed that thinhorn sheep, bighorn sheep and the Siberian snow sheep (*Ovis nivicola*) had a common ancestor in the early Pleistocene or late Pliocene (Cowan 1940). During the last ice age, the thinhorn sheep ancestor probably crossed to North American from Asia, through the Bering Land Bridge, and occupied a large ice-free region in Yukon and Alaska, known as Beringia (Pielou 1991). Beringia, as well as other smaller ice-free regions in British Columbia, are believed to have acted as refugia for thinhorn sheep populations, and to be partly responsible for today's genetic diversity observed between subspecies of thinhorn sheep (Loehr *et al.* 2006). The Richardson Mountains were located at the easternmost limit of Beringia, and were marked by three marginal glacial events during the Quaternary period, covering portions or the totality of the range (Catto 1996). This marginal ice was melted approximately 12 000 years ago (Dyke and Prest 1987) and Dall sheep could have inhabited the entire region since then.

Although the genetic structure and diversity across various thinhorn sheep populations in Alaska, the Yukon, and the Northwest Territories was recently investigated (Worley *et al.* 2004), the genetics of the Northern Richardson Mountains population have not yet been examined. Nevertheless, one could speculate that its genetic structure adheres to the isolation-by-distance pattern observed in other populations (Worley *et al.* 2004). As such, because of this population's relative isolation from other mountain ranges, its gene flow might be fairly restricted and its genetic variability correspondingly low, in comparison to more abundant populations living on a larger inter-connected range, such as the Mackenzie Mountains, NT. This hypothesis remains to be verified. Investigating the genetic structure of this population could bring additional insights about its level of isolation, its degree of exchange with other populations, and its evolutionary history.

2.3.2. Population parameters

Abundance

Historical trends based on local and traditional ecological knowledge

For the past centuries, aboriginal peoples inhabiting or traveling through the Richardson Mountains were likely aware of Dall sheep population cycles and shifts in composition. This information has however not been systematically recorded and is mostly unavailable. Nevertheless, some local and traditional ecological knowledge from Gwich'in elders and harvesters was documented in 2000 and 2001 when interviews were conducted in Aklavik, Fort McPherson, and Inuvik (Shaw *et al.* 2005). From observations recalled by the interviewees, no Dall sheep population trend was clearly apparent between the 1950s and the 1990s, although few participants mentioned that the population was larger at the time of the interviews than before, which would correspond to the population peak of the late 1990s estimated from aerial surveys, as described in the following sections. No information prior to the 1950s was mentioned. [1]

Earlier surveys: the 1970s until mid 1980s

A series of surveys conducted in the early 1970s and 1980s helped delimit the distribution of this Dall sheep population, estimate its abundance (Table 2.1),

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[1] Additional knowledge and insights are revealed in Chapter 6 of this thesis, documenting the traditional ecological knowledge about Dall sheep, grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) in the Richardson Mountains.

and acquire baseline ecological information in the face of potential threats to itself or its habitat (e.g., via overharvest (Simmons 1973), potential pipeline development (Hoffman 1974, Nolan and Kelsall 1977), or construction of the Dempster Highway (Hoefs 1978)). Hoefs (1978) subdivided Dall sheep range in the Northern Richardson in two: the “Mt. Goodenough” range, delimited by Black Mountain to the east, Willow River and the headwaters of Cache Creek to the north, Bell River to the west, and Rat River to the south; and the “Mt. Millen” population, covering the Mount Millen area, Sheep Creek area, and south of Summit Lake and the Rat Pass. This distinction was kept in subsequent surveys (Males 1980, Latour 1984b). These two regions as well as the areas covered during the surveys are shown in Figure 2.2.

For these earlier surveys, observers in fixed-wing aircrafts (1971, 1979, and 1983) were not able to accurately distinguish the sex and age class, and instead focused on the total number of sheep. Observers in helicopters however categorized the individuals into the following groups: adult rams, adult ewes, yearlings, and lambs. Because of the difficulty involved in distinguishing between yearlings and ewes from the air, and to minimize harassment from repeated overflights (Nolan and Kelsall 1977), the two groups were often merged and referred to as “nursery sheep”. The nursery sheep group may also include a small number of two-year-old rams (Nichols 1978b). These survey estimates were not corrected for observation error, except for Males (1980), who inflated his observed sheep number by 25% to account for unseen sheep. To facilitate the comparison and be consistent across surveys, numbers in Table 2.1 represent only raw counts.

In addition, Nolan and Kelsall (1977) conducted three aerial and one ground survey of the Black Mountain and surrounding areas during May and June 1973 to delineate lambing areas and estimate productivity. Their sheep counts ranged widely (from 37 to 122 within a week) and are not presented here. A one-day survey was also reportedly conducted in February 1974 over the Black Mountain winter range by Hoffman (as reported in Hoefs 1978, Males 1979; original document not located) and yielded a count of 47.

The sheep numbers reported between 1971 and 1984 show substantial fluctuations, likely due to a combination of factors: the use of various methods (fixed-wing, helicopter, and snowmobile), the inconsistent timing of the surveys, and most importantly, the difference between survey areas (Figure 2.2). This high variation may preclude comparing the estimates from this period to analyze the long-term population growth of Dall sheep in the Northern Richardson Mountains. Nevertheless, some surveys intensively covered most of the Northern Richardson Mountains (in 1972, 1973, 1977, and 1979) and all reported a fairly small sheep population (<500, with most <200). Previous authors (Simmons 1973, Hoefs 1978, Males 1980) were concerned that this population was small, potentially declining, and likely overharvested.

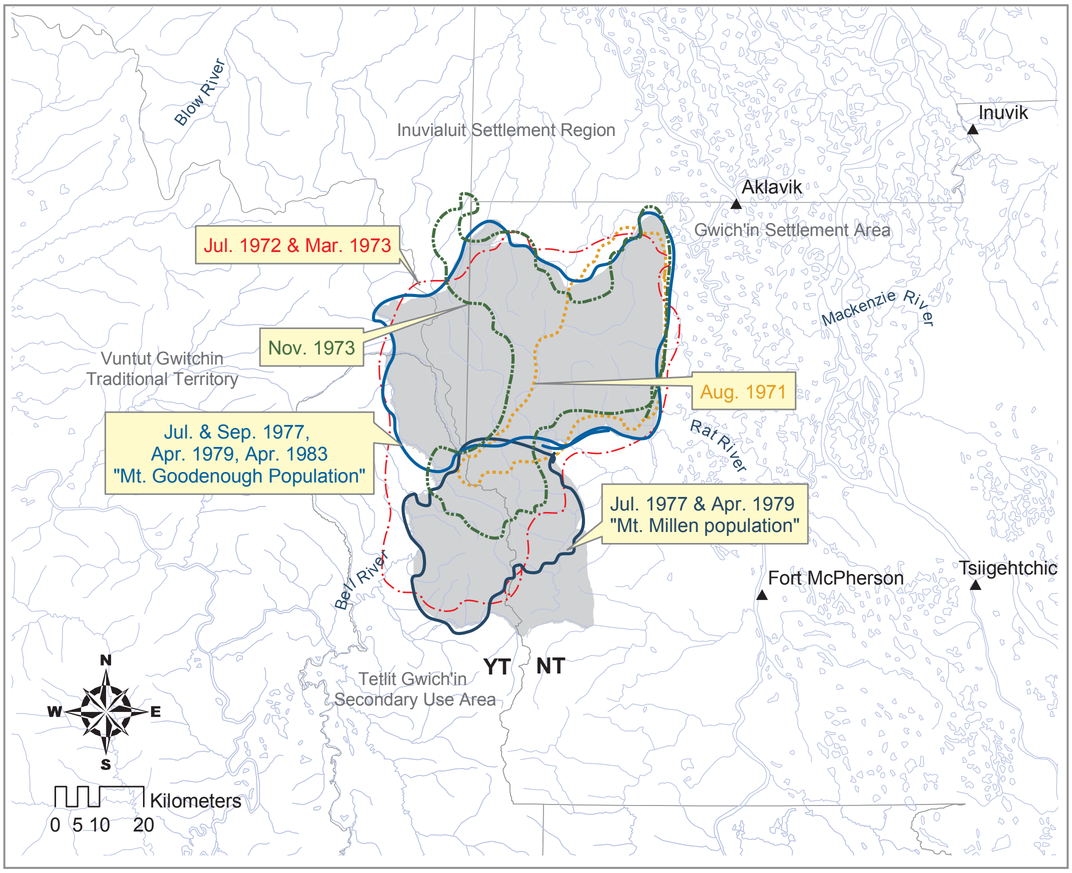

Figure 2.2. Approximate limits of the area covered by previous Dall sheep surveys in the Northern Richardson Mountains. The grey shaded area delimits the current survey area (since 1997).

Table 2.1. Dall sheep abundance estimates from earlier surveys (1971 to 1984) in the Northern Richardson Mountains.

Year	Month	Method	Rams	Nursery sheep	Lambs	Unc.[a]	Total	Area covered	Source
1971	Aug	Fixed-wing	37	---	---	---	193	Yellow line in Figure 2.2	Simmons 1973
1972	Jul	Helicopter	105	222	34	89	450	Red line in Figure 2.2	Nolan and Kelsall 1977
1973	Mar	Helicopter	30	60	25	4	119	Red line in Figure 2.2	Nolan and Kelsall 1977
1973	Nov	Helicopter	49	61	27	3	140	Green line in Figure 2.2	Nolan and Kelsall 1977
1977	Jul	Helicopter	46	121	48	---	215	Blue lines (Figure 2.2: "Mt. Goodenough & Mt. Millen")	Hoefs 1978
1977	Sep	Helicopter	33	107	42	---	182	Bright blue line (Figure 2.2: "Mt. Goodenough")	Hoefs 1978
1979	Apr	Fixed-wing	---	---	---	---	152[b]	Blue lines (Figure 2.2: "Mt. Goodenough & Mt. Millen")	Males 1980
1983	Apr	Fixed-wing	---	---	---	---	68	Bright blue line (Figure 2.2: "Mt. Goodenough")	Latour 1984a
1984	Mar & Apr	Snowmobile	---	---	---	---	130[c]	Black Mountain, Mt. Lang, and "Fish Hole" areas	Latour 1984b

Notes: [a] "Unc." stands for unclassified sheep; [b] Observed number of sheep, however Males judged that a 25% correction factor was needed to account for unseen animals and presented an estimate of 190; [b] Pooled observations of 3 crews over a one-month period (in three different areas).

Later surveys: 1984 to 2010

Concerns about the low abundance of this population during the early 1980s, combined with an interest in the region for oil and gas development, led to a comprehensive study on its ecology, range use, and movements between 1984 and 1986 (Barichello *et al.* 1987, Barichello and Carey 1989). This was also the start of a series of more standardized surveys. Barichello and colleagues surveyed the Dall sheep population by helicopter in June, July and March of 1984–1986 along the mountain contours and drainages of the Northern Richardson Mountains (as described in Hoefs 1978). They partitioned the area into 11 survey blocks that have been used since then. A 12th block, Sittichinli, was added in 1997 following a request from Fort McPherson residents (survey blocks are mapped in Figure 2.3); however sheep have not yet been observed in this block during aerial surveys. As in the previous helicopter surveys, Dall sheep were classified either as: lamb, nursery sheep (ewes, yearlings and some two-year old rams mixed with the group), and rams, which were further classed as into 1/2 curl, 3/4 curl or full curl (see Table 2.2 for results). Including an additional 10% to account for observation error or unseen sheep, the total population estimates for 1984, 1985, and 1986 were 597, 690, and 882 respectively. The trend observed during this period indicates a rapid population increase (15% and 27% annual increment in 1985 and 1986, respectively). Another survey done in 1987 yielded a count of 645 Dall sheep (Stenhouse and Kutny 1987). Authors reported lower survey efforts on the Yukon side compared to 1986 and concluded that the population was either stable or increasing.

Subsequent population surveys (1991 and afterwards) were not adjusted for observation error, like Barichello *et al.* (1987) had done, but were consistently flown in the same area by helicopter, either in June or August. The 1991 survey estimated the population at 1374, with a high lamb to nursery sheep ratio (see productivity section), and more sheep found in the Goodenough, Sheep, Lick and Rat block surveys (Nagy and Carey 2006a). The 1997 survey counted 1339[1] sheep for nine survey blocks (Nagy and Carey 2006b), however three blocks: Millen, Bear and White, could not be flown due to bad weather. When the 1997 estimate was adjusted based on the percentage of sheep found in these three blocks during the 1991 survey, the total came to 1730, which was the highest population abundance estimated to date. This said, the proportion of sheep in the different blocks in 1991 might not be an accurate indicator of the distribution in 1997; but, lacking the actual data for the 3 unsurveyed blocks of 1997, it is the best approximation available. The population declined thereafter, with 1057 sheep counted in June 2001 (Nagy *et al.* 2006b), 756 in August 2003 (Nagy *et al.* 2006a), 704 in 2006 (Davison and Cooley 2006), and 699 in 2010 (Kyle Russell, Yukon Department of Environment, pers. com.).

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[1] The reported total in Nagy and Carey (2006b) was 1344; but after calculating the sum of the survey counts presented in their report, the total was reassessed at 1339.

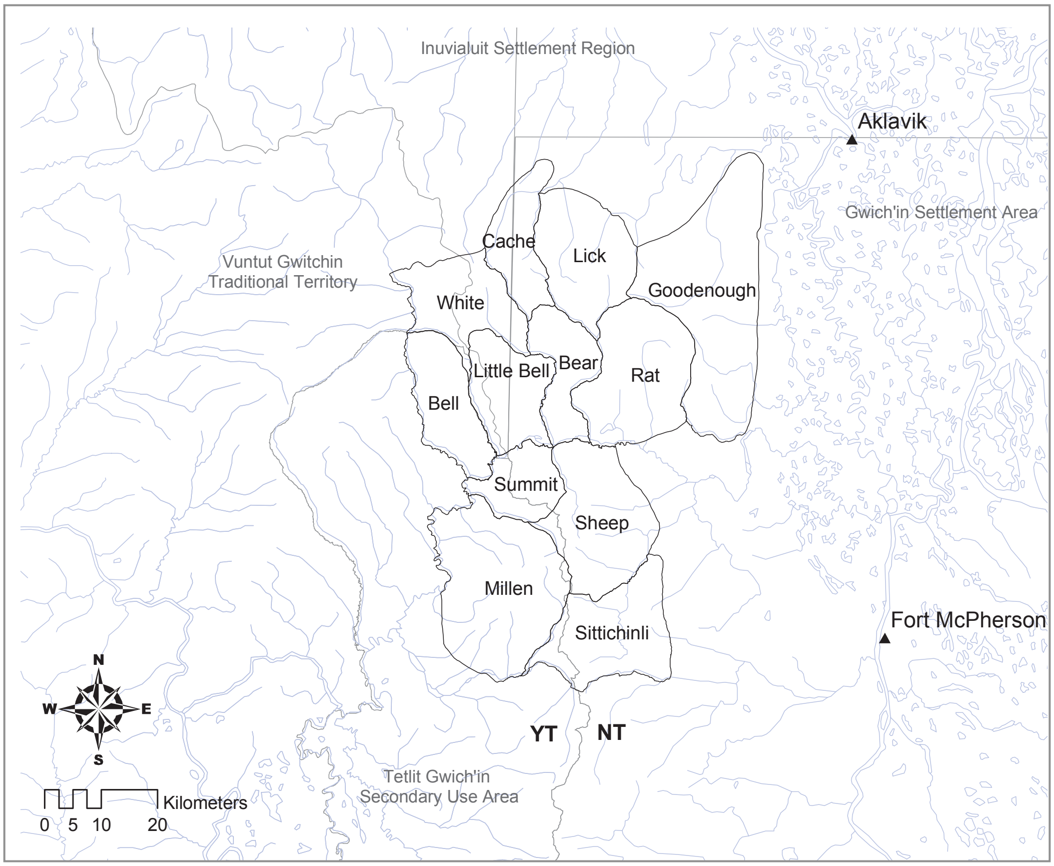

Figure 2.3. Current survey blocks for Dall sheep in the Northern Richardson Mountains, as established in 1984 (with the exception of the Sittichinli block, added in 1997).

Table 2.2. Dall sheep abundance estimates from aerial surveys conducted in helicopter between 1984 and 2010 in the Northern Richardson Mountains.

Year	Month	Rams				Nursery sheep[a]	Ewes	Yrl.[a]	Lambs	Unc.[a]	Raw count	Estimated total	Source
		½ c.	3/4 c.	Full c.	Total								
1984	Jun	48	33	49	131[b]	302	234	68	110	---	543	597[c]	Barichello *et al.* 1987
1985	Jun	46	49	51	148[b]	362	256	106	117	---	627	690[c]	Barichello *et al.* 1987
1986	Jun	78	50	67	197[b]	460	309	151	145	---	802	882[c]	Barichello *et al.* 1987
1987	Jun	60	42	49	151	310	---	---	143	41	645	645	Stenhouse and Kutny 1987
1991	Aug	99	92	182	373	675	---	---	289	37	1374	1374	Nagy and Carey 2006a
1997	Aug	76	74	136	286	802	---	---	250	1	1339	1730[d]	Nagy and Carey 2006b
2001	Jun	43	55	133	231	734	---	---	92	0	1057	1057	Nagy *et al.* 2006a
2003	Aug	35	42	100	177	429	---	---	121	29	756	756	Nagy *et al.* 2006b
2006	Jun	21	20	60	101	460	438	22	97	46	704	704	Davison and Cooley 2006
2010	Jun-Jul	50	37	73	165	384	154	10	150	0	699	699	Kyle Russell (pers. com.)

Notes: [a] The nursery sheep group combines ewes and yearlings, which sometimes could not be distinguished; "*Yrl.*" stands for yearlings and "*Unc.*" for unclassified sheep; [b] There were one unclassified ram in 1984, two in 1985, and two in 1986; [c] Adjusted by 10% to account for unseen sheep; [d] Adjusted to account for three blocks that could not be surveyed.

The realized population growth rate λ between each consecutive population survey estimates (Figure 2.4) was calculated as $\lambda = (N_{t+T} / N_t)^{1/T}$, where T is the time interval in years and N represents the authors' population estimates for each survey (Case 2000). A λ value of 1 indicates that the population is stable; a value above 1 indicates it is growing; and a value below 1 indicates it is declining. As such, λ assists managers in assessing at-risk populations and when compared to population size, can aid in determining need for quick recovery actions (i.e., there is likely less time available for taking recovery actions for populations with both low λ and small population size). Estimated annual realized growth rates for the 12 included surveys varied over the three decades of monitoring, ranging from 0.73 to 1.28, with a geometric mean of 1.00 and a standard deviation of 0.17 (Figure 2.5). Growth rates prior to 1991 were mostly indicative of an increasing population, with the exception of a decline between 1986 and 1987, possibly a result of the limited coverage of the 1987 survey. After the late 1990s, the rates reflect a declining population, however it now appears to have stabilized, as indicated in the latest survey. More frequent surveys would help refine these estimates.

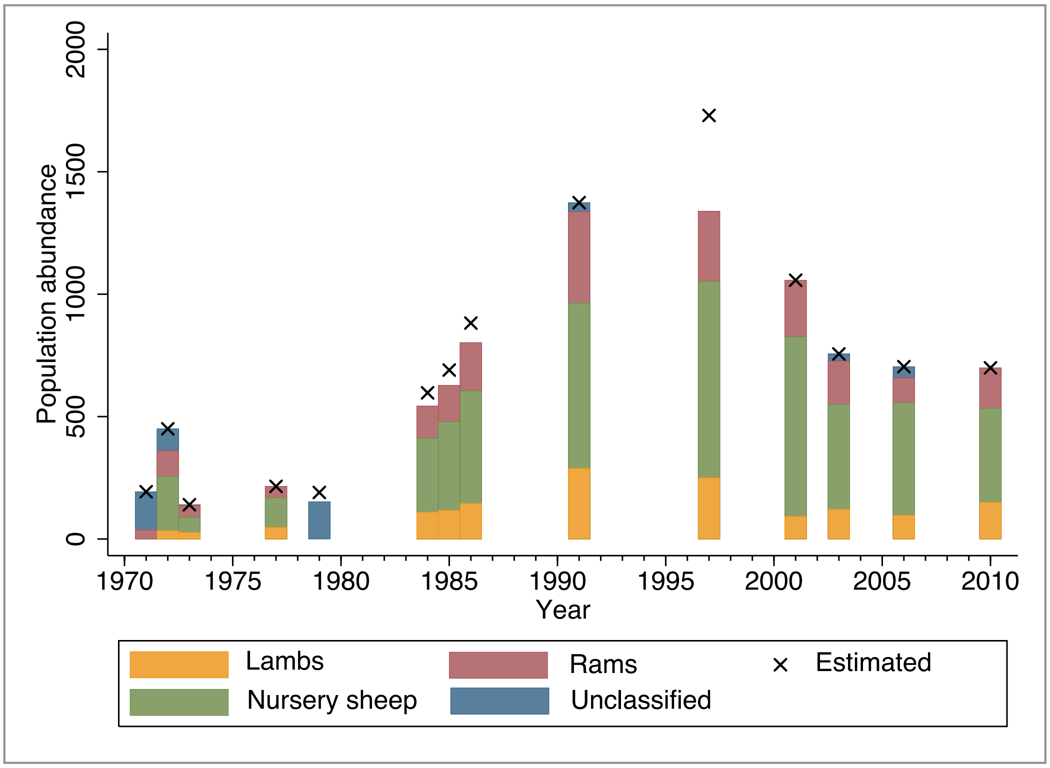

Figure 2.4. Raw counts and estimated Dall sheep abundance in the Northern Richardson Mountains, from summer helicopter surveys conducted between 1972 and 2010. The 1987 survey reportedly covered a smaller area and may be an underestimation. The counts of 1984, 1985, 1986 and 1997 were adjusted to account for unseen animals and missed survey blocks.

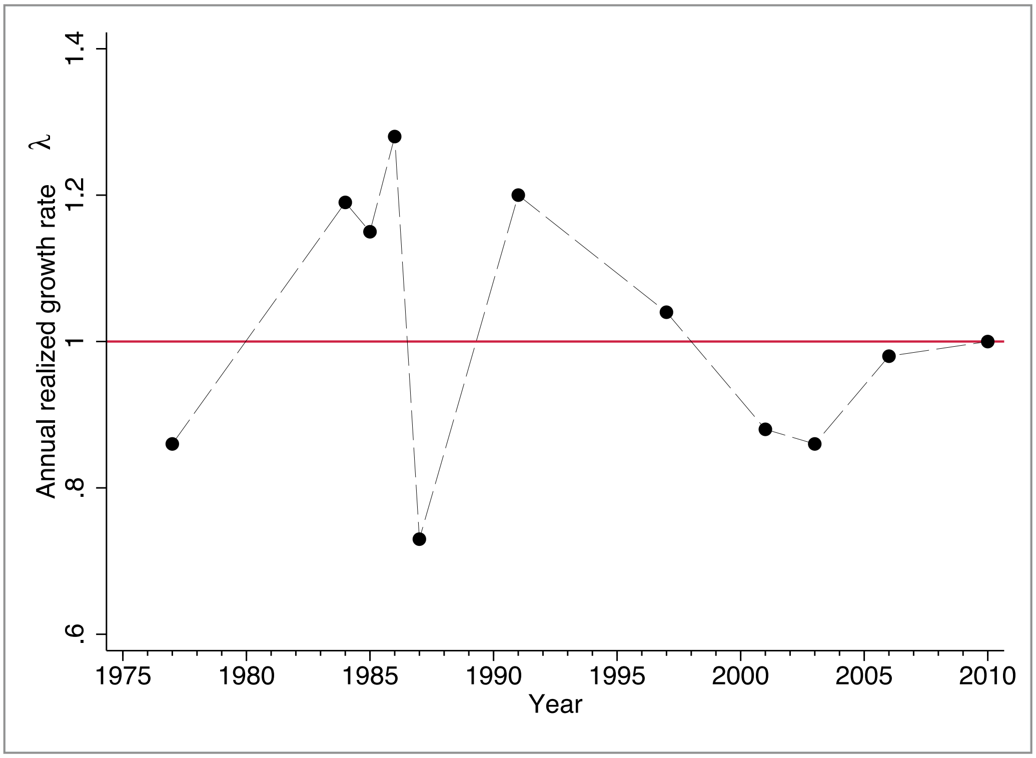

Figure 2.5. Estimated annual realized growth rates λ for Dall sheep in the Northern Richardson Mountains, from population estimates of summer helicopter surveys conducted between 1972 and 2010. Each point represents the growth rate between pairs of consecutive survey years, beginning with the rate observed between 1972 and 1977.

Note about observation error and survey methods

The accuracy and precision of population size and composition estimates are influenced by a combination of somewhat controllable factors, such as the survey method and intensity of efforts, the experience of observers, the level of enthusiasm and attitude of the survey team and pilot; and uncontrollable factors such as weather, light conditions, and distribution of sheep into habitats where sheep are easier or harder to see (Heimer 1994). Because mountain sheep tend to live in very rugged terrain (Geist 1971, Gwich'in Elders 1997), access to their range is very limited, and ensuring that all sheep are seen and counted during the survey is a challenge. In the Northern Richardson Mountains, there have been only few assessments of the proportion of sheep observed during the surveys, which is termed the visibility correction factor or sightability index. Based on a double sampling method (ground and aerial count), Barichello *et al.* (1987) recommended adding a 10% correction factor to survey estimates to account for unseen sheep. The same exercise was repeated by Stenhouse and Kutny (1987) in two sites, and their ground count was comparable to aerial results (differences of -2% and +5%). These were the best assessments of visibility conducted so far for this population, although there is a risk that some Dall sheep were missed by both ground and aerial crews. Based on a general evaluation of the survey, Males (1980) also inflated his fixed-wing estimate by 25%.

Failure to include a visibility correction factor may underestimate the number of animals present in the mountains and prevent the use of variance and related confidence intervals when estimating population size (Bodie *et al.* 1995). Under a designed assessment of the sightability index, the aerial relocation of collared mountain sheep (Bodie *et al.* 1995) and goats (Poole 2007) both yielded about 60% visibility; so a 10% or 25% correction factor may not suffice to account for the number of sheep missed during the survey. The estimation and use of a visibility correction factor during each survey would increase the precision of population estimates and variances in the future. Not including such a correction factor, as it is currently done, may yield conservative population estimates. Conservative estimates are however preferable to overly inflated estimates and may minimize the risk of overexploitation of this population. The need to adopt a consistent approach between surveys to enable results comparison cannot be overstated.

Choosing between aerial or ground technique is another important consideration when designing a population survey. Aerial surveys may inflict a higher level of stress to the population, despite being of relatively short duration. Mountain sheep have been observed to respond dramatically to helicopter or low fixed-wing overflights, and consequences of aerial disturbances may include high energy expenditures, reduced feeding, habitat shift, and potential abandonment of certain areas (Bleich *et al.* 1994, Frid 2003). The degree of response to the aircraft may however be reduced with increasing flying altitude (Krausman and Hervert 1983, who recommended survey aircraft staying at least 100 m over the animals). For the survey staff, there is also a considerable risk involved in flying over the mountains, which needs to be considered by wildlife managers (Heimer 1994).

On the other hand, ground techniques, like foot-based observations aided by a spotting scope or binoculars, are generally cheaper and cause fewer disturbances than aerial surveys. Humans can be seen as predators and elicit vigilance or even escape behaviours (Frid and Dill 2002), but probably to a lesser extent than aerial disturbances. Ground surveys may yield a more accurate population structure, as they allow the observers to get closer to the sheep groups and distinguish the sex and age classes more accurately. They also have the potential to involve community members into population monitoring and research. Ground surveys are however more laborious, of longer duration, and also limited in their ability to count simultaneously all the sheep groups and cover a large area. This downside could be partially overcome if multiple teams were deployed, although many people on the sheep range could then become disruptive.

Other than the snowmobile count reported in 1984 (Latour 1984a), there have been no extensive ground surveys of Dall sheep in the Northern Richardson Mountains. In 1985, Barichello *et al.* (1987) compared results from a simultaneous ground count and an aerial survey for two specific areas, and found a minimal difference between them (i.e., 180 sheep were observed on the ground, and 176 from the air). Ground surveys have also been conducted regularly to estimate the Dall sheep population in the Mackenzie Mountains (A. Veitch, Environment and Natural Resources, NT Government, pers. com.).

Productivity

Lamb to nursery sheep ratio

The recruitment of individuals, through the production and survival of lambs, is a key contribution to population growth. Even when adult sheep have relatively stable survival rates, survival rates of younger individuals can be highly variable. Low lamb production or high mortality rates for lambs and yearlings can be sufficient to trigger a population decline (Gaillard *et al.* 1998). There is insufficient knowledge of lamb births and deaths to accurately quantify this population's productivity. However, the number of lambs per 100 nursery sheep observed shortly after lambing season can provide a useful indicator of lamb production. This index does not consider stillbirths, perinatal mortality, deaths occurring before the conduction of the survey, or, for the June surveys, late births. Because lambs suffer higher mortality rates in their first few weeks of life (Simmons *et al.* 1984, Nichols and Bunnell 1999), the timing of the survey is crucial to the estimation of the lamb-to-ewe ratio.

In the Northern Richardson Mountains, the number of lambs to 100 nursery sheep ratio was determined from the population composition data reported in the periodic aerial survey estimates (Tables 2.1 and 2.2). Between 1972 and 2010, there were on average 32 lambs per 100 nursery sheep observed in the population (SD = 11, range = 13 to 46) (Figure 2.6). The counts were however done at various times of the year, and it is likely that counts in July or later were lower than if they had been done in June or late May because of the relatively high early mortality (Simmons *et al.* 1984). Generally, the production of thinhorn sheep lambs has been inversely associated with population density, severe winter weather, and heavy snow falls (Murphy and Whitten 1976, Nichols 1978a). The number of lambs born appears to relate to the density of sheep present the previous year, particularly in colder years (Geist 1971, Forchhammer *et al.* 2001 for Soay sheep). Moreover, there is evidence that large-scale weather phenomenon known as the Pacific Decadal Oscillation (PDO) is a driving force behind fluctuations in lamb production (Loehr 2006).

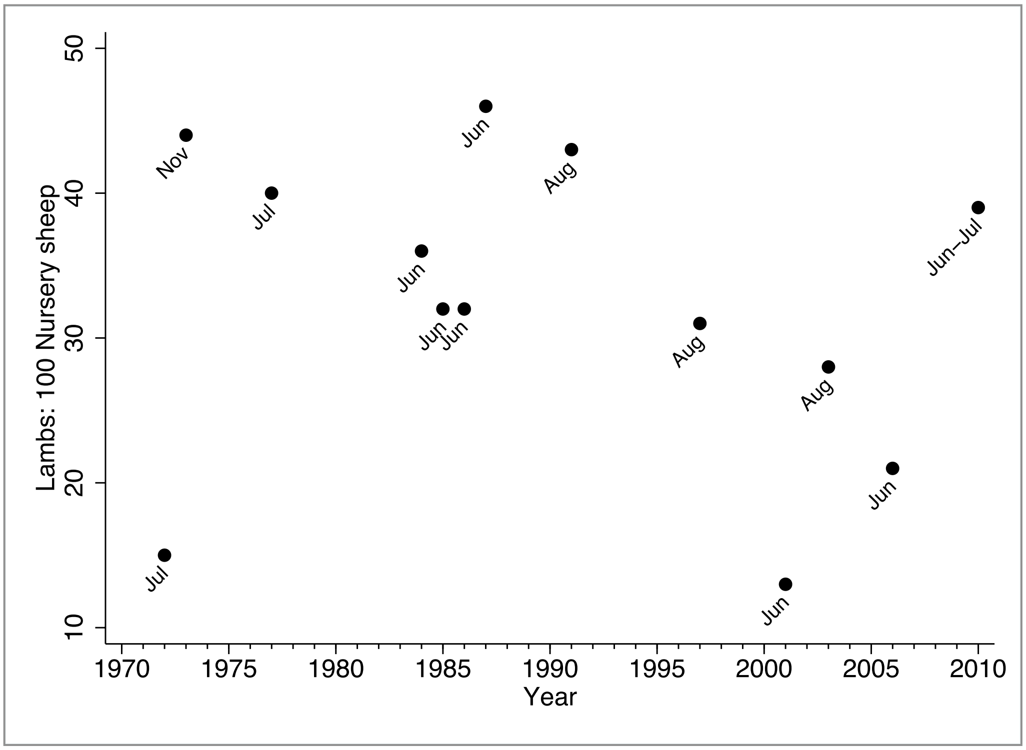

Figure 2.6. Lambs to 100 nursery sheep ratios estimated from aerial surveys (including composition counts) performed between 1972 and 2010 in the Northern Richardson Mountains. Surveys months are indicated.

Timing of the lambing season

Lambing season for this population is estimated to peak around the third and fourth weeks of May, but it has been observed to start as early as May 5 and end as late as June 15 (Nolan and Kelsall 1977, Barichello *et al.* 1987). Assuming the lambing period is regulated by similar processes affecting other populations in southwest Yukon, its onset and duration are likely related to photoperiod and energy constraints, with a shorter duration in environments of lower plant productivity (Bunnell 1980, Nichols and Bunnell 1999).

Age at first reproduction

In the Northern Richardson Mountains, Gwich'in Elders (1997) have mentioned that ewes can first give birth to a lamb when they are between two and four years old. In general, yearlings of 18 months of both sexes (or even younger with supplemental feeding (Hoefs and Nowlan 1993)) may be physiologically ready to reproduce, although only a small proportion of ewes may actually breed at that age. Most adult ewes (older than two years) should be able to engage in reproduction. Research in Alaska reported a 100% pregnancy rate for adult ewes (two years and older) and 75% for yearlings (Nichols 1978a). A much lower proportion will actually give birth to a lamb that will survive the first few weeks of life, which is reflected in the lower values of lamb-to-nursery sheep ratios (Nichols 1978a). In the Mackenzie Mountains (NT), 78% ($N = 94$) of adult ewes and less than half (three of seven) of the 18-month-old yearlings were pregnant (Simmons *et al.* 1984). Ewes were reported to produce lambs until 16 years of age, although no lambs were seen with ewes older than that (the oldest ewe recorded was 19 years of age, as described by Nichols, 1978). Twin births are very rare for thinhorn sheep and most ewes give birth to a single lamb (Nichols 1978a, Nichols and Bunnell 1999).

Rams usually have to wait a few more years (around seven years old) before being able to participate in the rut because of behavioural constraints imposed by older rams (Geist 1971, Nichols 1978b, Nichols and Bunnell 1999). In the Richardson Mountains, Barichello *et al.* (1987) reported that all five-year-and-older rams were accompanied by ewes during the 1985 rut, and observed a four-year-old ram courting a ewe. These observations were made when the population was low and increasing. Generally, the capacity of ewes and rams to participate in reproduction activities depends on how much energy reserves they were able to store during the previous summer (Nichols 1978a).

2.4. Limiting factors

Although causes of mortality for Dall sheep in the Northern Richardson Mountains have not been monitored, one may reasonably assume that fluctuations in this population are related to a combination of factors varying from year to year. As for other mountain sheep populations, factors that can limit or regulate population growth generally fall into one of the following categories: weather and snow conditions, density dependence, competition with other species, predation, diseases and parasites, and harvest. The following paragraphs describe how each of these factors may have a limiting effect on this population, based on knowledge acquired about this and other mountain sheep populations. Moreover, accidental falls and research-related mortality can cause occasional deaths and are discussed at the end of this section.

2.4.1. Weather and snow conditions

Environmental conditions can have a strong impact on thinhorn sheep survival and productivity. Being located at the northern edge of the species range, Dall sheep in the Northern Richardson Mountains are limited by a shorter plant growth season and exposed to more severe winter conditions than most other populations of mountain sheep. Prolonged periods of extremely cold temperatures consume large reserves of energy from the sheep, and therefore result in higher mortality and lower birth rates (Burles and Hoefs 1984). Cold summers are associated with brief periods of vegetation growth and the sheep may not be able to accumulate enough fat in such years to cope with the coming winter. On the other hand, warmer summers can be associated with increased plant productivity, which will often result in higher Dall sheep survival and productivity rates. Higher levels of spring and summer precipitation have been shown to improve neonatal survival for bighorn sheep (Portier *et al.* 1998). The snow layer on the ground can also affect the sheep in the winter, as more snow may translate to more energy spent to escape from predators and a reduced food intake (Murphy and Whitten 1976, Chappel and Hudson 1978, Goodson *et al.* 1991). Moreover, the horn growth of Dall sheep rams has been linked to cyclic climate and precipitation patterns in the southern Yukon, as warmer years were associated with greater horn growth (Hik and Carey 2000).

The weather station closest to the Northern Richardson Mountains is in Aklavik (Environment Canada) and has recorded temperatures, snow and rain precipitation since 1926 (data missing 1960 to 1991). Between 1928 and 2006[1], the average temperatures in January and July were –27.8°C and 13.6°C respectively; and the average annual precipitation was 236 mm. with snow comprising about half of the total. Additional weather stations are located in Fort

[1] Only years with 12 months of data were included ($N = 40$). Data accessed online at: http://www.climate.weatheroffice.ec.gc.ca, on June 1, 2009.

McPherson and Inuvik. To gain further insights into the climatic conditions prevailing in the sheep range itself, and to relate the weather to Dall sheep movements and habitat use, the Gwich'in Renewable Resources Board installed a weather monitoring station on top of Black Mountain in 2006. The station however malfunctioned shortly after deployment.

2.4.2. Density dependence

For Dall sheep, the carrying capacity of a habitat has been related to the capacity of the winter range to sustain a certain density of population (Nichols and Bunnell 1999). The effect of density dependence on mountain sheep populations has been documented in earlier studies (Murie 1944, Geist 1971) and recent investigations have continued to confirm its important role in population regulation. Bighorn sheep in the Canadian Rockies, particularly lambs, were found to have lower survival rates when the population was at high densities (Portier *et al.* 1998). For Soay sheep (*Ovis aries*) in Scotland, density dependence was identified as one major contributor to population growth, in combination with climate (Milner *et al.* 1999, Coulson *et al.* 2001, Forchhammer *et al.* 2001, Coulson *et al.* 2008). In general, high sheep density will make lambs and juveniles more sensitive to harsh environmental conditions (Portier *et al.* 1998, Forchhammer *et al.* 2001). A decline in the sheep population will usually reduce grazing intensity on the land and allow the vegetation to grow back.

Using available data, the lamb to nursery sheep ratios showed little correlation to the population abundance estimates for the same year (correlation coefficient r = -0.16), although it related to a certain extent to the previous survey abundance (r = 0.414). However, annual counts are necessary in order to accurately relate spring lamb production to the previous year density. Dall sheep population surveys in the Northern Richardson Mountains have not been conducted annually, making conclusions based on an evaluation of the effect of density dependence on the following year's lamb production tenuous.

2.4.3. Interspecific competition

Similar to density-dependent, competition with other species could result in lower population productivity and reduced survival. The influence of interspecific competition on thinhorn sheep has not been often investigated, but has been regarded as minimal because few other species occur on sheep wintering habitat (Nichols and Bunnell 1999). Potential competition interactions have however been suggested between mountain sheep and goats (*Oreamnos americanus*), barren-ground caribou (*Rangifer tarandus groenlandicus*), bison (*Bison bison*), marmots (*Marmota* spp.), ground squirrels (*Spermophilus parryii*), and free-ranging domestic horses and feral ass (*Equus* spp.) (Hoefs and Brink 1978, Nichols and Bunnell 1999, Marshal *et al.* 2008).

In the Northern Richardson Mountains, muskox (*Ovibos moschatus*), the Porcupine herd of barren-ground caribou, and moose (*Alces alces*) are the other ungulates sharing the land with Dall sheep and may compete with them through resource exploitation or direct interference. Ground squirrels and snowshoe hare (*Lepus americanus*) can also be found throughout the sheep range and could contribute to interspecific competition with sheep by reducing plant biomass during the summer season.

The Porcupine caribou is a large herd that migrates across northern Alaska, the Yukon, and the northwest limit of the Northwest Territories. Based on aerial surveys, the population was estimated at 123 000 in 2001, and is believed to currently number between 90 000 and 100 000 animals (Porcupine Caribou Management Board website[1]). The Richardson Mountains are located at the eastern limit of the herd's range, and groups of caribou can be seen in the area throughout most of the year, with higher densities during the spring and fall migrations (Russell and McNeil 2002). Caribou diet is similar to that of sheep and muskoxen (which are mostly grazers), and composed mainly of lichens and mosses during the winter, with an increase in vascular vegetation during the spring and summer (including cottongrass, willows, dwarf birch, forbs) (Thompson and McCourt 1981).

Moose, in contrast, do not migrate and are mostly browsers. Moose are usually found in the valleys and the lower slopes where they can find a higher abundance of willows (*Salix* spp.), one of their main food sources, especially in the winter (Risenhoover 1989). The moose density in the Richardson Mountains was estimated at 4.8 / 100 km^2 in 2000 (D. Cooley, Environment Yukon, unpublished), and at 3.78 / 100 km^2 in 2006 (Lambert Koizumi 2006).

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[1] Accessed at: http://www.taiga.net/pcmb/population.html, on April 6, 2010.

After being extirpated from Alaska in the late 1800s, a small group of muskoxen were reintroduced in 1969–1970 and have since expanded their range eastward into the Yukon North Slope and adjacent areas (Reynolds 1998). Muskoxen are now sharing the habitat occupied by this sheep population in the Northern Richardson Mountains and have been located several times in close proximity to Dall sheep groups. When Barichello and colleagues worked in the area, only one muskox was observed in 1984 (Barichello *et al.* 1987). A group of 46 muskoxen was observed in 2003 in the Goodenough survey block (Nagy *et al.* 2006a); 52 muskoxen were reported during a moose survey in March 2006 (Lambert Koizumi 2006); and 98 were counted during the 2006 Dall sheep survey, also in the same area (Davison and Cooley 2006; but the group may have been double-counted (D. Cooley, Environment Yukon, pers. com.)). Effect of muskoxen on this Dall sheep population have not been investigated, although Gwich'in elders and harvesters of Aklavik, Fort McPherson, and Inuvik have reported concerns of potential negative interactions (Shaw *et al.* 2005).

2.4.4. Predation

Dall sheep must be constantly vigilant to avoid predators. Escape to rugged areas is their main defense mechanism. Interviews with elders and active land users in Aklavik, Fort McPherson and Inuvik in 2000 and 2001 indicated that Dall sheep may be prey to wolves, grizzly bears, wolverines (*Gulo gulo*), black bears (*U. americanus*), golden eagles (*Aquila chrysaetos*), and potentially cougars (*Puma concolor*) that are believed to occasionally transit through the area (Shaw *et al.* 2005). Foxes (*Vulpes vulpes*) and lynx (*Lynx canadensis*) are also present and may occasionally prey on weak individuals or newborn lambs.

Barichello *et al.* (1987) found that one to three of the four ram mortalities recorded during monitoring of 12 collared sheep were likely caused by wolves. Research done in the 1990s indicated that wolves in the Northern Richardson Mountains and on the Yukon North Slope prey primarily on moose (*Alces alces),* and seasonally on the herd of Porcupine caribou crossing the area (Hayes *et al.* 1997, Hayes and Russell 1998, Hayes *et al.* 2000). However, in other areas it has been shown that wolf packs can significantly limit mountain sheep populations (Nichols 1978b, Sawyer *et al.* 2002). Research in Kluane and Denali National Parks demonstrated that predation can cause significant Dall sheep mortality (Murie 1944, Sumanik 1987, Mech *et al.* 2003). Moreover, recent declines of Cape Bathurst and Bluenose-West barren-ground caribou herds in the adjacent Northwest Territories (Nagy and Johnson 2006), combined with a decline in the Porcupine caribou herd (Porcupine Caribou Management Board 2007, Fisher *et al.* 2008) could mean that alternate prey such as Dall sheep will suffer from higher predation rates because of lower caribou availability (i.e., prey switching (Dale *et al.* 1994)). At present, there is subsistence harvesting of wolves in the area, with no management plan in place.

Grizzly bears are common in the Northern Richardson Mountains, and information from traditional knowledge (Shaw *et al.* 2005) and aerial surveys (Nagy *et al.* 2006a, Nagy *et al.* 2006b) indicate close spatial associations between grizzly bears and Dall sheep. During the 2001 surveys, most grizzly bears were observed along the continental divide (YT-NT border), with some individuals in the eastern part of the range (Nagy *et al.* 2006b). In 2003, dens were observed along the continental divide, but most grizzly bears were observed along the eastern limit of the range, in the Black Mountain and surrounding areas (Nagy *et al.* 2006a). Research in Alaska identified grizzly bears as the main predator of moose and caribou calves (Ballard and Miller 1990, Adams *et al.* 1995) and their potential as an ungulate predator seems to be higher when ungulates are only few weeks old (Zager and Beecham 2006). On the NT side, grizzly bear harvest is restricted to subsistence users and is regulated by a management agreement in the Gwich'in Settlement Area and quotas in the Inuvialuit Settlement Region. On the Yukon side, in addition to aboriginal subsistence harvest, resident hunters may harvest one grizzly bear every three years during the spring and fall hunting seasons (2009–2010 Hunting regulations summary booklet, YT Government, Department of Environment[1]). Since 1980, there has been only one grizzly bear killed by a licensed Yukon resident hunter in the Northern Richardson Mountains (Yukon Government, unpub. data).

Golden eagles can also prey on Dall sheep lambs, particularly during the first few days of life. Numerous attacks on lambs were recorded in the southern Yukon during an observation study (Barichello *et al.* 1991), although only one successful case of predation was observed. Ewes are highly protective of their lambs. Golden eagles are known to nest on the cliffs of the Richardson Mountains

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[1] Accessed online at:
http://www.environmentyukon.gov.yk.ca/huntingtrapping/documents/hunting_regs_0910web.pdf, on September 25, 2009.

in the summer and predation on neonates is believed to occur (Gwich'in Elders 1997, Shaw *et al.* 2005). The 2001 and 2003 aerial surveys reported observations of golden eagles throughout the range (Nagy *et al.* 2006a, Nagy *et al.* 2006b).

Because of the remoteness of this mountain range and the lack of an easy access, characterizing predation events and following the fates of a large number of Dall sheep would require intense monitoring and necessitate considerable financial and human resources. However, the investigation of indirect effects of predation is more easily done and may reveal important patterns and mechanisms underlying predator-prey interactions. Indirect, or non-consumptive, effects on prey species include vigilance behaviour, reduced feeding, altered activity budget, and habitat shift (Schmitz *et al.* 2004). These indirect effects are ubiquitous and can be determinants in shaping the spatial dynamics and behaviour of prey (Abrams 2008, Altendorf *et al.* 2001, Corti and Shackleton 2002, Peckarsky *et al.* 2008), which need to balance foraging needs and predation risk. Predators then respond to the prey behaviour and spatial distribution (Iwasa *et al.* 1981, Lima 2002).

In 2006, a study was launched to assess these indirect effects of wolves and grizzly bears on Dall sheep in the Northern Richardson Mountains (Gwich'in Renewable Resources Board and University of Alberta, C. Lambert Koizumi *et al.*[1]). The study focused on spatial interactions between the three species and their habitat use, on the wolves and the grizzly bears' diet, and on Dall sheep vigilance behaviour during lambing season. Six Dall sheep ewes, nine wolves, and 15

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[1] Refers to the research presented in this thesis.

grizzly bears were equipped with GPS satellite collars in 2006 and 2007. The last collars released in the autumn 2009 and results are presented in the subsequent chapters of this thesis.

2.4.5. Parasites and diseases

Neither parasites nor diseases have been documented as a primary factor in controlling thinhorn sheep populations (Nichols and Bunnell 1999). Elders and harvesters have characterized Dall sheep in the Northern Richardson Mountains as generally healthy with very few parasites or diseases (Shaw *et al.* 2005). Domestic sheep or goats are generally not present on the range of thinhorn sheep, and they have not been subject to epizootic pneumonia like the bighorn sheep (George *et al.* 2008, Schommer and Woolever 2008). Dall sheep can nevertheless carry a variety of disease agents. Gastrointestinal parasites are common but are not generally in high enough loads to impair digestive function. These parasites can be detected by examining the feces of the sheep or by conducting a necropsy. Other common parasites include few species of lungworms and other nematodes as well as various protozoa (see Bowyer and Leslie 1992). Common diseases include viral or bacterial infections such as arboviruses, contagious echthyma virus, brucellosis, parainfluenza virus, rickettsia, epizootic hemorrhagic disease, chronic pneumonia, and necrosis of the horn cores. Also quite common is mandibular osteomyelitis (lumpy jaw) (Murie 1944), affecting approximately 23% of a large sample of Dall sheep skulls (N = 1,481) from across the species range (Hoefs 2001). To our knowledge, this condition has not been reported for

Dall sheep in the Richardson Mountains. Mandibular osteomyelitis can lead to distorted jaw and tooth infections but has not been related to direct mortality of affected individuals –although they may become more prone to starvation or predation (Murie 1944, Bunch *et al.* 1999).

The emergence of new parasites in Dall sheep range could become more common in the future as global climate warming continues (Kutz *et al.* 2004, Jenkins 2005). For 12 of the 13 rams captured in the 1980s, fecal analysis identified the presence of larvae of undetermined species of the genus *Protostrongylus* (Barichello *et al.* 1987). More recently, two species of lungworms (protostrongylids: *Parelaphostrongylus odocoilei* and *Protostrongylus stilesi*) were detected in Dall sheep of the Mackenzie Mountains (Kutz *et al.* 2001), which led to more lungworm research in the population of the Northern Richardson Mountains. Three sheep harvested on Black Mountain were confirmed hosts of *P. stilesi* (Hoberg *et al.* 2002). The same parasite was also detected in two adult muskox on the Yukon North Slope (Hoberg *et al.* 2002). *P. stilesi* can switch between the two hosts, and the overlap between muskox and Dall sheep could cause the infection in the muskox population (Dall sheep are the typical host and are believed to be the original carrier of this lungworm (Hoberg *et al.* 2002)). On the other hand, *Umingmakstrongylus pallikuukensis*, a lungworm affecting muskox, could not switch to a Dall sheep host under experimental conditions (Kutz *et al.* 2004). No occurrence of *P. odocoilei* has been reported for Dall sheep in the Richardson Mountains (Jenkins 2005) but based on experimental infection trials, this parasite could lead to respiratory distress and increase chances of mortality (Jenkins *et al.* 2005). The effect of these parasites on the Northern Richardson population is unclear, and the massive die-offs observed in bighorn sheep populations (Bunch *et al.* 1999) have not been observed for Dall sheep.

2.4.6. Harvest

Mountain sheep are sensitive to harvest and this Dall sheep population is no exception. What is known of harvest levels and a discussion on the impact of hunting in the Northern Richardson Mountains can be found in Section 2.6.

2.4.7. Other mortality factors

Dall sheep are extremely agile and can admirably handle steep cliffs and rocky slopes. However, under certain icy conditions or as a result of avalanches, some individuals may lose their balance and die from an abrupt fall. Accidental falls are not believed to be very common, although some elders and harvesters have indicated observing such mortality events (Gwich'in Elders 1997). During the retrieval of radio-collars in 2005 and 2006, three sheep carcasses were found at the bottom of steep canyons (C. Lambert Koizumi, personal observation). While several factors could have lead to the death of those individuals, accidental fall stemmed as one potential reason. According to Nichols and Bunnell (1999), animals in poor body condition are more susceptible to accidental falls, as well as rams that are inattentive during the rut (i.e., during ram clash).

Moreover, there have been numerous concerns expressed about the effects of research on Dall sheep in the Northern Richardson Mountains (C. Lambert

Koizumi, personal observation from attendance at community meetings). Some elders have claimed that sheep die as a result of being captured or collared. Although the scientific community may minimize the impact of research activities, the effect of handling and collaring on sheep should not be understated. Capture has the potential to cause injuries, produce excessive stress, and lead to capture myopathy. Capture myopathy is a syndrome that can appear from several hours to two weeks after capture, and causes symptoms such as hyperthermia, renal failure, shock, muscle diseases, and sudden death (Bunch *et al.* 1999). Capture myopathy can be prevented by reducing chase time, handling time, and ensuring that few and only experienced people participate in the capture and handling. Other problems to consider are neck lesions and higher energy expenditures related to the wearing of a collar. Krausman *et al*. (2004) observed a high rate of neck lesions for bighorn sheep fitted with collars equipped with GPS and satellite technology, in contrast to the smaller VHF-only collars. Such lesions could be detrimental to the body condition, reproductive success, or even survival of the collared individuals. Continued improvement of radio collar equipment is needed so that smaller transmitters can yield the same amount and quality of information. Before starting research on this population, careful consideration should be given to the study question, experimental design, and selected methods. As much as possible, methods with less impact or disturbance should be chosen.

2.5. Habitat

2.5.1. Description

The Northern Richardson Mountains are located above the Arctic Circle ($67^{o}30'$ – $68^{o}30'$ N, $135^{o}30'$ – 137^{o} W) and are part of the British-Richardson Mountains ecoregion, in the Taiga Cordillera ecozone (Scudder 1997). The mountains in this ecoregion are largely unglaciated, resulting in steep, V-shaped valleys at higher elevations and more gentle lower slopes along the broader valleys. The mountains range between 400 and 1200 m, with the highest peaks in the centre of the range, at the NT-YT border (i.e., the Continental Divide). The Northern Richardson Mountains are bordered on the south by the Peel River Plateau, on the east by the Mackenzie Delta, on the north by the Yukon Coastal Plain (which ends in the Beaufort Sea), and on the west by the British Mountains and Old Crow Flats. Major rivers flowing through the range are the Bell River, Rat River, Fish Creek, Sheep Creek, and Willow River.

The vegetation of the Northern Richardson Mountains is dominated by alpine tundra, and treeline is located at approximately 300 m above sea level (Smith *et al.* 2004). Tree species, mostly black spruce (*Picea mariana*) and balsam poplar (*Populus balsamifera*), occur only in protected valleys with favorable exposure (Barichello *et al.* 1987). As discussed in section 2.3.1, most of the Richardson Mountains remained unglaciated during the Pleistocene, except for the eastern flanks of the range. The passage of the glaciers mostly affected the eastern valley bottoms, while the ridges and slopes stayed mainly free of ice. Repercussions of glaciations are evident in the plant communities today, with slopes dominated by lichens and forbs, and drift valley bottoms covered in moss, grass, and sedge communities (Smith *et al.* 2004). Typical plants of the Northern Richardson Mountains include cottongrass and other sedges (*Eriophorum* spp., *Carex* spp.), mountain avens (*Dryas* spp.), alpine bearberry (*Arctostaphylos alpina*), willows (*Salix* spp.), dwarf birch (*Betula glandulosa*), saxifrages (*Saxifraga* spp.), Arctic white heather (*Cassiope tetragona*), black crowberry (*Empetrum nigrum*), cloudberry (*Rubus chamaemorus*), blueberries (*Vaccinium* spp.), moss campion (*Silene acaulis*), peat moss (*Sphagnum* spp.), and diverse lichens (*Cladonia* spp., *Cladina* spp., *Stereocaulon pascale*, etc.) (Scudder 1997, personal observations). Higher peaks and steep slopes are mostly rocky and non-vegetated. The entire range is mainly composed of sedimentary rock (Smith *et al.* 2004), and underlaid by permafrost (Scudder 1997).

The area inhabited by Dall sheep covers approximately 4 000 km^2 (derived from the area encompassed by the 12 survey blocks), although only about 50% of the range appears suitable for Dall sheep (locations above treeline providing adequate access to pasture and escape terrain) (Barichello *et al.* 1987).

2.5.2. Dall sheep habitat use

Both traditional knowledge and scientific studies have confirmed that Dall sheep in the Northern Richardson Mountains move between various habitats during the year, depending on the available forage and on their reproductive status

(Barichello *et al.* 1987, Gwich'in Elders 1997). During winter, thinhorn sheep generally remain at higher elevation, and in proximity to rugged areas that act as escape terrain – taking advantage of wind-blown areas, which facilitate locomotion and food access, and minimize predation risk (Geist 1971, Nichols and Bunnell 1999). During the spring, they venture to lower elevations to take advantage of nutritious newly emergent vegetation and to drink from the creeks (Gwich'in Elders 1997). As the snow melts, pregnant ewes will then seek safe ground to give birth, usually in proximity to escape terrain (or right on a steep cliff), and rejoin the other ewes a few days after their lambs are born. Lambing areas have been identified around Black Mountain, Mount Lang, Sheep Creek, Summit Lake, Fish Creek headwaters, Bear Creek, Scho Creek, and Bell River (Barichello *et al.* 1987). The ewe and lamb pairs, along with yearlings and barren ewes, then form nursery groups and stay together for most of the summer, usually in proximity to escape terrain (Rachlow and Bowyer 1998). The groups of rams, being less susceptible to predation, tend to go further away from escape terrain and benefit from higher quality of forage. During the rut, in late autumn, bands of rams and nursery sheep congregate close to the winter range where they will stay for the following months. In late fall, the sheep who ventured to the western portion of the Richardson Mountains during the summer seem to return to the Black Mountain area (Simmons 1973).

In the early 1980s, 12 rams were fitted with VHF collars in the Northern Richardson Mountains and relocated on a monthly basis (Barichello *et al.* 1987, Barichello and Carey 1989). As with most other populations, the winter range of

Dall sheep in the Northern Richardson Mountains was constricted compared to the habitat used in other seasons, and Dall sheep seemed to move less extensively during the winter season (total home range size between 10 and 50 km^2, with a winter home range between 3 and 26 km^2) (Barichello *et al.* 1987). Longer movements were recorded in June and October. On an annual basis, rams appeared to be faithful to summer and winter ranges (Barichello and Carey 1989).

Because of the limited information yielded by VHF collars, a habitat selection study was started in 2004 and 2005 by the Gwich'in Renewable Resources Board (D. Auriat, unpub.), in collaboration with the NT Government. Eight rams were equipped with GPS satellite collars and their location was recorded every four hours. Random and used sites were sampled for vegetation and characterized during the summers 2004 and 2005, with the intent of analyzing fine-scale habitat selection of this population. Results have yet to be made available, but the ram locations were combined with the data of ewes collared in 2006 to provide a basis for evaluating habitat use of rams and ewes in this population[1].

To assess the productivity of this range and verify whether Dall sheep could be limited by density dependence or competition with other ungulates, four exclosures were installed in the Northern Richardson Mountains in 2004 (Gwich'in Renewable Resources Board, D. Auriat). The objective was to compare vegetation biomass and composition between grazed versus protected sites (similar to what Hoefs (1984b) did in Kluane National Park). The experiment was

[1] Habitat use analyses are presented in Chapter 4 of this thesis.

unsuccessful because the fence installations did not properly exclude ungulates (one was hit by a snowmobile and another was used as a scratching post by a herd of muskoxen). Little information is available regarding this range's productivity.

2.5.3. Mineral licks

Similar to other mountain sheep, minerals are vital to thinhorn sheep. Licks can be used for many years and are believed to provide important minerals necessary for growth (particularly sodium, magnesium, and calcium lost during the winter) and lactation, in the case of nursing ewes (Nichols and Bunnell 1999). Nursery groups stay in proximity of mineral licks, especially during the spring and summer seasons (Nolan and Kelsall 1977). In the Northern Richardson Mountains, the serum analysis of 12 rams identified low levels of copper, iodine, and calcium, which could indicate deficiencies in these minerals (Barichello *et al.* 1987). In their habitat assessment, Nolan and Kelsall (1977) identified four lick areas in the Northern Richardson Mountains: Bear Creek headwaters, southwest of Black Mountain, Rat River Pass, and south of Sheep Creek. A mineral analysis of the licks found the presence of silicon, barium, iron, manganese, titanium, rubidium, and zirconium (trace). Traces of zinc and lead or arsenic were also found in the Bear Creek lick, and arsenic in the Rat Creek lick (Nolan and Kelsall 1977). More licks were later identified between Black Mountain and Mount Lang and east of the headwaters of Little Bell River (Barichello *et al.* 1987). Local and traditional knowledge also reported licks along the valleys of Fish Creek, on a creek south of Twin Lake, and south of Long and Ogilvie Lakes (Shaw *et al.* 2005).

2.5.4. Land use, development and climate change

The Richardson Mountains are an area of high traditional use by the Gwich'in, Vuntut Gwitchin, and Inuvialuit peoples. A number of Gwich'in archaeological sites exist along the main drainages, and various routes and family trails were established generations ago to travel between hunting and meeting areas (Haszard and Shaw 2000). Today, the Richardson Mountains are still widely used by the Gwich'in from Fort McPherson and Aklavik, the Vuntut Gwitchin from Old Crow, and the Inuvialuit from Aklavik and Inuvik, and are considered a prime area for hunting large mammals like caribou, moose, Dall sheep, and grizzly bears. The Richardson Mountains fulfill the subsistence and recreational needs of many northern peoples.

A portion of the Northern Richardson Mountains in the Gwich'in Settlement Area was classified as a special management zone for *Vàdzaih* (Porcupine caribou) and the *Ddhah zhit han, Eneekaii han, Chii gwaazraii* (Rat River, Husky Channel, and Black Mountain area) form a conservation zone to protect wildlife, land, and traditional uses in these areas (Gwich'in Land Use Planning Board 2003). The potential for sport hunting (i.e., hunting by non-beneficiaries), particularly for Dall sheep, has been recognized and could be implemented if local organizations are supportive (Gwich'in Land Use Planning Board 2003). In the Yukon, west of the *Ddhah zhit han, Eneekaii han, Chii* *gwaazraii* conservation zone, the Summit Lake – Bell River area was designated as a protected area and the adjacent land is currently part of the North Yukon Land Withdrawal. As such, it is not available for mineral or oil and gas disposition or exploration (North Yukon Planning Commission 2009). In the Inuvialuit Settlement Region, the area is also subject to the Aklavik Community Conservation Plan (Wildlife Management Advisory Council (NWT) 2000). In this plan, the portion of this Dall sheep population within the Inuvialuit Settlement Region is contained in a special subregion managed to eliminate damage and disruption, as much as possible. This Aklavik subregion, *725D-Eastern North Slope, East of Babbage River* is also recognized to contain important habitat for thinhorn sheep, including lambing, rutting, winter range and migration corridors. Specific conservation measures in the Aklavik Community Conservation Plan include recommendations not to harvest when Dall sheep are pregnant (November to May), to harvest sustainably and to prevent disruptive land use by identifying and protecting important sheep habitats.

Although the area is presently relatively pristine, potential oil and gas development in the adjacent Mackenzie Valley, or on the Yukon or Alaska North Slope, could leave a heavy footprint. Oil reserves and gravel deposits may be found in the Rat River watershed, although there is currently no plan for a pipeline or gravel extraction (Gwich'in Land Use Planning Board 2003). However, if the Mackenzie Gas Project goes ahead, predictions are that the Richardson Mountains would be developed within 30 years (Holroyd and Retzer 2005). Exploration surveys started in 2006 (geological field trip of Devon

Canada) and more could happen in the future. As previously noted, mountain sheep are very sensitive to sensorial disturbances such as aerial overflights or nearby human presence, and can respond dramatically (Krausman and Hervert 1983, Bleich *et al.* 1994, Frid 2003, Loehr *et al.* 2005). The level of response varies between populations and depends on the perceived level of risk. If a disturbance is repeated and is not associated to a negative consequence; however, Dall sheep could become habituated and tolerant. Based on the research of Frid (2003), YT Government recommends that pilots should, in order to mitigate the effect of flying over the sheep ranges: (1) plan the route to avoid known sheep range and sensitive areas; (2) if flying near the sheep range is necessary, keep the distance from the aircraft to the sheep greater than 3.5 km (i.e., by increasing altitude of aircraft or deviating the flight path); (3) maintain an altitude lower than the sheep, when closer than 3.5 km; (4) minimize the number of flights; (5) fly during the sheep's active period; (6) fly at an angle (not directly towards) when approaching the sheep; and (7) not hover over or circle the sheep groups (Leberge Environmental Services 2002).

Additionally, the Aklavik weather data (Environment Canada[1]) reveal an increase in temperatures and in precipitation during the past few decades. Annual average temperature between 1928 and 1958 was –9.01°C and rose to –8.00°C between 1991 and 2006 (one-way t-test: $t_{38} = -2.96$, $P = 0.003$). Average precipitation (rain and snow combined) also increased from 213 to 273 mm for the same two periods ($t_{38} = -2.39$, $P = 0.011$). These trends are consistent with

[1] Data accessed online at: http://www.climate.weatheroffice.ec.gc.ca, on June 1, 2009.

regional and international climate analyses that have revealed warming temperatures in the Western Arctic, placing this area amongst the most affected by climate change (Walther *et al.* 2002, Parmesan 2006). A rapid warming will likely influence abundance and composition of vegetation, wildlife, and parasite agents. A longer plant growing season could mean enhanced productivity of this sheep population, although this simple relationship is complicated by a number of factors, including population fluctuations in some species (potential changes in competition and predation interactions), range shift in others (e.g., appearance of cougars), as well as the spread of new diseases and parasites (Kutz *et al.* 2004). The Northern Richardson Mountains are likely to undergo significant changes in the future, and there is a need to assess the current species' status and interactions in order to monitor future changes and ensure sustainable management of land and wildlife in this region.

2.6. Harvest and non-consumptive uses

2.6.1. Traditional use

Because they are associated with steep slopes, high peaks, and relatively inaccessible terrain, Dall sheep are notoriously challenging to hunt. Hunting Dall sheep can be dangerous and experienced hunters sometimes ambushed sheep at river crossings and in shrubs, where the escape terrain is generally more distant and the access easier (Gwich'in Elders 1997). Because Aklavik is the nearest community to the Northern Richardson Mountains, most sheep hunters are based in Aklavik. Eighteen interviews conducted with Elders and harvesters in the Gwich'in Settlement Area (Shaw *et al.* 2005) suggested that at least 130 sheep were harvested between the 1930s and the 1990s, mostly in the 1950s and 1960s. This is likely an artifact of the age of the interviewees, with the most active hunting period coinciding with their middle years. Interestingly, of the nine persons who reported hunting sheep (C. Lambert Koizumi, unpublished data), about half of the harvest was attributed to two hunters, who were apparently highly skilled in sheep hunting. Most of the harvest was done in the wintertime, with access facilitated by dog teams in the older days, and more recently by snowmobile. Moreover, the harvest tended to be equally distributed between adult ewes and rams, with very few lambs and younger animals taken (Shaw *et al.* 2005). This was a subsistence harvest and in times of scarcity, hunters would take whatever animals were available to them. When the hunters could choose, the rams were sometimes preferred because they had more meat; but after the rut, the ewes were fatter and tastier (Gwich'in Elders 1997). After a sheep was harvested, its muscles and organs were consumed (heart, kidney, liver and stomach; the lungs were dog food); its hide was used to make clothing, blankets or babiche; its gall bladder was used as a wound-healing medicine; and its horns were carved into various tools (e.g., spoons, forks, knife handles, fishing hooks) (Gwich'in Elders 1997).

2.6.2. Contemporary harvest levels

Inuvialuit in the Inuvialuit Settlement Region and Gwich'in in the Gwich'in Settlement Area have preferential rights to the harvest of Dall sheep, which means that their basic needs level has to be fulfilled before harvest can be allocated to other groups, such as residents and non-residents hunters (as described in the Inuvialuit Final Agreement, the Gwich'in Comprehensive Land Claim Agreement). The Vuntut Gwitchin First Nation Final Agreement does not make specific reference to Dall sheep harvest, but the species is addressed by the general provisions of the agreement.

In the Yukon, the Vuntut Gwitchin community of Old Crow is the primary user group of Dall sheep in the Northern Richardson Mountains, and there is only a small level of harvest. There has been no harvest of Dall sheep reported by the Vuntut Gwitchin in the last three years (Vuntut Gwitchin, unpub. data). Anecdotal information indicates a minimum of 11 sheep taken between 1995 and 2008 (S. Foss, Vuntut Gwitchin Government, pers. com.), corresponding to a mean of one per year for this period. Between 2004 and 2006, Yukon Government issued two annual resident hunting permits for full curl rams valid in a limited area on the Yukon side of the Northern Richardson Mountains. One kill was reported in each of 2004 and 2005 (J. Carey, unpub.). At the request of other stakeholders, these two permits were not issued in 2007 and 2008, while the management plan for this population was being developed and harvest recommendations formulated. Two permits were issued in 2009; one ram was reported killed (J. Carey, unpub.).

In the Northwest Territories, there is only aboriginal harvesting from this population. There are no limits or conditions on aboriginal harvest of Dall sheep, and reporting is voluntary. However, export permits are required to take wildlife parts out of the Northwest Territories. Also, aboriginal hunters are encouraged to bring all skulls to their local renewable resource office so that the horns can be plugged. This is a requirement for skulls leaving the Territories.

As mentioned in the preceding section, most users of this population come from the community of Aklavik; however the communities of Fort McPherson, Inuvik, and Tsiigehtchic also harvest Dall sheep. Current harvest information is not available for the whole population, but a minimal harvest is available from the horn plug records (Environment and Natural Resources, NT Government), the Inuvialuit Harvest Study (The Joint Secretariat 2003), the Gwich'in Harvest Study (GRRB 2009), and the Inuvialuit Harvest Data Collection Program (Aklavik Hunters and Trappers Committee (HTC)). Overall, the harvest reported in the 1970s was greater than the levels reported in recent years (Figure 2.7).

From 1966 to 1977, an estimated total of 329 sheep were harvested, with an annual average of 33 (range = 5 to 62), according to Simmons (1973) and estimates from the NT Government (letter from W. C. Cleghorn, Indian and Northern Affairs, Ottawa ON, dated May 30 1977). Harvest information is then missing until the Inuvialuit Harvest Study, which ran from 1987 until 1997. During that time, there was an estimated average harvest of two sheep per year (range = 0 to 4), for a total of 15 Dall sheep, all of which were harvested by Inuvialuit members of the Aklavik community (The Joint Secretariat 2003). The final report of the Gwich'in Harvest Study, conducted from 1995 to 2001, reported a Gwich'in participant harvest of nine Dall sheep between 1995 and 1999 (range = 0 to 5 per year) (GRRB 2009), although the published estimate may be revised to be ten Gwich'in participant harvests (K. Callaghan, pers. com.). Harvest by non-Gwich'in indigenous people also documented in this study was 11, for a total of 20 sheep harvested. This harvest by non-Gwich'in indigenous people was not included in other sources of harvest records used in this report (K. Callaghan, unpub.). Thirteen of the harvested sheep were rams, four were ewes, and three were of unknown sex. Most of the harvest ($N = 14$) was reported by Aklavik hunters, followed by Fort McPherson ($N = 4$), Inuvik and Tsiigehtchic ($N = 1$ each). The Aklavik HTC and Yukon Government estimated a small annual harvest between 2001 and 2006 (average = 1.3; range = 0 to 4, unpub. data). A large portion of the reported harvest of Dall sheep occurred in the Black Mountain area near Aklavik. In the Inuvialuit Harvest Study and the Aklavik HTC Harvest Study, 78% and 75% respectively of sheep harvested were harvested from Black or Red Mountain. In the Gwich'in Harvest Study, this proportion was 90% (K. Callaghan, unpub.).

Concerns have been raised in the community of Aklavik about a change in hunting practices where sheep are now being harvested for the commercial value of the cape and horns. In 2006, an Aklavik hunter was charged and convicted for meat wastage in Yukon; it was purported to be a subsistence kill, but the harvester took the cape and horns and left all of the meat behind (J. Carey, unpub.). There has been an increase in sheep parts exported from the Inuvik region during this past decade. There was a yearly average of three sets of horns exported from 2000 to 2003, which increased to seven in 2004, and nine in 2005 and 2006. There were also three hides exported without horns attached between 2000 and 2004. This number rose in 2005 and 2006, to three and five respectively (ENR export permits, unpub.).

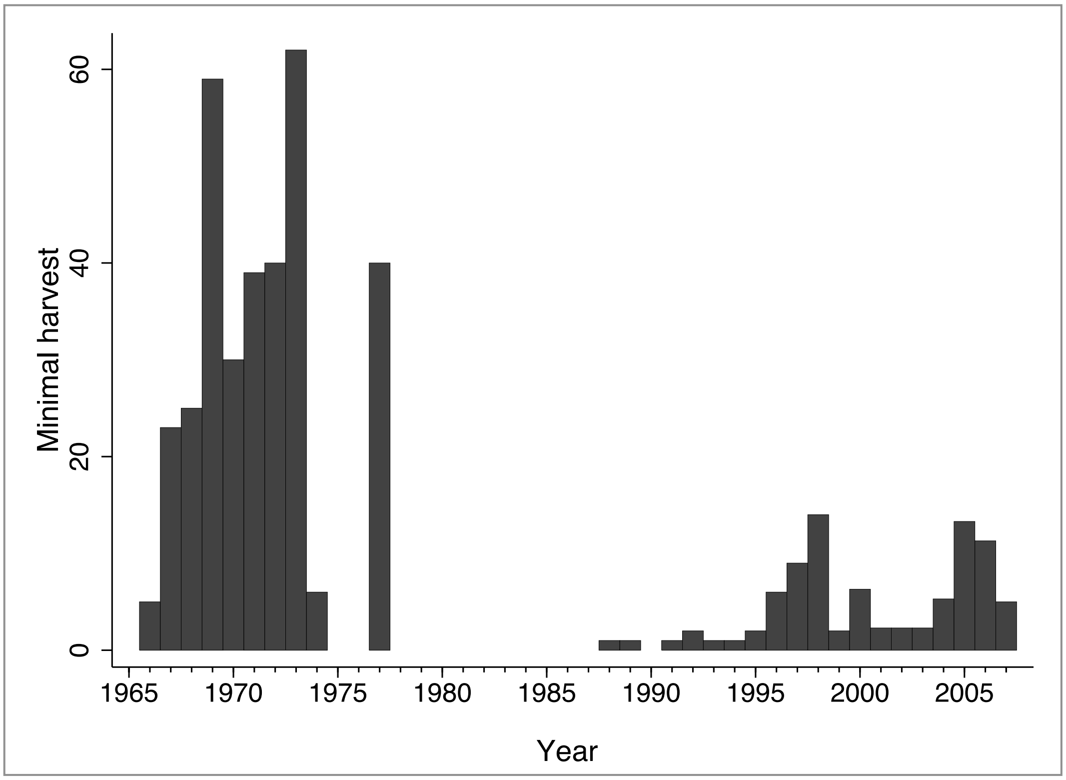

Figure 2.7. Minimum reported harvest between 1966 and 2008, with few missing years (1975-76 and 1978-1987 inclusive).

The harvest levels reported here are deemed minimum estimates and some harvest probably goes unreported. Recent community meetings (2005-06) in Aklavik and Fort McPherson have highlighted concerns related to a potential overharvest of Dall sheep by some harvesters. Meat wastage, caused by exclusive interest in rams with large horns for their economic or trophy value, has also been reported. Stakeholders interested in the management of this population (as listed in 2.2.2.) recommended a closer monitoring of sheep harvest to detect such situations and ensure that Dall sheep harvest remains within sustainable limits.

2.6.3. Estimated impact of harvest

In the 1970s, Simmons (1973) was concerned that the population of Dall sheep in the Northern Richardson Mountains was overharvested. At the time, he estimated that harvest rates were 11% higher than the recruitment rate of the population, and therefore unsustainable. If the aerial survey abundance estimates were correct in 1971, 1972, and 1973 (Table 2.1), between 8% and 60% of the adult population was harvested during these years. Simmons (1973) recommended better harvest monitoring and improved cooperation between hunters and wildlife managers. Nolan and Kelsall (1977) and Hoefs (1978) later reiterated his concerns.

In comparison, recent records show a much lower harvest. Based on the maximum reported value of 14 harvested individuals (in years 1998 and 2005) and applying this harvest level to the most recent (2010) population estimate (N = 699 – 150 lambs – 10 yearlings = 549 adults), the annual harvest would represent approximately 2.6% of the adult population. Based on demographic rates of Dall sheep in the Northern Richardson Mountains estimated in the 1980s, Barichello *et al.* (1987) recommended a harvest rate representing 2.5% of the adult population. However, this 2.5% was based on full curl rams harvest only, which is the regulation applicable for licensed harvest by resident and non-resident hunters in the Yukon. In the case of aboriginal hunting, immature rams and ewes are also harvested. Based on statistics from the Inuvialuit Harvest Study (The Joint Secretariat 2003), the Gwich'in Harvest Study (GRRB 2009) and statistics from NT Government export permits (Environment and Natural Resources, unpub.), the sex ratio of harvested sheep was about one ewe to four rams for the past two decades. In many cases, there is inadequate information on the age of the animals taken, so the proportion of full-curl ram harvest versus immature rams is unknown.

There is some controversy over the consequences of a selective full curl ram harvest versus the mixed harvest of sex and age classes in mountain sheep populations. The removal of ewes and rams younger than full curl could have a profound effect on recruitment and population growth because the reproductive value of these individuals, as actual and future contribution to population growth, is higher than that of full curl rams. In such a scenario, a sustainable harvest rate may in fact be much lower than the proposed 2.5%. This said, a full curl ram harvest only is not necessarily better, since it targets individuals of prime age that are most actively engaged in the rut (Geist 1971). The rams with larger horns socially dominate the younger or smaller rams, and by being reproductively active, are the ones passing their genes on to the next generation. For bighorn sheep (*O. canadensis*) populations that are under a sport-hunting regime, it has been demonstrated that older rams, or even the younger individuals that have faster horn growth, have lower survival rates due to harvest mortality (Bonenfant *et al.* 2009). This selective harvest could counter natural selection processes and lead to some important undesirable consequences at the evolutionary scale, such as reductions in body weight and horn size of rams in the population over time (Coltman *et al.* 2003). Additionally, at very high harvest levels, the loss of most or all of the larger rams could disturb the social structure of the population and favor a higher female ratio and a younger age of males, leading to higher energy expenditures of males during the rut (Singer and Zeigenfuss 2002), which could ultimately depress the recruitment rates (Milner *et al.* 2007).

However, the examination of horns from over 8000 rams in the southern Yukon indicated that horn growth is positively correlated with climate patterns and habitat productivity (Hik and Carey 2000, Loehr *et al*. 2010), suggesting that the removal of larger rams does not necessarily interfere with the capacity of producing high quality rams in the future. Investigations of hunted versus unhunted Dall sheep populations in Alaska indicated no impact of older ram removal on population productivity, nor on younger rams' survival (Murphy *et al.* 1990). Rams with larger horns are, in general, close to the end of their life and the hunting mortality of this older age class could be compensatory (i.e., the rams would have otherwise died of natural cause) (Hoefs 1984a). This argument seems supported by horn measurements of rams that died from hunting and from natural causes in the southern Yukon (Hik and Carey 2000, Loehr *et al.* 2007). In either case, rams with faster horn growth appeared to die earlier. This suggests a natural tradeoff between growth rate and longevity, and the selective hunting of large rams may have effects similar to natural mortality. A detailed assessment of sustainable harvest rates for this population has been regarded as necessary by the partners of the management plan for this Dall sheep population.

2.6.4. Non-consumptive use

Interest in this Dall sheep population is certainly not limited to harvest. Despite the sheep population being located in a range with limited access, community members and the public in general, greatly value the presence of sheep in the Northern Richardson Mountains and find it gratifying to know that there are Dall sheep in these mountains (C. Lambert Koizumi, unpub. results from Gwich'in Renewable Resources Board management questionnaire 2005). A number of people are also interested in viewing or photography opportunities. Some hunters and families from adjacent communities camp regularly in the area, monitoring the number of sheep year after year and watching for any unusual events disturbing to this population or its habitat. Tourists from the NT, YT, and elsewhere also venture into the Northern Richardson Mountains, sometimes through aircraft or boat access, and can spend days (or weeks) hiking, skiing, or paddling the range. This type of adventure tourism can be very lucrative for the local communities, and some people have expressed the wish to keep a section of the mountains unhunted and undisturbed by other activities, which would facilitate viewing opportunities and support non-consumptive use of this Dall sheep population (C. Lambert Koizumi, unpub. results from Gwich'in Renewable Resources Board management questionnaire 2005).

2.7. Education and information exchange

The management plan for Dall sheep in the Northern Richardson Mountains emphasizes the importance of educating youth in the nearby communities in regards to Dall sheep and keeping communities informed about research and management plans. As such, the following activities are important and may ultimately contribute to the conservation of this Dall sheep population: participation of community members (harvesters, youth, elders, etc.) in field studies, visits and public talks by Dall sheep researchers in schools and community halls, school trips bringing students on the sheep range (e.g., as the Moose Kerr School students in Aklavik have done in previous years), updates from renewable resource officers and councils to the communities, documentation of local and traditional ecological knowledge, and frequent exchanges about the status and concerns related to this population.

The implementation of these activities is an ongoing process contingent on the goodwill of individuals involved in the research and management of this Dall sheep population, and facilitated by permitting processes that are guided by legislation. For example, the acquisition of a NT wildlife research permit is associated with the obligation of producing a plain language research summary for the communities. As much as possible, individuals and organizations should be encouraged to share information and involve each others in the process of managing and conserving Dall sheep in the Northern Richardson Mountains, for the greatest benefit of this population.

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3. Spatial overlap of Dall sheep, grizzly bears and wolves in the Northern Richardson Mountains[1]

3.1. Introduction

Assessing the effects of predation on a declining prey population is a recurring but challenging assignment of wildlife managers and researchers (Burles and Hoefs 1984, Sawyer and Lindzey 2002, Festa-Bianchet *et al.* 2006). In remote and rugged environments, quantifying predation events (e.g., attack rates, mortality rates, and functional response) necessitates financial and logistic resources unavailable to most researchers. Indirect effects of predation, in contrast, are more easily investigated and can reveal important patterns and mechanisms underlying predator-prey interactions. Indirect effects, also called non-consumptive effects, include vigilance behaviour, reduced feeding, altered activity budget, and habitat shift of prey species (Schmitz *et al.* 2004). Such indirect effects are ubiquitous (Peckarsky *et al.* 2008) and can be a major factor shaping predator-prey spatial dynamics (Iwasa *et al.* 1981, Hebblewhite *et al.* 2005, Willems and Hill 2009).

Indirect effects at the spatial level may be revealed by the examination of home range overlap. The breadth of home range overlap between individuals or

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populations can be helpful to explore several types of interactions and space-use patterns. For example, measures of home range overlap have been used to detect mating associations of red foxes (*Vulpes vulpes*) (Doncaster 1990), kinship among bushbuck (*Tragelaphus scriptus*) (Wronski and Apio 2006), sexual segregation in racoons (*Procyon lotor*) (Gehrt and Fritzell 1998), Pacific tree frog (*Pseudacris regilla*) tadpole avoidance of predation by dragonflies (*Aeshna palmate*) (Hammond *et al.* 2007), temporal home range drift in grizzly bears (*Ursus arctos*) (Edwards *et al.* 2009), and wolf (*Canis lupus*) predation risk on migrant versus resident elk (*Cervus elaphus*) (Robinson *et al.* 2010). In this chapter, I use measures of home range overlap to assess the spatial associations and infer the potential risk of predation by grizzly bears and wolves on a declining population of Dall sheep (*Ovis dalli dalli*).

Dall sheep in the Northern Richardson Mountains, Northwest Territories and Yukon Territory, Canada, are located at the northeastern limit of the species range (Valdez and Krausman 1999). Sporadic aerial surveys revealed this population was small (N < 500) during the 1970s (Simmons 1973), grew steadily during the 1980s (Latour 1984, Barichello *et al.* 1987) and early 1990s (Nagy and Carey 2006a), until it reached a peak in the mid 1990s (N ~ 1730 in 1997) (Nagy and Carey 2006b), then declined consistently afterwards (Davison and Cooley 2006, Nagy *et al.* 2006a, Nagy *et al.* 2006b). The latest abundance estimate was 704 individuals in 2006 (Davison and Cooley 2006). The principal factors hypothesized to influence the dynamics of this population include predation, density-dependence, harvest, climate, and competition with other ungulates

(Lambert Koizumi *et al.* 2011). Following discussions with the local renewable resource councils, the role of predation in the recent population decline was identified as a research priority. Attempts of predation on Dall sheep by grizzly bears, wolves, wolverines (*Gulo gulo*), golden eagles (*Aquila chrysaetos*), and black bears (*Ursus americanus*) were reported by local community members, with wolves and grizzly bears being the most commonly mentioned (Shaw *et al.* 2005). Wolves in adjacent areas appear to feed mostly on moose (*Alces alces*), and seasonally on the Porcupine caribou herd (*Rangifer tarandus granti*) (Hayes and Russell 1998). Despite relying on other prey species, wolves have the potential to significantly limit mountain sheep populations (Murie 1944) and were suspected to have killed one to three radio-collared rams of four in one study (Barichello *et al.* 1987). Research in Alaska identified grizzly bears as the main predator of moose and caribou calves (Ballard and Miller 1990) and their potential as an ungulate predator seems to be higher when ungulates are only few weeks old (Zager and Beecham 2006). Grizzly bears and wolves have both been observed repeatedly in areas near Dall sheep (in aerial surveys and Gwich'in traditional ecological knowledge (Gwich'in Elders 1997)).

3.2. Study area

The study area encompasses approximately 9600 km^2 at the eastern limit of the Northern Richardson Mountains (Figure 3.1) (approximately 67°15'–68°24' N, 137°5'–135°12' W) and is part of the British-Richardson Mountains ecoregion, in the Taiga Cordillera ecozone (Scudder 1997). Steep, V-shaped valleys in the higher range, and gentle slopes where the valleys are broader characterize this ecoregion. The elevation ranges between 400 and 1200 m. The vegetation is dominated by alpine tundra, and the treeline is located at approximately 300 m asl (Smith *et al.* 2004). Average recorded temperatures in January and July at the nearest weather station, in Aklavik NT, are respectively -28°C and 14°C; with an average of 236 mm of precipitations annually (Environment Canada 2009). Climatic records for Aklavik show a recent increase in average temperature and precipitation (Lambert Koizumi *et al.* 2011), in accordance with climate analyses that have placed northern areas amongst the most affected by climate change (Hinzman *et al.* 2005).

Aboriginal claimed lands include the Gwich'in Settlement Area, the Tetlit Gwich'in Secondary Use Area, the Inuvialuit Settlement Region, and the Vuntut Gwich'in Traditional Territory. The closest human settlements are Aklavik and Fort McPherson (each about 12 km east and southeast of the study area). Only aboriginal people can harvest this Dall sheep population and a multijurisdictional management plan is in the process of being adopted. Grizzly bear harvest is also restricted to aboriginal users and is regulated by a management agreement in the Gwich'in Settlement Area and quotas in the Inuvialuit Settlement Region. In the Yukon, in addition to aboriginal harvesters, residents and non-residents may harvest grizzly bears during the spring and fall hunting seasons. Wolves may be harvested throughout the study area, and there is no management plan for them.

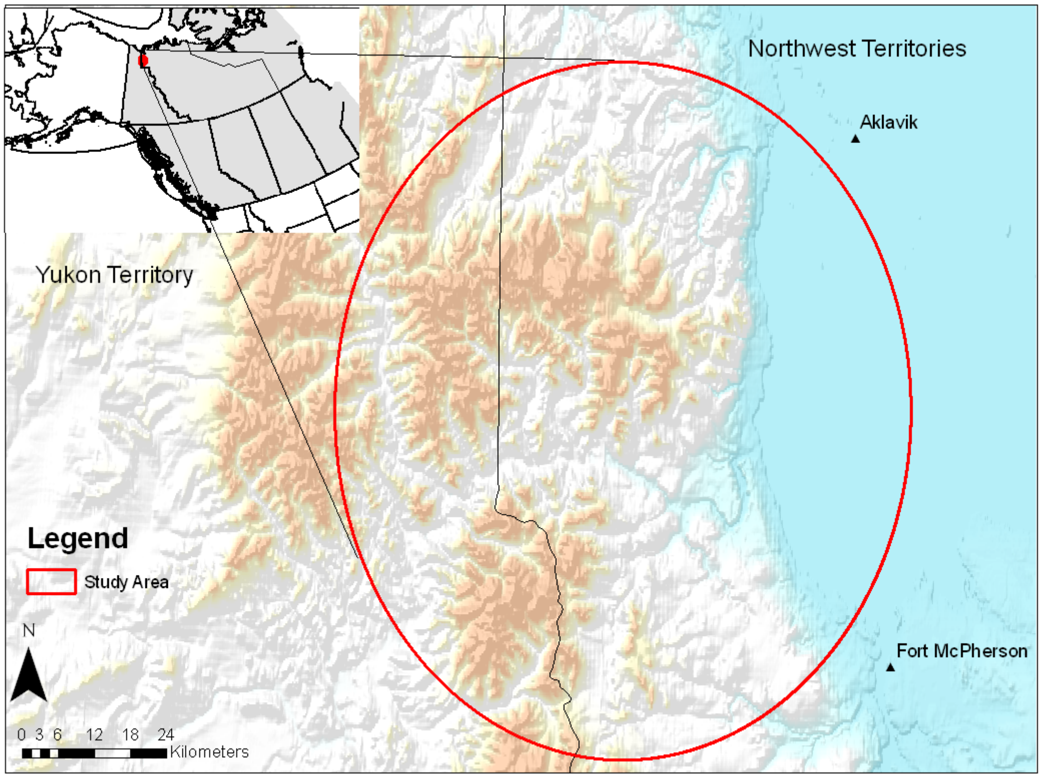

Figure 3.1. Location of the study area in the Northern Richardson Mountains, Northwest Territories and Yukon Territory, Canada.

3.3. Material and methods

In 2006 and 2007, Dall sheep ewes, grizzly bears and wolves were equipped with GPS collars (Telonics© Gen II and Gen III TGW-3580 & TGW-3680 (Mesa Arizona, USA); and Lotek© 3300W (Newmarket Ontario, Canada)). Locations of Dall sheep rams monitored in the same area in 2004-05 (D. Auriat, Gwich'in Renewable Resources Board, unpub.) were also incorporated in analyses. Ewes were selected randomly in different subgroups, and most adult grizzly bears and at least one wolf per pack were collared in the Dall sheep range within the study area (three packs were identified based on capture sightings and GPS locations, although those were not entirely cohesive, as some wolves did move between pack boundaries). Animal captures were performed from helicopter (net gunning for Dall sheep and wolves; dart injection of Telazol©, a mixture of tilatemine HCl and zolazapam HCl, for grizzly bears (dosage: 8 mg/kg) and wolves when net gunning was impossible to perform (5 mg/kg)). Capture and handling protocols were approved by the Government of the Northwest Territories Wildlife Care Committee (research permits WL003119 and WL003319) and followed the guidelines on the care and use of wildlife of the Canadian Council on Animal Care from Environment and Natural Resources, GNT). Locations were recorded every two hours between May 15 and June 15, to get a fine resolution of spatial dynamics during the lambing season, and every four hours the rest of the year. Collars were programmed to release automatically from the animals' necks after 15-28 months of wear, and data were retrieved following collar recovery. Daily to biweekly locations were also sent through the Argos satellite system for all Telonics collars.

To standardize the time interval between animal relocations and reduce bias from temporally correlated data (Börger *et al.* 2006), only one daily location per individual was randomly selected and used in home range analyses. Species composite home ranges were calculated with a 50% and 95% fixed-kernel density estimate (Worton 1989) from the species-specific daily locations of individuals monitoried throughout the study period. Home ranges were calculated with Hawth's Analysis Tools, version 3.27 (Beyer 2006). I used two indices to evaluate home range overlap between Dall sheep and the two potential predators. First I calculated the two-dimensional overlap between core areas (50% kernel contour) and high-use areas (95% kernel contour) of Dall sheep, grizzly bear and wolf composite home ranges (Ostfeld 1986). I quantified the overlap in core and high-use areas as the proportion of Dall sheep composite home range that is intersected by the grizzly bear and wolf core and high use areas. Second, I converted the composite kernel home ranges into utilization distributions (UD), which provide a probabilistic measure of use, and calculated the three-dimensional overlap (volume of intersection) between the three species (Kernohan *et al.* 2001).

3.4. Results

Capture efforts resulted in the monitoring of six Dall sheep ewes, 15 grizzly bears (11 females and four males), and nine wolves from three different packs (three females and six males), in addition to eight Dall sheep rams monitored in 2004-05. Because some collars were unavailable when conducting this analysis, the data presented here stem from the combined locations of 14 Dall sheep (N = 20 189 locations), 14 grizzly bears (N = 16 279), and six wolves (N = 11918). The average time interval between locations selected for this analysis was 1.24 days per individual (SD = 3.15).

The composite 50% and 95% kernel home ranges for each population covered respectively 46 and 213 km^2 for Dall sheep; 252 and 1662 km^2 for grizzly bears; and 434 and 3385 km^2 for wolves (Figure 3.2). Considerable spatial overlap was observed between the monitored individuals. Most of the Dall sheep high-use areas (95% composite kernel home range) were included in the high-use areas of grizzly bears and wolves (77% and 97% overlap, respectively). Over a third (36%) of the Dall sheep core area (50% composite kernel home range) overlapped the core areas of grizzly bears, compared with an overlap of 15% with the core areas of wolves. An examination of the animal locations indicates that six grizzly bears were in Dall sheep core areas and used these intensively, in comparison with three wolves, from three different packs, that passed through them briefly. The volume of intersection of UDs was 20% between Dall sheep and grizzly bears; and 80% between Dall sheep and wolves.

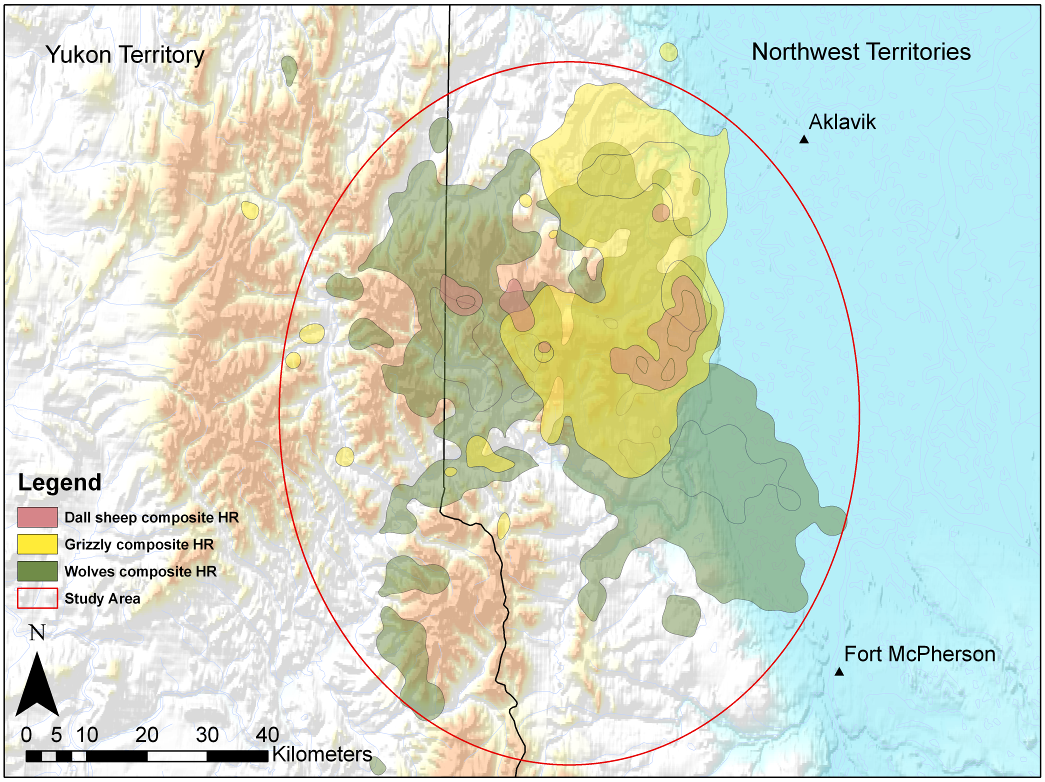

Figure 3.2. Composite 50% and 95% kernel home ranges of Dall sheep (N = 14), grizzly bears (N = 14) and wolves (N = 6) monitored between 2004 and 2009 in the Northern Richardson Mountains, Canada.

3.5. Discussion

My results suggest that on most of their range, during this study, Dall sheep had a higher probability of encountering wolves. Wolves had large home ranges that encompassed those of several Dall sheep and covered a larger proportion of the Dall sheep composite home range. However, when only core areas are considered, grizzly bears were more likely to be encountered. The overlap between composite home ranges of Dall sheep, grizzly bears and wolves reveal probabilities of encounter that might correspond to levels of predation risk associated with each predator population. Predation risk is a determinant of mountain sheep habitat selection (Bleich 1999) and can influence their sexual segregation and social behaviour (Frid 1997). Predation risk has been related to the degree of vigilance exhibited by prey and predation risk can vary with group size and habitat characteristics (Frid 1997), and to the probability of occurrence of predators within the landscape (Hebblewhite *et al.* 2005, Walker *et al.* 2007, Willems and Hill 2009). In the Northern Richardson Mountains, predation risk from grizzly bears appears higher in Dall sheep core areas, and wolf predation risk seems higher in other areas used by Dall sheep.

Because individual predators may specialize in their own prey niche, mortality rates from grizzly bears and wolves may be difficult to assess from this index of predation risk. The degree of carnivory of grizzly bears varies greatly among individuals (Hilderbrand *et al.* 1999) and wolves belonging to the same pack may select different food sources (Urton and Hobson 2005). As such, grizzly bears in Dall sheep core areas may vary in their predation of Dall sheep. Holders of traditional ecological knowledge have suggested that a high concentration of grizzly bears in prime Dall sheep habitat may occur because of the area's abundance in Arctic ground squirrels (*Spermophilus parryii*) and forage availability (C. Lambert Koizumi, unpub.). Similarly, other prey species present in Dall sheep high-use areas could influence the occurrence of wolves. However, some predators may specialize on certain prey, and few of these specialized predators may be needed to cause a population decline (Festa-Bianchet *et al*. (2006). In the absence of known mortality rates, a higher probability of encounter is likely to correspond to higher predation risk.

Further analyses are needed to improve our understanding of the indirect effects of predation by grizzly bears and wolves. At the spatial level, the investigation of animal locations at a finer scale (at the individual and seasonal levels) and the characterization of habitat use patterns from the UDs (Marzluff *et al.* 2004) have the potential to provide more detailed insights on the interactions between these three populations. In the next chapters, I pursue these analyses in combination with other techniques like grizzly bears and wolves diet analysis, Dall sheep behaviour observations, and documentation of aboriginal traditional knowledge, to better assess how grizzly bears and wolves may impact Dall sheep in this secluded northern ecosystem.

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4. Assessing grizzly bear and wolf predation on Dall sheep from spatial and nutritional ecology

4.1. Introduction

Determining the impact of predators on a prey population is an enduring ecological challenge, especially for wide-ranging species in secluded areas. Not long ago, predation events were mainly tracked through field observations (Murie 1944, Mech 1970, Geist 1971), requiring exceptionally committed temporal and spatial monitoring. The advent of radio or global positioning system (GPS) telemetry, paired with thorough ground investigations, provided means to lessen time in the field and focus sampling on locations that correspond to a kill (Hayes and Russell 1998, Hebblewhite *et al.* 2005, Cooley *et al.* 2008, Merrill *et al.* 2010). However, reliably detecting kills depends on a stringent combination of intense field efforts and short-time interval telemetry monitoring (Zimmermann *et al.* 2007).

These limitations have promoted the investigation of indirect, or non-consumptive, aspects of predator-prey interactions (Abrams 2007, Peckarsky *et al.* 2008). Although direct consequences of predation (the immediate decline in prey abundance) are obvious, indirect consequences are subtle –but nevertheless widespread and multifaceted. For prey, the need to avoid predation may lead to changes in foraging and vigilance (Kie 1999), group size (Elgar 1989), sexual segregation (Corti and Shackleton 2002), as well as habitat utilization (Lima and Dill 1990, Bergerud and Luttich 2003, Hebblewhite *et al.* 2005). In this chapter, I concentrate on the latter two components.

Sexual segregation occurs in many ungulates and the major hypotheses proposed to explain it (reviewed in Main *et al.* (1996) and Ruckstuhl and Nehaus (2000)) are based on predation risk (also known as the reproductive strategies hypothesis) (Main and Coblentz 1996, Corti and Shackleton 2002), forage selection (Beier 1987), scramble competition (Clutton-Brock *et al.* 1997), and activity budgets (Ruckstuhl 1998). The predator risk hypothesis stipulates that males need to frequent habitats of higher foraging quality in order to increase their reproductive success (most of the year except rut), whereas females need to focus on protecting their offspring from predators –particularly when they are young and most vulnerable. This constrains females to stay in safer areas, even if those offer lower nutritive value.

At the spatial level, predators can influence the movement patterns and resource utilization of prey (Lima 2002, Willems and Hill 2009), which can have cascading effects on other elements of the ecosystem (Schmitz *et al.* 2004, Beschta and Ripple 2009). As such, spatial dynamics can provide insights into associations at the individual or species level. For instance, analyses of habitat utilization have helped characterize wolf predation risk for elk (*Cervus elaphus*) (Hebblewhite *et al.* 2005), or wolf and grizzly bears predation risk for Stone sheep (*Ovis dalli stonei*) (Walker *et al.* 2007). Similarly, the degree of home range overlap may indicate various types of associations, including: home range fidelity

(Edwards *et al.* 2009), mating and territoriality (Doncaster 1990), sexual segregation (Gehrt and Fritzell 1998), and social organization or matrilineal structure (Wronski and Apio 2006), interspecific competition (Minta 1992) or predator risk (Hammond *et al.* 2007, Robinson *et al.* 2010, Lambert Koizumi and Derocher 2010).

Although spatial associations between predators and prey are a necessary precursor to predation events, an alternate approach is required to assess actual prey consumption. Naturally occurring stable isotope ratios of carbon and nitrogen in consumer tissues can help estimate the proportion of assimilated food sources and reconstitute food webs (Post 2002, West *et al.* 2006). For instance, $\delta^{13}C$ and $\delta^{15}N$ stable isotopes have been used to distinguish diet variability, identify foraging profiles, and quantify the importance of several food sources into the diet of wolves (Szepanski *et al.* 1999, Darimont and Reimchen 2002, Urton and Hobson 2005, Darimont *et al.* 2008, Adams *et al.* 2010) and grizzly bears (Hilderbrand *et al.* 1999, Robbins *et al.* 2004, Edwards 2009, Edwards *et al.* 2011).

In this research, I examined the risk posed by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) to Dall sheep (*Ovis d. dalli*) in the Northern Richardson Mountains, Canada, based on habitat utilization, seasonal home range overlap, and stable isotopes. This Dall sheep population numbered between 1400 and 1700 animals in the 1990s (Nagy and Carey 2006a, 2006b) then rapidly declined to about 700 animals based on aerial surveys in 2003, 2006 and 2010 (Nagy et al 2006b, Davison and Cooley 2006, K. Russell, Yukon Department of

Environment, pers. com.). This large decline may be mostly attributed to a combination of climate, density dependence, predation, and harvest (Lambert Koizumi *et al.* 2011, Chapter 2). Wolves and grizzly bears have been identified as two main predators of this population (Barichello *et al.* 1987, Shaw *et al.* 2005) although the evidence remains limited.

I started by assessing predation risk from the Dall sheep perspective. If the predation risk hypothesis drives sexual segregation, Dall sheep rams would be expected to frequent habitats of higher nutritive quality and be exposed to greater predation risk levels during most of the year. Ewes would be expected to stay in areas of lower predation risk than rams, particularly perinatal, and choose habitats based on safety rather than forage quality. I tested those predictions by comparing Dall sheep rams and ewes seasonal habitat utilization patterns under predation risk. Then, I investigated the issue from the grizzly bear and wolf perspective. In the previous chapter (Lambert Koizumi and Derocher 2010), I calculated the spatial overlap between Dall sheep and these two predators using their composite home range, merging individuals from each species in unique categories. Because predation risk is likely to vary among individual predators based on their size, nutritional constraints (Welch *et al.* 1997) and unique foraging patterns (Urton and Hobson 2005, Edwards *et al.* 2011), I analyzed variations among individual predators in terms of spatial home range overlap with Dall sheep. Furthermore, I estimated the proportion of Dall sheep in the predators diet using stable isotopes analyses. By integrating spatial ecology with isotopic diet analysis, this chapter constitutes a step fowards regarding the acquisition of new insights about predator-prey dynamics in remote ecosystems.

4.2. Study area

The Northern Richardson Mountains are located in the Canadian Arctic and overlap the Northwest Territories (NT) and the Yukon Territory (YT) border. All animals were captured within the Gwich'in Settlement Area, but some movements were monitored in the adjacent Inuvialuit Settlement Region and Vuntut Gwitchin Traditional Territory (Figure 4.1). The study area encompasses approximately 5900 km^2 (67°20'–68°20' N, 137°2'–134°50' W), which corresponds to the 99% combined kernel home range of all study animals.

The Northern Richardson Mountains are occupied by other prey species including the Porcupine barren-ground caribou (*Rangifer tarandus granti*), moose (*Alces alces*), muskox (*Ovibos moschatus*), snowshoe hare (*Lepus americanus*), arctic ground squirrel (*Spermophilus parryii*), and beavers (*Castor canadensis*). Other predators include wolverines (*Gulo gulo*), Canada lynx (*Lynx canadensis*), red foxes (*Vulpes vulpes*), and golden eagles (*Aquila chrysaetos*), which nest throughout the area during summer. The area is pristine with no road access. The closest human settlements are Aklavik and Fort McPherson, NT.

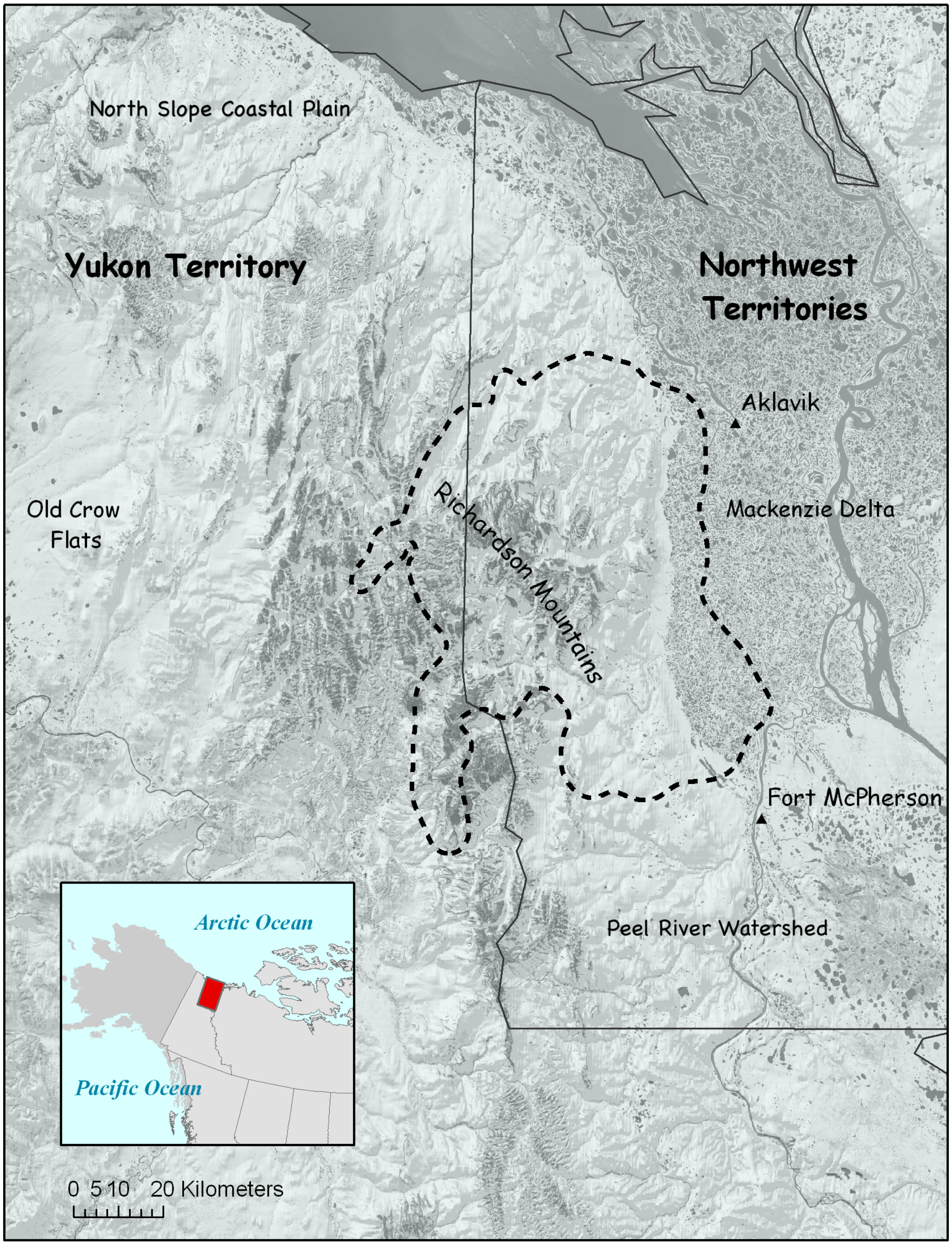

Figure 4.1. Study area in the Northern Richardson Mountains, NT and YT, Canada. The dashed line shows the 99% combined kernel home range of all study animals (excluding dispersal movements of one wolf).

4.3. Methods

4.3.1. Animal capture and monitoring

Collar deployment occurred in autumn 2004 (rams) and spring 2006 (ewes) for Dall sheep, and spring 2006 and 2007 for wolves and grizzly bears. A handheld net gun was fired from a Bell 206B or Astar 350 helicopter to capture all Dall sheep and most wolves. Dart injection of Telazol®, a mixture of tilatemine HCl and zolazapam HCl, was used for some wolves (5 mg/kg) and all grizzly bears (dosage: 8 mg/kg). Capture and handling protocols were approved by the Government of the Northwest Territories Wildlife Care Committee (research permits WL003119, WL003319, WL005590, and WL007406) and respected guidelines on the care and use of wildlife of the Canadian Council on Animal Care. Animals were equipped with GPS collars linked to Argos satellites (Telonics Gen II and Gen III TGW-3580 & TGW-3680 (Mesa Arizona, USA) and Lotek 3300W (Newmarket Ontario, Canada)). Collars deployed in 2004 recorded locations every eight hours. Collars deployed in 2006 and 2007 recorded locations every two hours between May 15 and June 14, to get finer resolution of spatial dynamics during lambing season, and every four hours the rest of the year. Each collar had a programmable release mechanism.

4.3.2. Dall sheep seasonal habitat utilization

Dall sheep seasonal habitat utilization patterns were estimated from their fixed-kernel utilization distribution constructed with GPS telemetry data

(Marzluff *et al.* 2004, Millspaugh *et al.* 2006). I employed linear regression models to relate habitat attributes and predation risk, the independent variables, to a probabilistic measure of Dall sheep space use, the dependent variable. This probability was represented by rasterized values of individual Dall sheep utilization distributions (Marzluff *et al.* 2004), thereby using each animal as an experimental unit and avoiding pseudoreplication (Hurlbert 1984). To assess temporal variations in resource use and predation risk, I calculated Dall sheep fixed-kernel home ranges for five seasons: winter (November 15 to March 30), spring (April 1 to May 14), lambing (May 15 to June 14), summer (June 15 to August 31), and autumn (September 1 to November 14). For each monitored Dall sheep, I set the extent of the habitat use analysis as its minimum convex polygon home range buffered by one kilometre, to include cells of the utilization distribution located at the outer limits of the range. This scale corresponds to third order selection defined by Johnson (1980), pertaining to the choice of habitat features within individual home ranges. Dall sheep utilization distributions (h = 750) were generated at a 30-m resolution using the program Hawths Analysis Tools 3.27 (Beyer 2006) for ArcGIS 9.2 (ESRI, Redlands, California, USA).

Seasonal utilization distributions for each Dall sheep were described by topographical features (elevation, slope, aspect, ruggedness), greenness based on the normalized difference vegetation index (NDVI), land cover, and predation risk. Topographical features were calculated from a 30-m grid digital elevation model (Natural Resources Canada). Aspect was categorized as 0 or 1 in the classes N (316°-45°), E (46°-135°), S (136°-225°), W (226-315)), or nil if the slope was <5°. Terrain ruggedness was derived from slope and gradient heterogeneity following that developed for desert bighorn sheep (*Ovis canadensis nelsoni*) habitat selection (Sappington *et al.* 2007). The NDVI layer corresponded to average values for northern Canada from satellite data collected between 1986 and 2006 (Olthof *et al.* 2008). I used the 90 m resolution land cover circa-2000 vector (Olthof *et al.* 2005) and aggregated land cover classes into seven categories (coded as 0 or 1): barrens (moraines, exposed soil, rocks), bryoids (bryophytes and lichens), forests (conifers, deciduous and mixed), herbs (grasses, tussocks, graminoids), shrubs (tall and low), snow or ice, and water (wetlands, lakes and rivers). Land units obscured by clouds or shadows (<2% of the area used by Dall sheep) were omitted. I interpreted grizzly bear and wolf predation risk as the probability of encountering these species within the study area, which was calculated from the predators' composite utilization distribution (h = 3500). In order to assess the influence of predation risk from each species on a seasonal basis, I built seasonal species-specific utilization distributions (5 layers for wolves and 4 layers for grizzly bears).

Due to collinearity (correlation coefficient > 0.5) with elevation and the barren land cover class, NDVI was excluded from regression models. My results present robust estimates of variance (multiplied with N/(N-k), where n is the number of observations and k the number of parameters (StataCorp 2009)) and standardized regression coefficients (variance scaled to 1), which facilitate comparison between the relative effect of habitat attributes and predation risk on Dall sheep habitat use, regardless of the variables' differing units (Millspaugh *et* *al.* 2006). If a variable coefficient (β) was significantly different from 0 (at α = 0.05), I interpreted that it was either highly used for (β > 0) or less used (β < 0). Rams and ewes exposure to predation risk, based on the coefficient value, were compared using one-way ANOVA. Because I did not aim to predict habitat use by Dall sheep over other areas, models were not tested with cross-validation procedures (Boyce *et al.* 2002, Wiens *et al.* 2008). I conducted all statistical analyses in Stata 11.2 (Stata, College Station, Texas, USA).

4.3.3. Individual predator overlap with Dall sheep

I calculated home range overlap between each predator and the composite Dall sheep home range using the volume of intersection (Fieberg and Kochanny 2005), at 100 m resolution. The composite home range corresponds to the fixed-kernel utilization distribution from the combined locations of all monitored Dall sheep. Because individuals were captured in various subgroups of this population, the composite home range is thought to be representative of Dall sheep distribution within the study area centre. Utilization distributions were scaled to sum to 1, to correspond to true probability distributions and facilitate the calculation of spatial overlap between predators and prey. To systematize the monitoring frequency of each species throughout the year and yield unbiased utilization distributions (Börger *et al.* 2006), I sub-sampled GPS locations at the lowest frequency recorded for each species (eight hours for Dall sheep; four hours for grizzly bears and wolves). Because winter corresponds to the denning period of grizzly bears, I also excluded Dall sheep winter locations, between November

15 and March 30) from the overlap analysis with grizzly bears. I compared levels of predation risk of grizzly bears and wolves using the *t*-test, and calculated home range overlaps in ArcGIS 9.2.

4.3.4. δ^{13}C & δ^{15}N stable isotopes

I collected sample guard hairs from the forelegs of grizzly bears and wolves handled in 2006 and 2007. For both grizzly bears and wolves, moulting occurs annually, starting in late spring to early summer (Mech 1970, Darimont and Reimchen 2002, Schwartz *et al.* 2003). Because capture occurred in spring, right before the moult, the collected hair samples should reflect the previous year diet (Hobson *et al.* 2000, Edwards *et al.* 2011). Samples were rinsed with distilled water, soaked for 24h and rinsed twice in 2:1 chloroform: methanol solvent to remove oils, air-dried, then finely homogenized to a fine powder with scissors (Wassenaar 2008). Approximately 1.0 mg of each resulting sample were loaded into tin capsules for isotopic analyses. The ratios of δ^{13}C and δ^{15}N isotopes were analyzed using a continuous-flow ratio mass spectrometry at the Stable Isotopes Facilities of the University of Saskatchewan, SK. Results are reported in δ notation as deviations in parts per thousands (‰) relative to an international standard (Vienna PeeDee Belemnite (VPDB)).

I merged potential food sources with similar isotopic signature in the following groups: aquatic browsers (beavers and moose), arctic ground squirrels, caribou, Dall sheep, fish (arctic charr (*Salvelinus alpinus*) and broad whitefish (*Coregonus nasus*)), and small rodents (lemmings and microtines). Vegetation (berries, horsetail, grass, sedge, alpine sweetvetch (*Hedysarum alpinum*)) was also considered for grizzly bears. Except for Dall sheep samples, which I collected in the field, and arctic charr values taken from the literature (Doucett *et al.* 1999), isotopic ratios of sources were provided by M. Edwards (2009).

Because the isotopic signature of prey tissues is enriched at varying turnover rates within the consumer's tissues (Hobson and Clark 1992, Hilderbrand *et al.* 1999), I adjusted the δ^{13}C and δ^{15}N values of the prey sources to incorporate fractionation rates, also called trophic enrichment. Fractionation has not been documented for wolf and grizzly bear hair, so I used rates published for another terrestrial carnivore, the captive red fox (*Vulpes vulpes*) (2.6 ± 0.1‰ for δ^{13}C and 3.4 ± 0.1‰ for δ^{15}N) (Roth and Hobson 2000). These rates are within the range of values estimated for other mammalian species (Caut *et al.* 2009).

I assessed the contribution of the examined food sources into the predators' diet using a Bayesian mixing model that allows the inclusion of several sources and their variability, resulting in dietary solutions in terms of true probability distributions (Moore and Semmens 2008, Parnell *et al.* 2010). The model was built using the software package SIAR (Stable Isotope Analysis in R), based upon a Gaussian likelihood with a mixture dirichlet-distributed prior on the mean (Jackson *et al.* 2009, Parnell *et al.* 2010). I set uninformative priors for all food sources. For the proportion of each considered food source, SIAR provided a posterior distribution described by a mean and a true probability density function.

4.4. Results

4.4.1. Dall sheep, grizzly bear and wolf monitoring

Movement data were obtained for 12 Dall sheep (four ewes and eight rams), 15 grizzly bears (ten females and five males), and five wolves (two females and three males). Two additional Dall sheep and four more wolves were collared, but I had to exclude their locations due to collar malfunction ($N = 3$), mortality (harvest ($N = 1$) and undetermined cause ($N = 2$)) within weeks of capture. The dispersal movement of one wolf after a year of monitoring was also excluded. In total, my analyses are based on 19 940 Dall sheep locations (mean ± SE = 1662 ± 328 per individual), 22 596 grizzly bear locations (1506 ± 284 per individual), and 11 116 wolf locations (2223 ± 364 per individual). The sizes of home ranges averaged 80 ± 12 km^2 for Dall sheep (no statistical differences between sexes), 548 ± 88 km^2 for grizzly bears (males had larger home ranges than females: 760 ± 163 km^2 versus 442 ± 92 km^2; $t_{13} = 1.84$, $P = 0.04$), and 1777 ± 531 km^2 for wolves (no statistical differences between sexes). For stable isotopes analysis, I collected hair samples from 19 grizzly bears, 9 wolves, and tissue (hair, heart, kidney and muscle) from 13 Dall sheep. Samples were taken from animals that were handled during this study, or carcasses found during fieldwork.

4.4.2. Dall sheep seasonal habitat utilization

Dall sheep seasonal habitat utilization varied among individuals, but some patterns emerged both for rams and ewes. During winter, rams were positively associated with rugged terrain, steep slopes, and barren lands (Table 4.1). In contrast, ewes were associated with eastern and western slopes, and exposed to high wolf risk (Table 4.2). During spring, rams infrequently used northern slopes and ewes were frequently associated with steep slopes. During lambing, rams highly used southern slopes as well as land covered by barrens, forests, herbs, shrubs, and water. Ewes tended to stay in rugged and steep terrain and used less northern slopes. During summer, rams used less northern aspects but highly used rugged terrain, steep southeast oriented slopes, as well as barrens, bryoids, and water land covers. Rams were exposed to significantly high grizzly bear risk, although their exposure to wolves was low. Ewes frequented higher elevations, rugged and steep terrain, eastern slopes, and did not use south and west oriented aspects, barrens, forests, herbs, shrubs, snow, and water land covers. Finally, in autumn, rams highly used habitats of lower elevations, southeast oriented slopes, as well as barrens, bryoids, forests, herbs, shrubs, snow and water land covers. No habitat use pattern emerged for ewes in autumn.

Throughout the year, there were considerable variations in exposure to predation risk among Dall sheep individuals, although rams were overall exposed to higher grizzly bear risk than ewes ($F_{1,40} = 6.07$, $P = 0.02$) (Figure 4.2). Ewes exposure to wolf risk was highest during winter (Figure 4.3), but no statistical difference was found between the two sexes ($F_{1,52} = 2.32$, $P = 0.13$).

Table 4.1. Standardized coefficients (β) and standard errors (SE) of seasonal resource utilization for Dall sheep rams in the Northern Richardson Mountains under wolf and grizzly bear predation risk. Regression coefficients in bold had confidence intervals that did not include 0.

Variables	**Winter**		**Spring**		**Lambing**		**Summer**		**Autumn**	
	β	SE	β	SE	β	SE	β	SE	β	SE
Elevation	-0.039	0.027	0.100	0.064	-0.038	0.073	-0.071	0.048	**-0.211**	0.046
Ruggedness	**0.063**	0.032	0.081	0.054	0.028	0.028	**0.082**	0.018	0.029	0.030
Slope	**0.048**	0.024	0.036	0.042	0.008	0.026	**0.081**	0.033	0.011	0.029
N	-0.012	0.045	**-0.102**	0.038	-0.056	0.038	**-0.063**	0.025	0.006	0.026
E	-0.010	0.041	-0.029	0.041	-0.021	0.037	**0.031**	0.005	**0.049**	0.021
S	0.014	0.022	0.034	0.025	**0.042**	0.016	**0.041**	0.011	**0.098**	0.032
W	-0.009	0.021	-0.018	0.014	-0.022	0.014	0.025	0.022	0.019	0.014
Barrens	**0.143**	0.069	-0.082	0.084	**0.202**	0.079	**0.184**	0.064	**0.463**	0.073
Bryoids	0.019	0.029	0.000	0.058	0.035	0.034	**0.088**	0.042	**0.122**	0.040
Forests	0.059	0.037	-0.098	0.053	**0.127**	0.056	0.021	0.042	**0.201**	0.056
Herbs	0.114	0.079	-0.125	0.094	**0.240**	0.090	0.119	0.081	**0.455**	0.091
Shrubs	0.074	0.053	-0.101	0.070	**0.172**	0.061	0.093	0.052	**0.299**	0.065
Snow	0.042	0.038	-0.046	0.058	0.040	0.044	-0.028	0.059	**0.103**	0.035
Water	0.026	0.016	-0.009	0.014	**0.017**	0.008	**0.061**	0.017	**0.065**	0.012
Wolf risk	0.038	0.083	0.032	0.107	0.022	0.062	**-0.142**	0.042	-0.066	0.065
Grizzly risk	NA	NA	0.110	0.115	0.046	0.087	**0.258**	0.118	0.129	0.095

Table 4.2. Standardized coefficients (β) and standard error (SE) of seasonal resource utilization for Dall sheep ewes in the Northern Richardson Mountains under wolf and grizzly bear predation risk. Regression coefficients in bold had confidence intervals that did not include 0.

Variables	Winter		Spring		Lambing		Summer		Autumn	
	β	SE	β	SE	β	SE	β	SE	β	SE
Elevation	-0.075	0.052	-0.032	0.080	0.021	0.048	**0.286**	0.035	0.038	0.179
Ruggedness	-0.020	0.023	0.062	0.055	**0.184**	0.055	**0.090**	0.031	0.012	0.046
Slope	0.020	0.078	**0.054**	0.016	**0.127**	0.032	**0.121**	0.044	0.003	0.033
N	0.075	0.040	-0.041	0.031	**-0.063**	0.032	-0.062	0.032	-0.021	0.025
E	**0.127**	0.051	0.075	0.087	0.006	0.031	**0.085**	0.013	0.060	0.037
S	0.037	0.041	0.018	0.017	0.037	0.049	**-0.022**	0.010	0.030	0.039
W	**0.055**	0.012	-0.041	0.022	0.010	0.026	**-0.073**	0.017	-0.024	0.030
Barrens	0.119	0.116	0.190	0.173	0.060	0.086	**-0.395**	0.109	0.234	0.369
Bryoids	0.001	0.030	0.022	0.029	-0.038	0.053	-0.125	0.067	-0.050	0.049
Forests	0.003	0.036	0.003	0.071	-0.071	0.060	**-0.214**	0.077	-0.052	0.094
Herbs	0.076	0.113	0.143	0.165	-0.004	0.080	**-0.484**	0.092	0.184	0.356
Shrubs	0.027	0.068	0.075	0.080	-0.017	0.040	**-0.256**	0.049	0.052	0.196
Snow	0.011	0.035	0.028	0.036	-0.017	0.038	**-0.082**	0.038	-0.035	0.057
Water	0.036	0.025	0.023	0.020	0.010	0.008	**-0.062**	0.007	0.016	0.045
Wolf risk	**0.218**	0.059	0.008	0.141	-0.003	0.106	-0.004	0.070	0.115	0.159
Grizzly risk	NA	NA	-0.031	0.122	-0.081	0.119	-0.048	0.071	-0.069	0.163

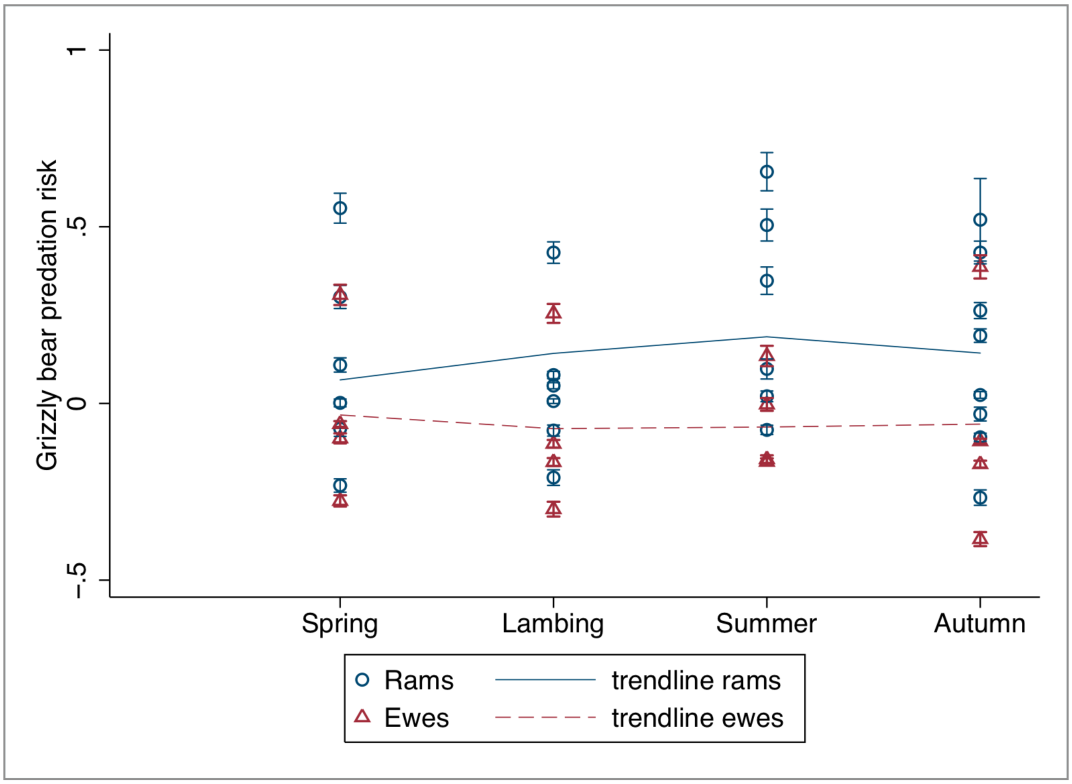

Figure 4.2. Regression coefficients representing seasonal exposure to grizzly bear predation risk for individual Dall sheep rams and ewes, from spring to autumn, in the Northern Richardson Mountains. Error bars on each data point correspond to the 95% confidence interval, using robust estimates of variance. A fractional polynomial trendline for rams and ewes is shown.

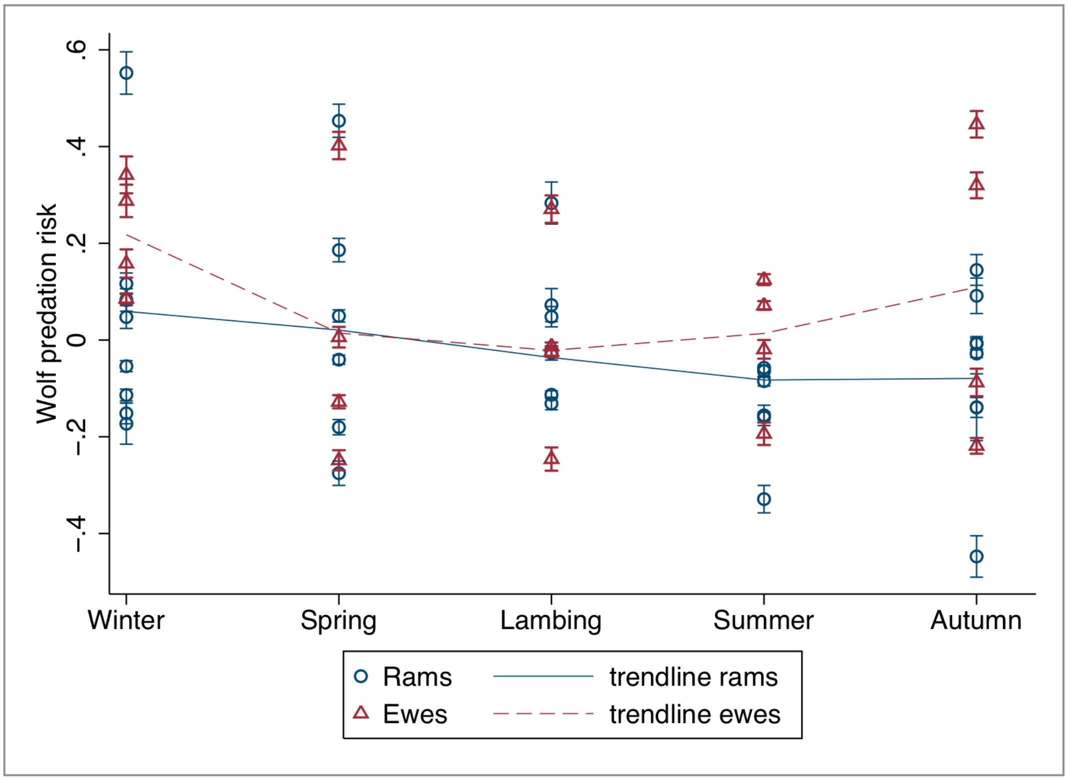

Figure 4.3. Regression coefficients representing seasonal exposure to wolf predation risk for Dall sheep rams and ewes in the Northern Richardson Mountains. Error bars on each data point correspond to the 95% confidence interval, using robust estimates of variance. A fractional polynomial trendline for rams and ewes is shown.

4.4.3. Individual predator overlap with Dall sheep

The spatial overlap between individual predators and the Dall sheep home range varied between 0 and 32% for grizzly bears (9.8 ± 3.0%) and between 0 and 20% for wolves (5.9 ± 3.7%), indicating no significant difference between the two predator species ($t_{18} = 0.68$, $P = 0.25$) (Figure 4.4). Further, no differences between sexes were detected for either species.

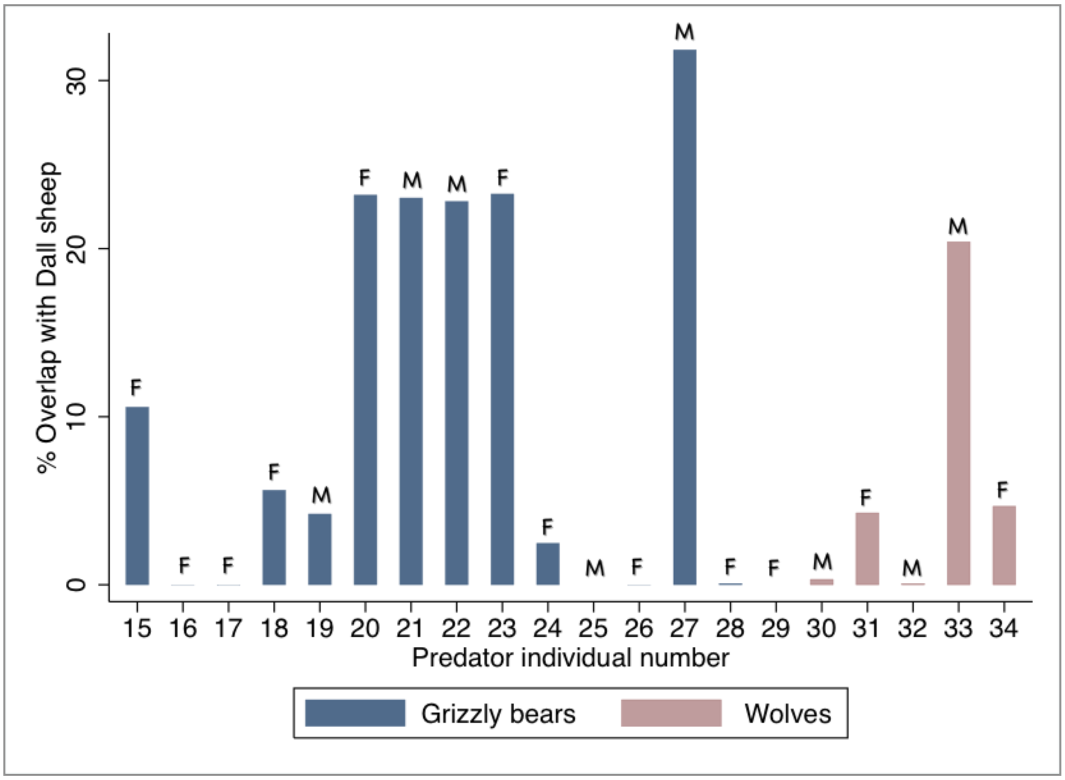

Figure 4.4. Home range overlap (%) between individual predators (grizzly bears numbered from 15 to 29; wolves numbered from 30 to 34) and the composite home range of Dall sheep monitored in the Northern Richardson Mountains. The sex (M = male, F = female) of each predator is indicated above bars.

4.4.4. Dall sheep consumption by grizzly bears and wolves

Stable isotope values for grizzly bears and wolves in the Northern Richardson Mountains reflect a broad range of signatures. Mean carbon and nitrogen isotope values (± SE) were respectively -23.17 ± 0.14‰ δ^{13}C (range -23.93 to -22.02) and 5.07 ± 0.18‰ δ^{15}N (range 3.46 to 6.61) for grizzly bears, and -21.53 ± 0.20‰ δ^{13}C (range -22.34 to -20.69) and 5.87 ± 0.17‰ δ^{15}N (range 5.46 to 6.98) for wolves (Figure 4.5). Overall, the estimated proportion of Dall sheep in the predators diet averaged 12.9% for grizzly bears (95% credible interval (CI) =

0 – 29%) and 27.1% for wolves (95% CI = 0.01 – 52.0%). The single most important food source group for grizzly bears was vegetation, followed by aquatic browsers (beavers and moose), small rodents, then Dall sheep. On average, animal sources accounted for approximately 70% of the grizzly bear diet (Table 4.3). For wolves, their principal food source was aquatic browsers, followed by Dall sheep, then caribou. Fish were the least used resource for both species (Table 4.3).

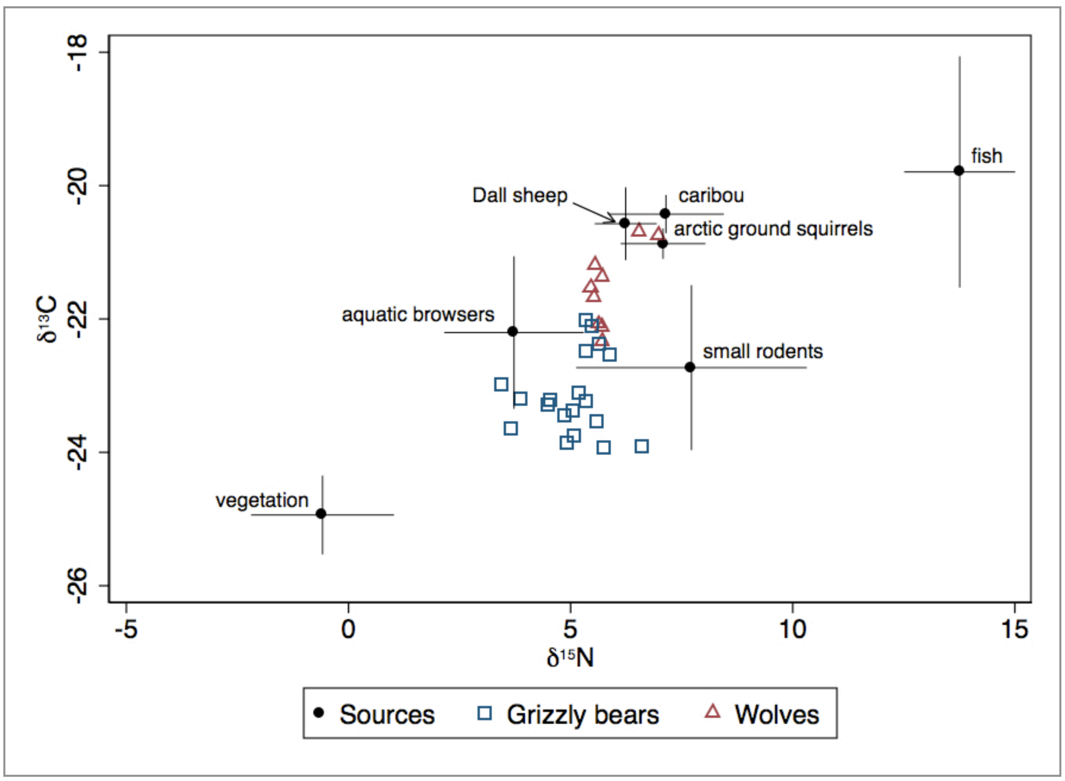

Figure 4.5. $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) stable isotope signatures for grizzly bears and wolves monitored in the Northern Richardson Mountains. Food sources values were adjusted to account for fractionation, and cross bars on food sources show standard deviations.

Table 4.3. Mean proportion and 95% credible interval (CI) of various food sources in the assimilated diet of grizzly bears and wolves.

Source	Grizzly bears		Wolves	
	Mean (%)	95% CI	Mean (%)	95% CI
Aquatic browsers	20.5	0.2-40.0	38.6	17.0-59.0
Arctic ground squirrels	11.9	0.0-28.0	12.0	0.0-3.0
Caribou	11.4	0.0-26.0	15.3	0.0-35.0
Dall sheep	12.9	0.0-29.0	27.1	0.8-52.0
Fish	4.9	0.0-12.0	2.7	0.0-7.9
Small rodents	8.0	0.0-18.0	4.3	0.0-13.0
Vegetation	30.3	19.0-41.0		

Similar isotopic ratios may interfere with our capacity to distinguish between related sources (Phillips and Gregg 2003). Because Dall sheep isotopic signature was similar to that of caribou and arctic ground squirrels (Figure 4.5), I redid the analysis *a posteriori* by pooling these three species into a new group, which I called mountain mammals. This posterior model contained five groups of food sources instead of seven and yielded a mean dietary proportion of 27.5% mountain mammals for grizzly bears, and 42.3% for wolves (Table 4.4). Figures 4.6 and 4.7 illustrate the relative proportion of these food sources in the grizzly bear and wolf diet, respectively.

Table 4.4. *A posteriori* mean proportion and 95% credible interval (CI) of various food sources in the assimilated diet of grizzly bears and wolves, after Dall sheep, arctic ground squirrels and caribou were merged into mountain mammals.

Source	Grizzly bears		Wolves	
	Mean (%)	95% CI	Mean (%)	95% CI
Aquatic browsers	28.6	3.8-50.0	48.3	29.0-69.0
Mountain mammals	27.5	8.3-47.0	42.5	17.0-66.0
Fish	6.7	0.0-15.0	3.8	0.0-10.0
Small rodents	8.6	0.0-20.0	5.3	0.0-15.0
Vegetation	28.6	17.0-41.0		

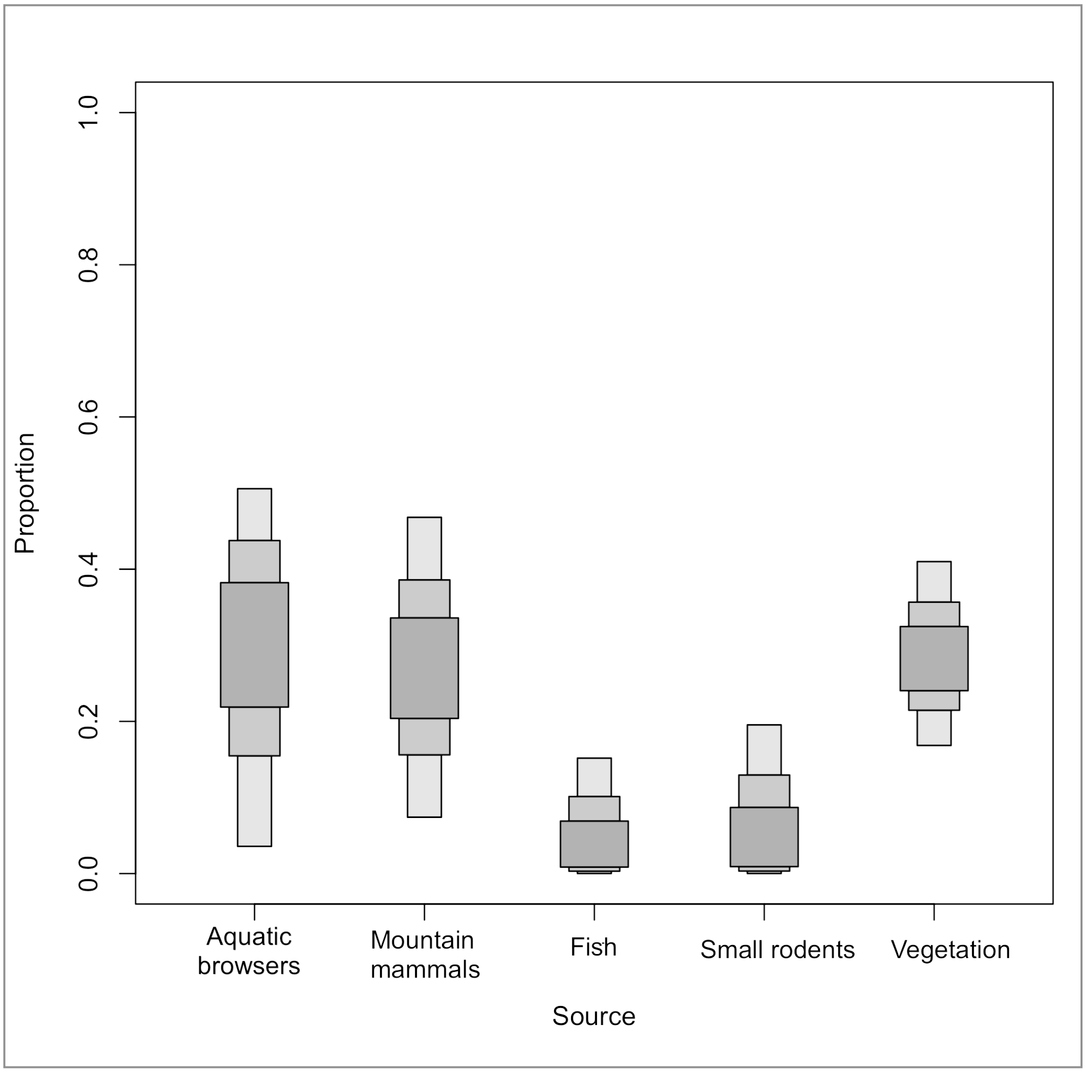

Figure 4.6. Estimated proportions of various food source groups in the diet of grizzly bears in the Northern Richardson Mountains, after combining Dall sheep, caribou and arctic ground squirrels in the mountain mammals group. Darker, medium and lighter grey bars respectively indicate the 25, 75, and 95% credible intervals.

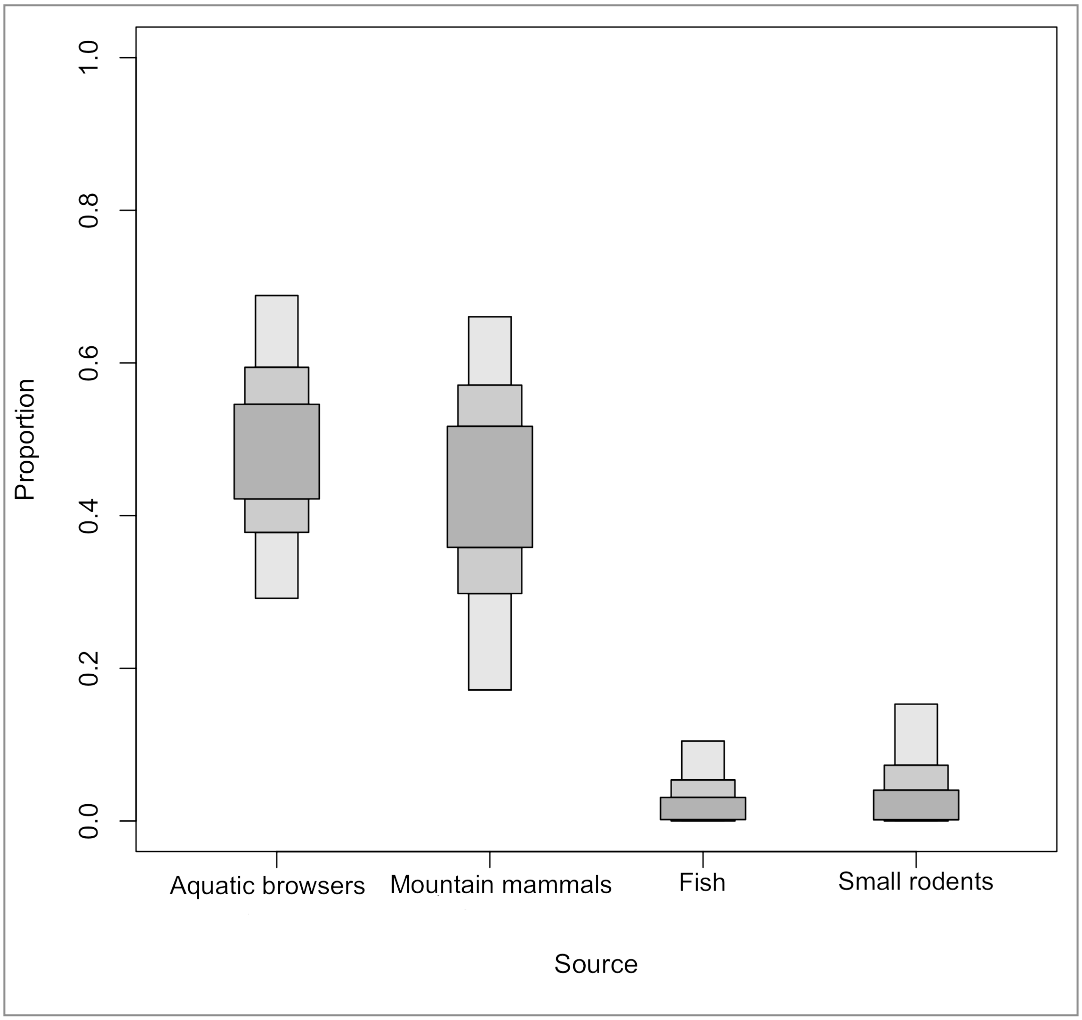

Figure 4.7. Estimated proportions of various food source groups in the diet of wolves in the Northern Richardson Mountains, after combining Dall sheep, caribou and arctic ground squirrels in the mountain mammals group. Darker, medium and lighter grey bars respectively indicate the 25, 75, and 95% credible intervals.

4.5. Discussion

I am starting this section by highlighting few limitations and assumptions underlying this chapter. Although studying several species simultaneously offers an unrivalled opportunity to increase our understanding of their interactions, it often implies that available resources need to be divided among the monitored species. In my case, this resulted in restricted sample sizes, particularly for wolves and Dall sheep. For wolves, I had identified three packs that overlapped with the Dall sheep range and monitored at least one wolf per pack. Based on ground and aerial observations, pack sizes were estimated to range between two and eight individuals, although packs were not always cohesive and some exchange movements seemed to occasionally occur among them. Nevertheless, even if wolf packs are not continually cohesive (Meier *et al.* 1995), wolves often hunt in social units (Mech 1970) and it seemed reasonable to assume that the space used by monitored wolves adequately represented that of other pack members.

Also, despite most adult grizzly bears and wolves within the composite Dall sheep utilization distribution were monitored (where capture efforts were concentrated), not all Dall sheep groups were monitored within the larger predators' home ranges; possibly leading to an underestimation of home range overlap. Specifically, some grizzly bears or wolves with no or little overlap with the monitored Dall sheep could have been living nearby other groups of uncollared Dall sheep. Such unmonitored Dall sheep could have minimized the estimated home range overlap with predators, but would have had no incidence on results related to Dall sheep habitat utilization or diet analyses.

Finally, I would like to mention the earlier monitoring of Dall sheep rams compared to other animals in this study. I assumed that rams were subject to the same levels of predation risk as ewes, despite being monitored 1-2 years before.

Shifts in predators' home ranges may occur and have been documented before (Edwards *et al.* 2009). Although it could be the subject of further investigation, I did not monitor such shifts in my research. In spite of potential annual home range drift, my research covered a relatively short time span and I assumed that seasonal patterns of habitat utilization and predation risk remained similar within the time frame of this study.

4.5.1. Dall sheep habitat utilization, predation risk, and sexual segregation

Sexual segregation was evident in this Dall sheep population, as revealed by the different seasonal habitat use patterns of rams and ewes. Throughout the year, habitat features most often used by rams were barrens; followed by water and southerly aspects; then ruggedness, slope, avoidance of northerly aspects, use of bryoids, forests, herbs, and shrubs. All of these categories, except ruggedness and slope, may be linked to ground vegetation and foraging needs. Dall sheep are primarily grazers of grasses and sedges, but also browses, forbs, moss, and lichens (Nichols 1978, Nichols and Bunnell 1999). It is likely that the barrens, which rams used four out of five seasons, provide sparse vegetation and wind-swept ridges or slopes that are critical to insect avoidance during harassment periods in northern ungulates (Walsh *et al*. 1992) and access to forage during winter. Associations with water features from lambing to autumn may be linked to the dryness of this environment after the snowmelt. Similar positive associations with rocky land and riparian habitat were reported for Stone sheep ewes (Walker *et al.* 2007). Finally, the use of south-oriented and avoidance of north-oriented slopes are likely related to the availability of better forage on slopes with maximal sun exposure as well as the need to minimize body heat loss in this northern ecosystem. For rams, predation risk from grizzly bears was higher in the summer, which coincided with lower wolf predation risk.

In contrast, habitat variables most often used by ewes were steep slopes, followed by ruggedness and eastern aspects. The use of steep or rugged escape terrain is a well-documented behaviour of predator avoidance for Dall sheep (Geist 1971, Gwich'in Elders 1997, Rachlow and Bowyer 1998). In this study, ewes highly used steep slopes and rugged terrain during lambing and summer, when lambs are youngest and most vulnerable to predation (Hass 1989, Festa-Bianchet *et al.* 2006). The importance of safety for ewes was reflected in their habitat use patterns, at the cost of land cover classes that could provide higher foraging. Dall sheep ewes were overall less exposed than rams to grizzly bear predation, although their exposure to wolf predation increased during winter – when lambs are less vulnerable and factors like foraging and thermoregulation may gain importance.

4.5.2. Grizzly bear predation on Dall sheep

I documented a wide range of overlap with Dall sheep among individual grizzly bears. Males did have larger home ranges than females; however no difference in overlap was detected between the two sexes. Overall, the observed range of isotopic signatures indicated individual variations in dietary habits. However, the diet of grizzly bears in the Northern Richardson Mountains appeared much less diverse than in the adjacent Mackenzie Delta, where distinct foraging profiles were identified (Edwards *et al.* 2011).

Over two-thirds of the grizzly bears' assimilated diet appeared to be composed of animal sources, with vegetation providing the remaining portion. Aquatic browsers (composed of beavers and moose) emerged as their main animal food source, in equal proportion as vegetation, although with greater variability. Grizzly bear predation on moose has been reported in few populations (Boertje *et al.* 1988, Mattson 1997) and it is likely that moose, rather than beaver, constitutes an important component of grizzly bear diet in the Northern Richardson Mountains. Dall sheep, caribou and arctic ground squirrel composed altogether over one-quarter of their diet. For several coastal bear populations, fish, particularly salmon or trout (*Salmo* spp., *Oncorhynchus* spp.), has been reported as a major food source (Hilderbrand *et al.* 1999, Gende *et al.* 2001). In the adjacent Mackenzie Delta, grizzly bears were also observed feeding on broad whitefish (Barker and Derocher 2009). My results suggest that, in the Northern Richardson Mountains, the consumption of fish by grizzly bears is minimal compared to other food sources.

4.5.3. Wolf predation on Dall sheep

Wolves' spatial overlap with Dall sheep also varied greatly among individuals. Given the individual variations in isotopic signatures among this population, it is likely that some wolves were more reliant on Dall sheep than others. Variations in wolves' diet have been documented in other populations

(Urton and Hobson 2005) and can be a consequence of some individuals specializing in certain prey species. Specialized predators can lead to stochastic predation events that may adversely affect mountain sheep populations, as reported for cougars (*Puma concolor*) and bighorn sheep (Ross *et al.* 1997, Festa-Bianchet *et al.* 2006).

Overall, the wolves' main food sources in the Northern Richardson Mountains appeared to be aquatic browsers (moose and beavers) followed closely by mountain mammals (Dall sheep, caribou and arctic ground squirrels). My results corroborate findings reported elsewhere: wolves in central Yukon relied primarily on moose (Hayes *et al.* 2000), wolves in Northwest Alaska preyed almost equally on moose and caribou (Ballard *et al.* 1997), and wolves in Nunavut mostly followed the migration route of the barren-ground caribou (Walton *et al*. 2001). In the Northern Richardson Mountains, wolves were previously reported to prey on the Porcupine caribou herd, although kill rates greatly varied among packs (between 0.01 to 0.21 caribou killed/day/wolf) (Hayes and Russell 1998). During my study, caribou almost certainly formed part of the wolves' diet; however I did not monitor migratory movements of wolves into the calving grounds, which are located on the coastal plain (Russell *et al.* 1993). This suggests that wolves of the Northern Richardson Mountains are mostly sedentary and rely on prey within their territories.

4.5.4. Conclusion

From the Dall sheep's perspective, my analyses revealed seasonal habitat utilization patterns that varied for rams and ewes. Foraging needs emerged as a key factor driving the rams' habitat choices, whereas ewes' habitat choices seemed to be motivated by predator avoidance –particularly when lambs were most vulnerable. My results suggest that predation risk plays an important role in Dall sheep' sexual segregation and habitat use, thereby supporting the predation risk hypothesis and corroborating findings for other mountain sheep populations (Festa-Bianchet 1988, Corti and Shackleton 2002). This study also shows that individuals were exposed to various levels of risk throughout the year. Precisely, ewes exposure to wolf predation risk peaked during the winter; whereas rams were more at risk to grizzly bear predation than ewes, with an increased exposure during the summer.

From the predators' perspective, I described variations in levels of risk posed by each individual by calculating their home range overlap with Dall sheep, and characterized their reliance on Dall sheep by estimating its proportion in their diet. My results suggest that meat is critical to this grizzly bear population and that mountain mammals constitute an important part of both the grizzly bear and wolf diets. Due to their close isotopic signatures, methods other than carbon and nitrogen stable isotopes analysis are required to distinguish the exact dietary proportion of Dall sheep from caribou and arctic ground squirrels. The spatial proximity of these food sources further confounded my attempts to assess grizzly bear and wolf predation. For instance, arctic ground squirrels select for steep slopes (Barker and Derocher 2010) that are also used by Dall sheep. Holders of Gwich'in and Inuvialuit traditional ecological knowledge have mentioned that vegetation (mostly berries) and arctic ground squirrels are important factors driving grizzly bears near Dall sheep groups (Chapter 6). Intrinsically, predator-prey interactions are intricate and challenging to investigate, particularly in remote ecosystems. Even if some questions remain, this chapter contributes to raise our understanding of Dall sheep, grizzly bear and wolf interactions through an innovative combination of approaches. My results have revealed important patterns related to Dall sheep seasonal habitat utilization, sexual segregation, predation risk, and delineated grizzly bear and wolf diets in the Northern Richardson Mountains. In the following chapter, I examine Dall sheep behaviour and sexual segregation in early summer, in relation with wolf and grizzly bear predation risk.

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5. Dall sheep behaviour and sexual segregation under wolf and grizzly bear predation risk

5.1. Introduction

Predator avoidance is pivotal to the survival and fitness of ungulates. To minimize the odds of being killed by predators, prey may be forced to increase vigilance, reduce foraging, use suboptimal habitat and minimize energy gain (Kie 1999). Vigilance behaviour, a key mechanism to detect predators and avoid their attack, is recognized to increase along levels of perceived predation risk (Lima and Dill 1990, Quenette 1990, Hunter and Skinner 1998). However, this relation is not straightforward and the level of vigilance exhibited by individual animals is also influenced by factors like group size (Elgar 1989, Roberts 1996, Beauchamp 2008), group composition and status (e.g., presence of offspring, lactating versus non-lactating females) (Corti and Shackleton 2002, Hamel and Côté 2008), conspecifics behaviour (Childress and Lung 2003), feeding sites (Dumont and Boissy 2000) and distance from refuges or escape terrain (Frid 1997).

Predation risk can also lead to sub-optimal or altered feeding patterns, which has been reported for several ungulates. For example, increased vigilance induced foraging costs, in terms of reduced bite rate and forage consumption, for both bison (*Bison bison*) and elk (*Cervus canadensis*) observed during the summer (Fortin *et al.* 2004). Moreover, adult females accompanied by offspring appear to be particularly affected by predator avoidance, in contrast to males. For instance, moose (*Alces alces*) cows with calves remained longer than bulls in poor quality habitats, likely to avoid predation (Edwards 1983). Similar findings were reported for Dall sheep (*Ovis dalli dalli*), with ewes frequenting habitats with low forage indices during lambing season (Corti and Shackleton 2002). In ungulates, sexual segregation may occur at various scales (Bowyer and Kie 2006) and has often been linked to predator avoidance (for a review, see: Main *et al.* 1996, Ruckstuhl and Neuhaus 2002).

The predation risk hypothesis, also called the reproductive strategies hypothesis (Main and Coblentz 1996, Corti and Shackleton 2002, Hamel and Côté 2007), states that females increase their reproductive success through the survival of their young, which leads them to prioritize safe environments, even if those offer low nutrition. In turn, the males' reproductive success depends on their ability to breed with females and compete with other males, which is often determined by their energy level and body condition. This leads males to select habitats based on available forage, even if those habitats expose them to higher predation levels. The varying nutritional needs and movement rates of adult males and females may naturally lead to the formation of groups with similar activity budgets (i.e., the amount or proportion of time allocated to various behaviours), which has also been suggested to explain sexual segregation (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2000, Ruckstuhl and Neuhaus 2002). Other major hypotheses of sexual segregation are related to forage selection, stating that females need high quality forage due to their increased protein requirement (particularly at lactation), compared to larger-bodied males that need high forage biomass (Beier 1987, Barboza and Bowyer 2000); and density dependence, which presumes that the population sex ratio leads to various levels of associations between males and females (Clutton-Brock *et al.* 1997).

Although literature abounds on the relation between predation risk and ungulate behaviour, predation risk itself too often remains an unknown factor. Except for few studies that have compared ungulates in environments where predators were either present or absent (Hunter and Skinner 1998, Creel and Winnie 2005), or documented predator observations (Corti and Shackleton 2002) and actual kill sites (Pierce *et al.* 2004), predation risk is routinely assumed to correspond to the level of vigilance itself (Altendorf *et al.* 2001, Mooring *et al.* 2004, to cite only few). This is based on the premise that vigilance level corresponds to perceived predation risk, which in turn is equivalent to the actual risk of being killed. Measuring predation risk in the field is not straightforward because it is not only linked to the proximity between predators and prey, but also to their numbers, the availability of alternative prey, individual body condition and behavior, individual abilities, and habitat features. Nevertheless, it appears reasonable to assume that the probability of occurrence of predators within the prey environment correlates with actual predation risk, and is a worthy measurement variable compared to vigilance behavior alone. Despite the importance of predation avoidance on prey behaviour, rare are the studies that link ungulate behaviour with an actual measure of predator risk, perhaps because monitoring predators can be a laborious and costly process (one exception is the work of Liley and Creel (2008) based on elk and wolf (*Canis lupus*) monitoring). However, knowing the predators' spatial distribution within a prey's home range can help assess how, and if, prey adjust their behaviour in when predators are more likely to occur; which would further increase our understanding of predation avoidance and sexual segregation in ungulates.

In this chapter, I aimed to investigate Dall sheep behaviour and sexual segregation at lambing and early summer in relation to predation risk, which was assessed by the movements of simultaneously monitored wolves and grizzly bears (*Ursus arctos*), as well as predator sightings. To examine the predictions of the "predation risk" and "activity budget" hypotheses of sexual segregation, I started by investigating the prevalence of sexual segregation among adults in early summer, then compared their activity budget and levels of predation exposure. I subsequently focused on the impact of predation risk on the vigilance and foraging behaviours of adult ewes and rams. Because of their essentially treeless environment with easily defined escape terrain, mountain ungulates, like bighorn sheep (*Ovis canadensis*), thinhorn sheep (*O. dalli*), Tibetan argali (*O. ammon hodgsoni*) and mountain goats (*Oreamnos americanus*), represent a group of choice to study activity budget and vigilance behaviour (Singer *et al.* 1991, Frid 1997, Ruckstuhl 1998, Corti and Shackleton 2002, Mooring *et al.* 2004, Loehr *et al.* 2005, Walker *et al.* 2006, Hamel and Côté 2008, Singh *et al.* 2010).

5.2. Methods

5.2.1. Study area

I studied Dall sheep behaviour in the Northern Richardson Mountains (68°N, 135°W), in vicinity of Mount Goodenough (also called Black Mountain), within the Gwich'in Settlement Area, Northwest Territories, Canada. Most of my observations were concentrated in about 58 km^2. The range of this population (estimated between 500 and 1730 in aerial surveys since 1984 (Lambert Koizumi *et al.* 2011)) extends to approximately 4000 km^2, with about half constituting suitable Dall sheep habitat (Barichello *et al.* 1987). The study area is part of the Taiga Cordillera ecozone (Scudder 1997), with elevations ranging from 400 m to 1200 m. The climate is characterized by long, cold winters and short, cool summers. Vegetation is dominated by alpine shrub tundra, with dwarf willows (*Salix* spp.), mountain avens (*Dryas* spp.), lichen and sparse vegetation cover on ridges; shrubs on upper and middle slopes; sedge (*Carex* spp.) tussock communities in lower slopes; and trees limited to river valleys and lower slopes with favourable aspects (Smith *et al.* 2004). In the Northern Richardson Mountains, wolves and grizzly bears are two potential predators of Dall sheep (Barichello *et al.* 1987, Gwich'in Elders 1997, Shaw *et al.* 2005, Lambert Koizumi *et al.* 2011). Golden eagles (*Aquila chrysaetos*) also present some risk, particularly during lambing (Barichello *et al.* 1991). Other species present in the area include: red foxes (*Vulpes vulpes*), wolverines (*Gulo gulo*), Canada lynx (*Lynx canadensis*) and rare cougars (*Puma concolor*) that may transit through the area (Shaw *et al.* 2005, Chapter 6). Approval for this study was obtained from the Gwich'in Renewable Resources Board, the Tetlit and Ehdiitat Renewable Resource Councils, the Gwich'in Tribal Council, and the Government of the Northwest Territories (research permit WL003319).

5.2.2. Observations

Three teams of two observers recorded Dall sheep behaviour and noted the presence of predators between June 4 and 28, 2007. Lambing season for this population was estimated to peak around the third and fourth weeks of May, but could start as early as May 5 and end as late as June 15 (Nolan and Kelsall 1977, Barichello *et al.* 1987). This investigation coincided with the end of lambing season and the beginning of the summer. We alternated eight-hour shifts and conducted continuous observations, which was made possible due to the all-day illumination at this northern latitude. Teams were sometimes changed to ensure that all workers followed the same protocol and recorded observations in similar ways. We hiked from our base camp until we detected a group of Dall sheep (typically after 5 to 12 km). Using binoculars (10X) and spotting scopes (20-60X), we recorded group size and composition, estimated distance and bearing to sheep (which we later used to determine the actual Dall sheep position coordinates). We tried to record the horn curvature (¼, ½, ¾, or full curl) of all rams observed, however some observations were uncertain or missing. To maximize sample size, we pooled all adult rams together for data analysis, yielding the following categories: ewes, rams, yearlings, and lambs.

In each Dall sheep group, we randomly selected one focal individual and recorded its behaviour for approximately 30 minutes (less if animals went out of sight). Peripheral animals may be subject to increased predation risk and exhibit more vigilance compared to animals at the centre of a group (Blanchard *et al.* 2008). However, since animals regularly switched positions during the observation period, we did not record spatial position within a group. Because I was interested in understanding what factors influence the behaviour of the adult segment of the population, the majority (87%) of our observations focused on ewes and rams. We also observed, albeit in smaller proportion, yearlings and lambs to document their activity budget in contrast with the activity patterns of adult classes. During observation bouts, we categorized and timed focal animals' behaviour into one of the following activities: (1) rest (lying down), (2) vigilant, (3) travel (walk, trot or run), (4) forage, (5) nurse, (6) play (frolic jumps and kicks), (7) dominance behaviour (horn clash, mount another sheep), and (8) other, such as groom, scratch or stretch. We considered an animal to be vigilant whenever it stood still, head above shoulders, and attentively scanned its surroundings (Frid 1997). Activities were not mutually exclusive, as a sheep could for example forage and walk simultaneously, or chew food while being vigilant (Fortin *et al.* 2004). We tried not to disturb the observed animals nor be noticed by them. If Dall sheep changed their behaviour noticeably due to our presence (i.e., stared at us, increased vigilance, took flight), we recorded the incident and discarded these data points from behavioural analyses.

5.2.3. Estimation of predation risk

Predation itself may be decomposed in two stages: the encounter between predator and prey, then the probability of a successful attack given an encounter (Holling 1959, Hebblewhite *et al.* 2005). In this study, I did not monitor actual attacks by predators, but I interpreted the first component of predation, the probability of encounter, as an index of predation risk. I estimated predation risk based on the probability of occurrence of wolves and grizzly bears monitored in the study area during the observation period, from their GPS collar locations recorded at four hours interval (Lambert Koizumi and Derocher 2010). From observations made in the field and at the time of capture, at least one wolf per pack (four wolves, out of a minimum of seven wolves distributed in two packs overlapping the observation area) and several adult grizzly bears (11 during that period, out of at least 15 that were identified) were monitored. I calculated the predators' probability distribution from the rasterized value (100 m grid cell) of wolf and grizzly bears fixed-kernel home range for June 2007 (bandwidth = 2500), following utilization distribution methods described by Marzluff *et al.* 2004 and Millspaugh *et al.* 2006. I then computed predation risk for each estimated Dall sheep location using Hawth's Analysis Tools (Beyer 2004) and ArcGIS 9.2 (ESRI, Redlands, California, USA). Additionally, we recorded predators observed in vicinity of Dall sheep during behavioural observations. The distance between predators and Dall sheep was estimated and their interaction was noted, if any. Whether predators were observed near a Dall sheep group constituted one dependent binomial variable of my models, as described in the next section.

5.2.4. Statistical analyses

The normality of all variables was examined with quantile-normal plots. I transformed non-normally distributed variables with standard methods (i.e., $\log_{10}$, square-root, arcsine) to conduct parametric statistical analyses, and then back-transformed in result statements where relevant (Zar 1999). For activity budget analyses, I arcsine square-root transformed the proportion of time spent conducting each behaviour type. To assess differences in group size (number of individuals observed together, log-transformed), activity budget, and exposure to predation between ewes and rams, I used the *t*-test. To examine variations between additional classes (yearlings and lambs), I used one-way ANOVA followed by post-hoc Tukey-Kramer multiple pairwise comparisons (Day and Quinn 1989) if differences (using α level = 0.05) were found among groups.

To assess factors that might affect the foraging and vigilance behaviours of Dall sheep ewes and rams, I built *a priori* a series of linear regressive models that I fitted to observations for both sexes. The models I considered included up to eight independent variables related to either (1) Dall sheep social organization: group size (log-transformed), presence of at least one lamb (coded as 0 or 1), mixed adult sexes (whether opposite sex was present in group, coded as 0 or 1);

(2) the environment: distance to escape terrain (square-root transformed), time of the day (0 to 1, starting at midnight, square-root transformed); and (3) predation risk: probability of occurrence of the simultaneously monitored wolves and grizzly bears (both log-transformed), and whether predators were observed during the observation (coded as 0 or 1). Models were run twice for each sex; one with the proportion of time being vigilant as the dependent variable, and one with the proportion of time spent foraging (both arcsine square-root transformed). I could have combined variables in up to 245 different ways, or more if I had considered interactions; however I restrained my selection to a set of 33 models that include a combination of prey, environmental, and predator variables (Table 5.2), based on my knowledge of the species and findings from previous studies.

I identified which model(s) best fitted the data using a multi-model inference approach (Burnham and Anderson 2002). Competing models were evaluated with a corrected version of Akaike's information criterion (AIC_c), suitable for small sample sizes and when the number of fitted parameters represents a moderate to large fraction of the sample $w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)}$ size (Hurvich and Tsai 1989). The weight w_i of each model was calculated as: , Δ_i being the difference between each model's AIC_c score with the score of the model with the smallest AIC_c value. Models with $\Delta AIC_c < 2$ were considered as the most suitable ones (Burnham and Anderson 2002). The relative importance of each variable was assessed as the cumulative weight of models in which variable appeared. To assess how each variable related to ewes and rams' behaviours, I averaged the regression coefficients and their standard errors across all competing models, based on each model's weight (Anderson 2008). Moreover, I used unconditional variance estimators that have the quality of incorporating both sampling variance, given a model, and a variance component for model selection uncertainty (Anderson 2008). Statistical analyses were conducted in Stata 11.2 (Stata, College Station, Texas, USA).

5.3. Results

5.3.1. Behavioural observations

A total of 194 observation bouts were recorded, on groups composed between one and 75 Dall sheep. I excluded bouts (N = 38) that lasted less than ten minutes, whenever Dall sheep seemed to have noticed our presence, and incomplete records. As such, I retained 156 bouts for activity budget analyses, corresponding to 73.9 hours of observations (mean ± SE = 28.4 ± 0.5 minutes per bout) for 63 ewes, 72 rams, 6 yearlings, and 15 lambs. The mean distance between observers and Dall sheep was estimated at 682 ± 33 m. Group size varied between age and sex classes ($F_{3,152}$ =16.35, $P < 0.01$), as rams (mean group size = 8.4 ± 1.3 animals) stayed in smaller groups compared to ewes (18.2 ± 1.8 animals) and lambs (24.1 ± 4.2 animals) (post-hoc Tukey-Kramer comparison, $P < 0.05$). In 34% of observations (n = 65), adult ewes and rams were mixed together. Single adult sex groups (i.e., ewes, nursery groups, or bachelors only) formed the rest of the observations.

5.3.2. Activity budget

The activity budget of focal animals varied individually and across demographic classes (Figure 5.1). When all focal animals were pooled together, the four most important activities were foraging (a proportion of 0.38 ± 0.04 of the observation bout), resting (0.30 ± 0.04), travelling (0.22 ± 0.03), and vigilance (0.10 ± 0.01). Other behaviours accounted on average for a proportion less than 0.01 of activity budgets. Examining differences between sexes revealed that rams spent more time resting (0.41 ± 0.07 versus 0.24 ± 0.06; $t_{133} = 2.01$, $P = 0.02$) and exhibiting dominance behaviour (0.0004 ± 0.0003 versus 0.00002 ± 0.00003; $t_{133} = 1.66$, $P = 0.05$) than ewes; but spent less time foraging (0.29 ± 0.05 versus 0.50 ± 0.06; $t_{133} = 2.71$, $P < 0.01$), being vigilant (0.08 ± 0.01 versus 0.13 ± 0.03; $t_{133} = 1.69$, $P = 0.05$), and, naturally, nursing (0 versus 0.002 ± 0.002; $t_{133} = 3.21$, $P < 0.01$). When yearlings and lambs were also considered, further differences emerged related to: time spent being vigilant (($F_{3.152} = 2.87$, $P = 0.04$), with ewes being more vigilant (0.13 ± 0.03) than lambs (0.03 ± 0.02)); and playing ($F_{3,152} = 26.38$, $P < 0.01$, with lambs playing more than any other class (0.07 ± 0.04 versus 0.002 ± 0.004 for yearlings, 0.00002 ± 0.00003 for rams, and 0 for ewes)). Nursing was also exclusive to ewes and lambs (respectively 0.002 ± 0.002 and 0.004 ± 0.004 of their average time budget).

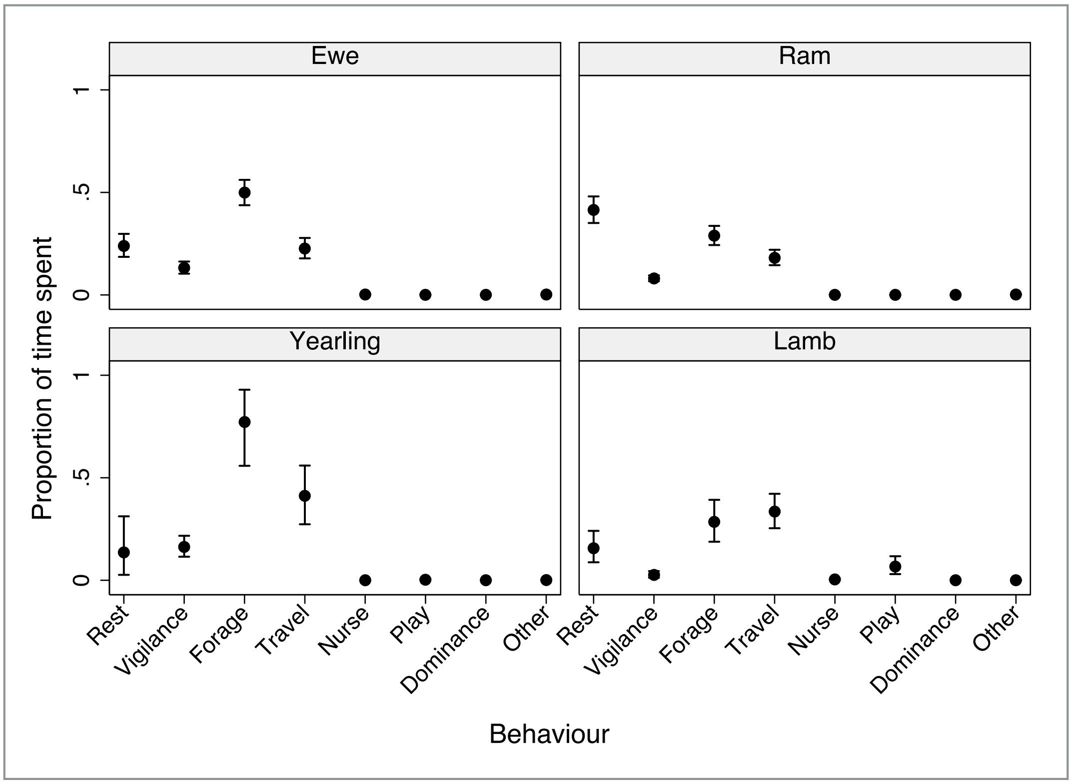

Figure 5.1. Activity budget of Dall sheep ewes, rams, yearlings and lambs in the Northern Richardson Mountains, June 2007. Shown are the means and standard errors for each activity, which were back-transformed from arcsine square-root transformed proportions of time spent in each activity.

5.3.3. Predation risk

The wolf predation risk layer was estimated from 539 locations recorded for four wolves (average of 135 ± 33 locations per wolf), between 1-30 June, 2007. The grizzly bear risk was based on 1896 locations from 11 grizzly bears (172 ± 24 locations per bear) monitored during the same period. The overall probability of occurrence of wolves and grizzly bears varied throughout the study area (Figure 5.2), leading to different levels of predation risk across observed groups. Exposure to wolf predation risk was higher for rams compared to ewes ($F_{3,152}$ = 12.42, P < 0.01), yearlings, and lambs (Tukey-Kramer tests, P < 0.05,

Table 5.1). There were however no significant differences across sex and age class regarding exposure to grizzly bear risk ($F_{3,152}$ = 1.31, P = 0.27). Overall, all demographic classes were exposed to greater levels of grizzly bear predation risk compared to wolf predation risk (t_{310} = 19.49, P < 0.01, Table 5.1).

Table 5.1. Exposure to wolf and grizzly bear predation risk (mean and standard error (SE), log-transformed) of focal animals by demographic class.

Demographic class	N	Wolf risk (log)	SE	Grizzly bear risk (log)	SE
Rams	63	-10.933*	0.176	-8.970	0.068
Ewes	72	-12.085	0.207	-8.990	0.073
Yearlings	7	-13.018	0.313	-8.857	0.104
Lambs	15	-12.889	0.226	-8.695	0.075

(*) = Statistically significant difference

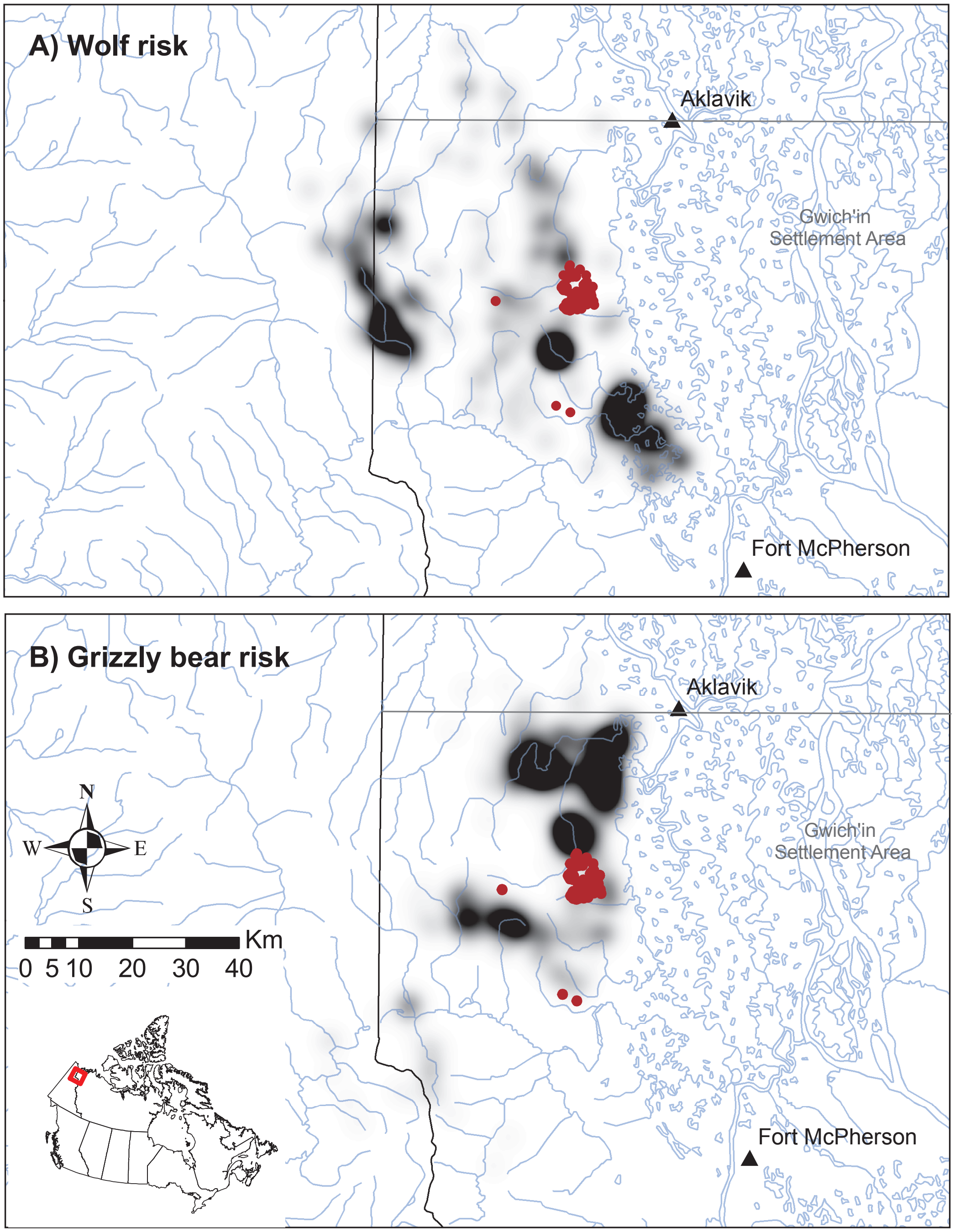

Figure 5.2. Study area in the Northern Richardson Mountains, showing locations of the Dall sheep behavioural observations (red circles) as well as variations in wolf (A) and grizzly bear (B) predation risk (darker shades indicate higher risk), estimated for June 2007 from the movements of animals equipped with GPS collars.

Predators were recorded nearby Dall sheep groups in 15 occasions. In total, 14 grizzly bears (five groups of mother and cubs and two single bears), five golden eagles, two wolves, and two red foxes were observed. Estimated distances between predators and Dall sheep varied between 10 m to over 1.5 km. The closest observation was for a pair of golden eagles that hovered above one group of ten Dall sheep (nine ewes and one lamb). Grizzly bears were the closest terrestrial predators observed, with eight individuals recorded within 250 m of Dall sheep. No successful predation event was witnessed, however a grizzly bear sow and her two cubs were observed stalking a group of 12 Dall sheep (seven ewes and five lambs) from above a steep cliff. After waiting for several minutes, the bears ultimately caused a rockslide that scared the sheep away. One lone collared wolf was also observed travelling in direction of a Dall sheep group, but reoriented its trajectory after noticing the observers' presence.

5.3.4. Vigilance and foraging behaviour models

For Dall sheep ewes, the best vigilance behaviour models (with $\Delta AIC_c < 2$) included time of the day, distance to escape terrain, group size, presence of lambs, and grizzly bear risk (models 23 and 27, Table 5.2, Figure 5.3). Foraging behaviour of ewes was best described by, in order of importance, increasing distance to escape terrain, lower wolf risk, higher grizzly bear risk, increasing time of the day, and increasing group size (models 25 and 22, Table 5.2). For rams, the best predicator variables of vigilance behaviour were grizzly bear risk and wolf risk (models 2 and 3, Table 5.2). Several models came out nearly equal in explaining rams' foraging behaviour (models 3, 9, 8, 2, 13, and 12, Table 5.2). The most influential variables were wolf risk, grizzly bear risk, group size, time of the day, and distance from escape terrain.

Although a combination of variables were found to affect the behaviour of both ewes and rams, model averaging revealed that only one variable, time of the day, had a coefficient significantly different from 0, when related to ewes' vigilance (Table 5.3). Specifically, ewes were increasingly vigilant as the time of the day advanced (Figure 5.3). No clear pattern or relationship emerged between other variables and vigilance (Figure 5.3) or foraging (Figure 5.4) behaviours, for neither ewes nor rams.

Table 5.2. Ranks for regressive models on vigilance and foraging behaviours of Dall sheep ewes and rams.

	Prey			Environment		Predation				Ewes ranks		Rams ranks	
Model No.	Group size	Lambs present	Mixed adult sexes	Escape distance	Time of the day	Wolf risk	Grizzly risk	Predator seen	*K*	Vigilance	Foraging	Vigilance	Foraging
1	+								1	26	26	29	27
2							+		1	10	28	***1****	***4****
3						+			1	21	12	***2****	***1****
4					+				1	9	30	27	9
5				+					1	32	31	30	29
6			+						1	33	33	32	32
7		+							1	30	9	33	33
8	+						+		2	13	25	5	***3****
9	+					+			2	23	16	8	***2****
10	+			+					2	27	23	28	30
11						+	+		2	14	18	3	7
12					+		+		2	8	27	4	***6****
13					+	+			2	19	20	7	***5****
14				+				+	2	31	32	31	31
15					+			+	2	11	29	16	14
16	+			+			+		3	17	24	6	12
17	+					+	+		3	16	21	10	10
18	+			+		+			3	25	5	12	8
19	+	+	+						3	29	11	26	24
20					+	+	+		3	3	22	11	13
21						+	+	+	3	15	15	9	11
22	+			+		+	+		4	20	***2****	14	15
23	+	+		+	+				4	***1****	7	19	16
24	+	+		+				+	4	28	17	25	28
25				+	+	+	+		4	6	***1****	13	17
26	+			+		+	+	+	5	22	3	17	18
27	+	+		+	+		+		5	***2***	13	15	19
28	+	+	+	+	+				5	4	14	22	21
29	+	+		+	+	+			5	5	10	18	20
30	+	+	+	+		+	+		6	24	6	20	22
31	+	+		+	+	+	+		6	7	4	21	23
32	+	+	+	+	+	+	+		7	12	8	23	25
0	+	+	+	+	+	+	+	+	8	18	19	24	26

(*) = Models with $\Delta AIC_c > 2$

Table 5.3. Regression coefficients (β) and standard errors (SE) from model averaging, using AIC_c weights and based on transformed variables (as described in text).

	Prey			**Environment**			**Predation**		
Behaviour	Variable	β	SE	Variable	β	SE	Variable	β	SE
Ewe vigilance	Group size	-0.013	0.044	Escape distance	0.013	0.008	Wolf risk	0.012	0.022
	Lambs present	-0.206	0.151	Time of the day*	***0.628***	***0.239***	Grizzly bear risk	-0.020	0.027
	Rams present	-0.004	0.040				Predator seen	0.008	0.064
Ewe foraging	Group size	0.014	0.063	Escape distance	0.026	0.019	Wolf risk	-0.080	0.102
	Lambs present	0.091	0.316	Time of the day	0.208	0.303	Grizzly bear risk	0.071	0.105
	Rams present	0.011	0.061				Predator seen	-0.029	0.153
Ram vigilance	Group size	0.001	0.020	Escape distance	0.000	0.004	Wolf risk	-0.007	0.022
	Lambs present	-0.002	0.026	Time of the day	0.017	0.262	Grizzly bear risk	-0.022	0.014
	Ewes present	0.000	0.009				Predator seen	0.003	0.030
Ram foraging	Group size	0.034	0.075	Escape distance	0.000	0.006	Wolf risk	-0.025	0.045
	Lambs present	0.000	0.057	Time of the day	0.115	0.211	Grizzly bear risk	-0.017	0.026
	Ewes present	-0.002	0.027				Predator seen	0.014	0.079

* = Statistically significant (α = 0.05)

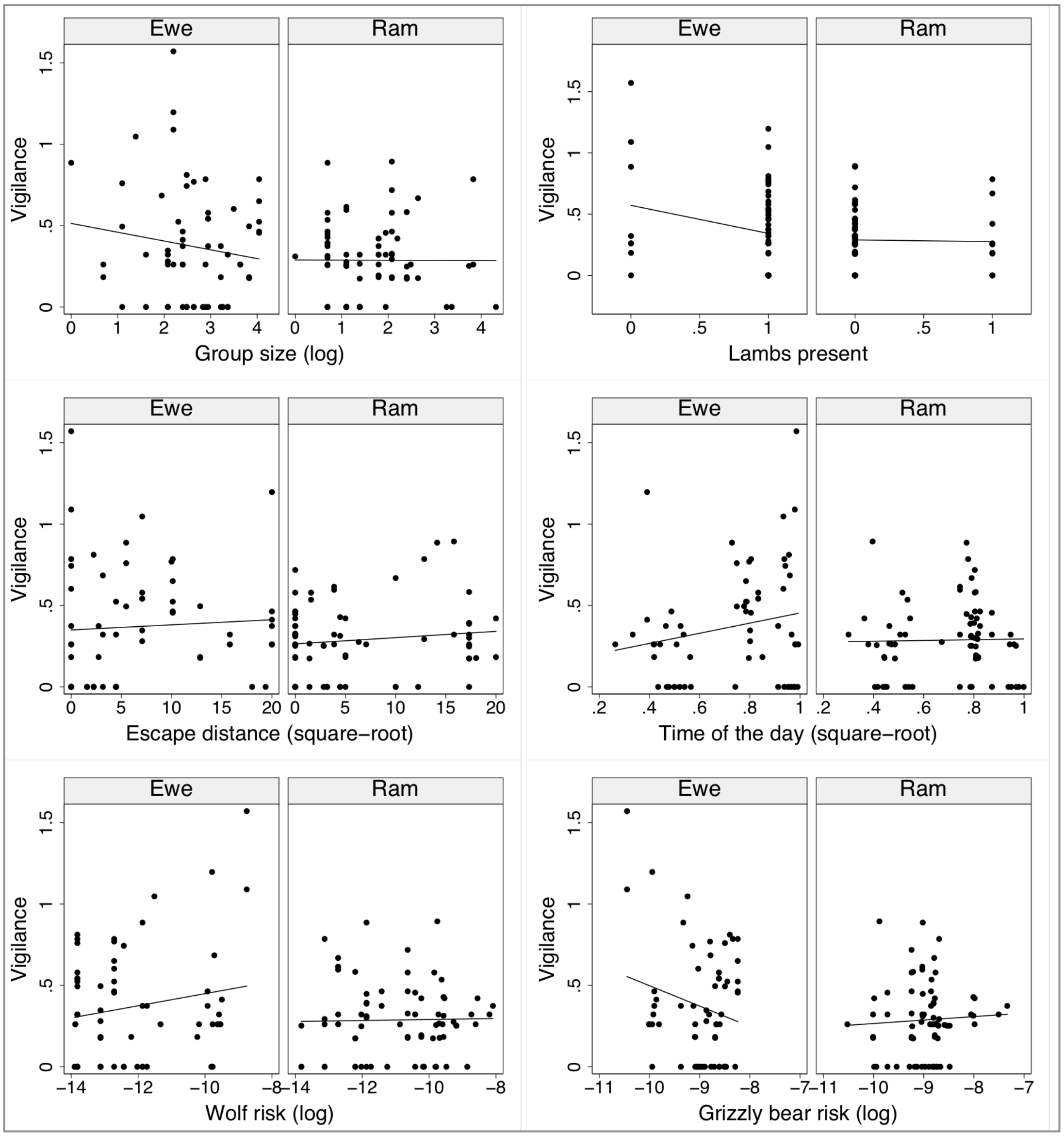

Figure 5.3. Dall sheep ewes and rams' vigilance behaviour (proportion of time spent being vigilant, arcsine square-root transformed) in relation with variables that were included in the most suitable models ($AIC_c < 2$). Linear regression lines are shown for all graphs, although only the relationship between time of the day and ewes' vigilance was significantly different from 0 ($\alpha = 0.05$).

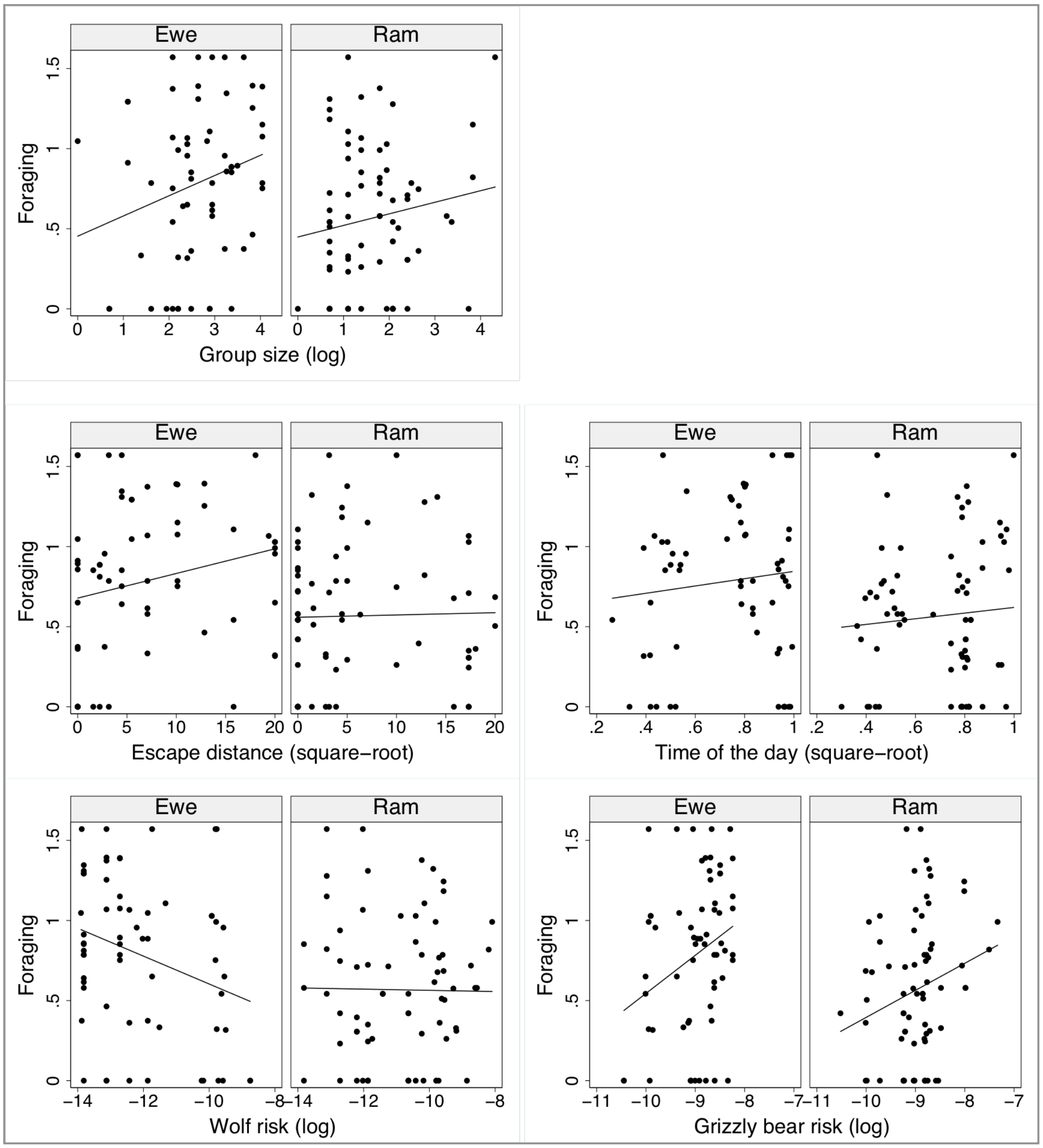

Figure 5.4. Dall sheep ewes and rams' foraging behaviour (proportion of time spent being foraging, arcsine square-root transformed) in relation with variables that were included in the most suitable models ($AIC_c < 2$). Linear regression lines are shown for all graphs, although none actually came out as statistically different from 0 ($\alpha = 0.05$).

5.4. Discussion

In this study, I examined Dall sheep sexual segregation and activity budget through ewes and rams' vigilance and foraging behaviours during lambing and early summer. As pointed out by Bowyer and Kie (2006), the study time scale may affects our interpretation of several processes like sexual segregation, habitat use, and animal behaviour. In my case, observations were limited to a one-month period. Perhaps due to this short time period, I did not detect some relationships often reported in the literature, for example a decreased vigilance with increased group size (Elgar 1989, Roberts 1996, Beauchamp 2008) or nearer escape terrain (Frid 1997). Repeated observations during other months or in other areas could have increased the statistical power of my analyses. Nevertheless, this chapter reveals important patterns of Dall sheep behavior, and highlights the complexity and plurality of factors affecting ungulate behaviour.

5.4.1. Sexual segregation and differences in activity budgets

I found that sexual segregation occurred in about two-thirds of observations. Although the majority of adults were grouped according to sex, sexual segregation during lambing was far from complete, because a substantial portion of the population remained in mixed groups. Although I pooled adult rams together for data analysis, notwithstanding the size of their horns, *a posteriori* examination of my records indicated that rams that stayed with ewes and nursery groups were mostly young ones, based on their horn curl. Full curl rams were observed with nursery bands in only two instances, in larger groups (≥ 29 animals). This provides evidence that young rams remain with the maternal groups until they join bachelor bands, when they get older and possibly reproductively active.

Comparisons between the behaviour of Dall sheep age and sex classes revealed several distinctions. Overall, ewes were found to forage more, be more vigilant, rest less, and exhibit less dominance behaviour compared to rams. Lambs were also found to play more than any other group. Social play is an important mechanism to familiarize with other group members and learn proper communication and social cues; its preponderance in lambs has also been noted in bighorn sheep (Berger 1980). On one hand, my findings concord with the main prediction of the "activity budget hypothesis" to explain sexual segregation –i.e., ewes and rams exhibited different activity patterns, which could preclude them from staying together. Another key prediction of that hypothesis is that females compensate for their lower digestive efficiency and higher energy requirements during lambing by foraging for longer than males, while males spend more time ruminating or lying than females to digest forage (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2002). I also observed this phenomenon, with ewes foraging more and resting less than rams. In contrast, my results also indicate that rams were subject to higher exposure to wolf predation risk and stayed in smaller groups. This particularity, combined with increased vigilance in ewes, equally concords with the "predation risk hypothesis" (Main *et al.* 1996), suggesting that ewes prioritize predator avoidance and their progeny's safety, while rams are exposed to greater predator risk, potentially to benefit from higher quality forage in other habitats. As others have concluded (Ruckstuhl and Neuhaus 2002, Singh *et al.* 2010), the two hypotheses are not mutually exclusive, and my research provides support for both.

5.4.2. Vigilance and foraging behaviours

When assessing which factors most affected the vigilance and foraging behaviours of ewes and rams, I attempted to select the most relevant variables, while keeping models simple and easily interpretable. The models I considered suggest that the vigilance and foraging behaviours of ewes are influenced by the interplay of several variables related to prey social organization, the environment, and predation. These results concur with those of Liley and Creel (2008), who also found that complex models best described elk vigilance behaviour. The vigilance of rams, in constrast, was mostly influenced by wolf and grizzly bear predation risk. This difference might be related to the higher levels of wolf predation risk rams endure in comparison to ewes, which exhibited greater vigilance. Predation risk also affected the time rams spent foraging, in combination with other variables related to their social organization and their environment. Segregation of Dall sheep groups did not have a noticeable effect on the vigilance or foraging behaviours of ewes and rams. The observation of predators nearby also did not appear to be a great indicator of predation risk, or at least was not related to Dall sheep behaviour, perhaps due to our limited sample size (15 observations) and the wide variation in distances between sheep and predators.

Despite the exposure to grizzly bears being more important than to wolves for both Dall sheep adult sexes, ewes' vigilance was not related to grizzly bear risk, in contrast to wolf predation risk; suggesting that ewes perceive grizzly bears as a lesser threat than wolves. Previous analyses have revealed that Dall sheep shared a greater spatial overlap with grizzly bears than wolves in intensively used areas, although the overlap with wolves was greater in other areas (Lambert Koizumi and Derocher 2010, Chapter 3). During summer, I also found that rams were subject to higher exposure to grizzly bears than ewes, while ewes' exposure to wolves peaked at wintertime (Chapter 4). In this chapter, I documented a predation attempt by grizzly bears on Dall sheep, albeit unsuccessful. Meat constitutes an important part of the diet of these grizzly bears, although they also rely on other food sources present on the Dall sheep range (Chapter 4, Edwards *et al.* 2011). The lack of relationship between the ewes' vigilance and grizzly bear risk could be related to the fact that the ewes' close associations with bears occur in intensively used areas that provide a multitude of escape terrain and steep cliffs, in contrast with areas of wolf exposure that may offer less opportunity for predator avoidance.

Although a combination of several variables best described Dall sheep vigilance and foraging behaviours, only time of day was statistically significantly when related to ewes' vigilance. This increase in ewes' vigilance later in the day could correspond to times when predators are more likely to attack. The Northern

Richardson Mountains being located in the Arctic, this study area is characterized by full daylight (midnight sun) during summer solstice, a particularity lacking from most other mountain sheep studies. It is unclear how the circadian rhythm of wolves and other predators may be affected by this full daylight, but at lower latitudes wolves exhibit greater movement rates (Merrill and Mech 2003) and higher incidence of kills (depredation cases (Ciucci and Boitani 1998)) at night. During the long Arctic summer, thinhorn sheep have been seen foraging at all times of the day (Nichols and Bunnell 1999). In southern latitudes, nocturnal foraging and walking behaviours, along with increased vigilance, were also reported in bighorn sheep (Woolf *et al.* 1970). In my study, the proportion of time spent foraging, travelling or resting varied throughout the day with no particular pattern (based on post-hoc examination). Only vigilance appeared to increase for ewes (Table 5.3). It is worth noting that more variables, such as traits inherent to each individual's personality (Buirski *et al.* 1978, Réale *et al.* 2000), could also affect the prey behaviour and lead to varying displays of vigilance, playfulness, or dominance interactions.

Intrinsically, ungulate behaviour is complex and disentangling the various influencing factors is rarely straightforward. My research described sexual segregation in Dall sheep, along with activity patterns and exposure to predation risk that varied among age and sex classes. Although I did not test all proposed hypotheses of sexual segregation in ungulates, my results support two main hypotheses, related to predator risk and disparity in activity budgets, and further enrich the debate regarding causes of sexual segregation in ungulates. This study also provides a unique glimpse of Dall sheep behaviour in early summer, and deepens our understanding of Dall sheep, wolves, and grizzly bears interactions in the Northern Richardson Mountains. In the next chapter, I further complement the results obtained so far with the documentation of Gwich'in and Inuvialuit traditional ecological knowledge.

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6. Traditional ecological knowledge of Dall sheep, grizzly bears, wolves, and their interactions, in the Richardson Mountains

6.1. Introduction

Traditional ecological knowledge (TEK) stands as a body of information stemming from careful observations of the natural world, either passed down in oral tradition or shared among users of a resource (Huntington 2000). When TEK is compared with science, several parallels and contrasts may be highlighted (Berkes *et al.* 2000, Pierotti and Wildcat 2000). For instance, TEK holders and scientists are similar in that they both have acquired their knowledge through a series of observations. Typically, however, TEK is collected over a much longer time period (from the lifetime of an individual to several generations), in contrast with a few days, months or years for scientific studies. Additionally, science is more systematic and planned than TEK, which focuses on the connectivity and relationships between humans and the natural world (Pierotti and Wildcat 2000).

Emerging from the use of TEK in research and management of natural resources is the complementary nature of the two approaches (Huntington *et al.* 2004, Moller *et al.* 2004). TEK can be a useful tool to gain additional insights on ecosystems, address management problems, and provide a bridge between local communities, resource users, and managers (Berkes *et al.* 2000, Usher 2000, Ellis 2005). TEK and aboriginal wisdom may also provide a model for sustainable resource management (Turner *et al.* 2000).

In northern Canada, where the inclusion of TEK in management policies prevails (Ellis 2005), aboriginal knowledge has been documented in relation to several wildlife populations and ecological processes. For example, TEK has been collected to assess the impacts of climate change (Riedlinger 1999, Berkes and Jolly 2001, Cruikshank 2001) and understand the ecology, abundance, and movements of harvested species like polar bears (*Ursus maritimus*) (Keith 2005, Dowsley 2007) and barren-ground caribou (*Rangifer tarandus*) (Ferguson and Messier 1997, Parlee *et al.* 2005). Increasingly, there is a tendency to document TEK in association with scientific studies as a complementary aspect for co-management (Berkes *et al.* 2007).

For several generations, the remote Richardson Mountains, overlapping the Yukon (YT) and Northwest Territories (NT), Canada, have been travelled and inhabited by two groups of aboriginal people: the Gwich'in and the Inuvialuit. The Gwich'in live at the northwest limit of the boreal forest and belong to the larger family of aboriginal people known as Dene or Athapaskans. Today, the Gwich'in live in several communities of the Northwest Territories, the Yukon, and Alaska. Hunting, fishing and trapping remain important both culturally and economically, with caribou, moose (*Alces alces*) and whitefish (*Coregonus nasus*) being the staples of their diet (Gwich'in Social and Cultural Institute, 2003). In the community of Aklavik (NT), located about 20 km east of the Richardson

Mountains, Gwich'in cohabit with the Inuvialuit. The Inuvialuit primarily live above the treeline and represent one group of Inuit inhabiting Canada's Western Arctic. The Inuvialuit culture and way of life is closely linked to marine mammals as well as barren-ground caribou (Alunik *et al.* 2003). Both Gwich'in and Inuvialuit have maintained strong ties to their natural environment and, whenever possible, families live out on the land in seasonal camps. They hold a rich history of oral tradition and comprehensive TEK about the species living in the Richardson Mountains.

For my research, I focused on three species of this mountain range: Dall sheep (*Ovis dalli dalli*) and two potential predators: grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*). Dall sheep have suffered a sharp decline since the mid-1990s and are now managed under a collaborative plan developed by aboriginal, territorial and other partners[1]. Some traditional and local knowledge had been documented for these species before (Gwich'in Elders 1997, Shaw *et al*. 2005, Wildlife Management Advisory Council (North Slope) and Aklavik Hunters and Trappers Committee 2008), however little attention had been devoted to their interactions.

From the scientific side, aerial surveys of Dall sheep were initiated in the 1970s (Simmons 1973, Hoffman 1974, Nolan and Kelsall 1977, Hoefs 1978) and continued every few years afterward (Males 1980, Latour 1984a, Latour 1984b, Barichello *et al.* 1987, Stenhouse and Kutney 1987, Davison and Cooley 2006,

[1] Draft management plan available at: http://www.env.gov.yk.ca/mapspublications/documents/N-Richardson_Sheep_Mgmt_Plan_DRAFT_2008.pdf [Accessed July 25 2011]

Nagy and Carey 2006a, Nagy and Carey 2006b, Nagy *et al.* 2006a, Nagy *et al.* 2006b). These surveys have revealed large fluctuations in population abundance, with an important decline from about 1700 to 700 individuals between the mid 1990s to mid 2000s. Factors driving the abundance of this population may include harvest, climate, predation, density dependence, competition with other species, and diseases (see Lambert Koizumi *et al.* (2011). The role of predation by grizzly bears and wolves in the recent decline was unclear but suspected to be important by some community members (Shaw *et al.* 2005; communications during co-management meetings, unpub.). The productivity of grizzly bear females in the Richardson Mountains was studied from 1992 to 2000 (M. Branigan, ENR NT Government, unpub.). In this region, wolves were documented to depend mostly on moose and, seasonally, on the Porcupine Caribou herd (Hayes and Russell 1998, Hayes and Harestad 2000b). The home range overlap of grizzly bears and wolves with Dall sheep (Lambert Koizumi and Derocher 2010, Chapter 3), their assimilated diet and relation with Dall sheep habitat utilization patterns (Chapters 4), in addition to their effect on Dall sheep behaviour (Chapter 5) were recently investigated as part of my research. However, many questions remained on grizzly bears and wolves, particularly on their population status, habitat use, nutrition, ecology, and overall impact on Dall sheep.

To understand the ecology and interactions between Dall sheep, grizzly bears and wolves and complement findings from other scientific methods (i.e., satellite collars, behavioural observations and stable isotope analyses), I turned to Gwich'in and Inuvialuit TEK. My main objective was to document TEK about these three species ecology and interactions, focusing on predator-prey dynamics. Additionally, I gathered the views, wisdom, and recommendations of study participants regarding anthropogenic disturbances as well as the conservation and management of Dall sheep, grizzly bears and wolves in the Richardson Mountains.

6.2. Methods

In July and August 2008, I conducted 23 interviews with Gwich'in (N = 21) and Inuvialuit (N = 2) elders and active land users living in the communities of Aklavik and Fort McPherson, Northwest Territories, Canada (Figure 6.1). Interviewees were reputed in their communities for being knowledgeable about the studied species and research area, and were selected in collaboration with the Ehdiitat and Tetlit Gwich'in Renewable Resources Councils and / or referred by their peers. Although I initially planned to document only Gwich'in TEK, two Inuvialuit persons were referred by their peers during the interviews. After consideration (and as per our research license), I decided to adopt an inclusive approach and listen to all participants, Gwich'in and Inuvialuit, willing to share knowledge about this study system. It is my hope that this decision will be well received, as I hold much respect for both Gwich'in and Inuvialuit people.

A consent form explaining the study was presented to the participants before the interviews (Appendix A). Interviews were semi-directed (Huntington

1998) and questions (Appendix B) addressed the origin and extent of the knowledge of the interviewees on Dall sheep, grizzly bear and wolf ecology – including population trends, habitat use and diet, limiting factors, predator-prey dynamics, as well as impacts of development and climate change. Management recommendations were also documented. Maps of the study area were presented to the interviewees, who delimited their own travel routes as well as habitats used by Dall sheep, grizzly bears and wolves. In this research, I broadened the TEK concept to also include local knowledge, which may not come from oral tradition, but from personal experience and may also be shared amongst resource users (Gilchrist *et al.* 2005, Anadón *et al.* 2009). Results included a broad collection of traditional knowledge about the Gwich'in and Inuvialuit way of life. Only information pertaining to Dall sheep, grizzly bears and wolf ecology or their interactions is however presented here.

A coordinator was hired in each community to help schedule and record (audio and video, if consented by the participants) the interviews. The interview process followed guidelines of the Gwich'in Tribal Council and underwent ethical review from the Gwich'in Social and Cultural Institute, the Aurora Research Institute (research licenses #14110, #14758 and #14370), and the Arts, Science and Law Research Ethics Board of the University of Alberta. I transcribed the interviews as accurately as possible and individual transcripts were sent back to the interviewees, along with a video copy of the interview (if filmed) for verification. Audio and video files as well as transcripts were deposited at the

Gwich'in Renewable Resources Board. Copies were also sent to the Gwich'in Social and Cultural Institute.

Throughout the result section, I summarized and interpreted the knowledge shared by Gwich'in and Inuvialuit participants in a narrative format, and complemented TEK with scientific literature where relevant. I also inserted selected interview quotes throughout the chapter as a complement to the result description. Unless otherwise indicated, all information presented in the results comes from the knowledge shared by participants during this study.

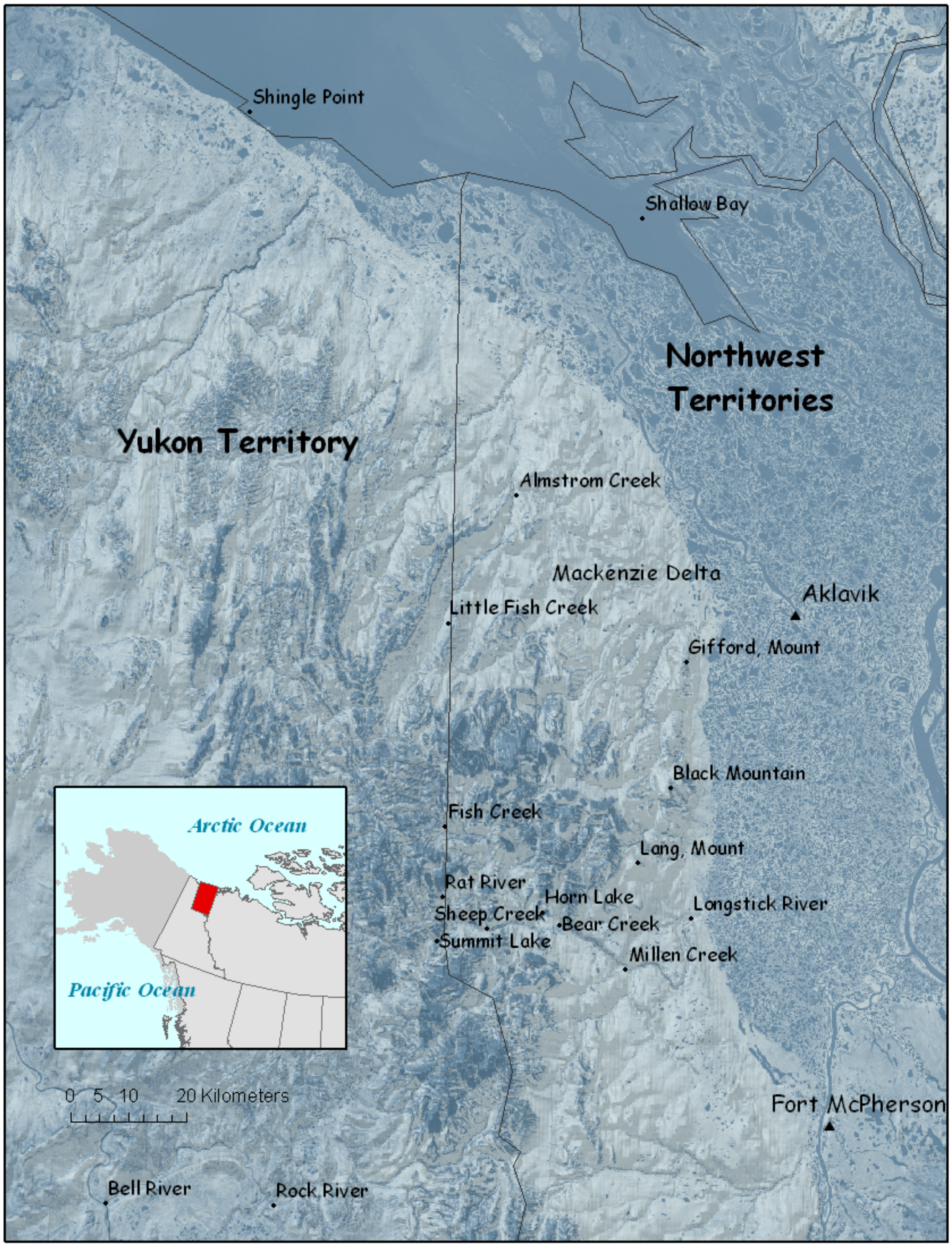

Figure 6.1. Satellite view of the Richardson Mountains and surrounding areas. Place names identified on the map were cited by the interviewees and are referred to in the text.

6.3. Results

6.3.1. Interviewees and their knowledge

Eleven participants were interviewed in Aklavik and 12 in Fort McPherson. All interviewees were men, except for one woman. Each interview lasted between 40 and 100 minutes (mean ± SE = 69 ± 4 minutes). Twenty-one participants were Gwich'in and two were Inuvialuit. Participants acquired their knowledge of this area from a young age. For several centuries, the Rat River watershed has been an area of high cultural and historical significance to the Gwich'in (Haszard and Shaw 2000). Elders were raised in the mountains with their families where they lived a nomadic life and moved on the land by foot, dog team, or boat.

> We used to live up there. We lived at the Rat Pass. We lived in the mountains. (Ernest Vittrekwa, 26 July 2008)

As they indicated, younger participants grew up in settlements but spent a considerable part of their life on the land, mostly hunting, trapping, and fishing. Snowmobiles and boats became the most common form of transportation in recent years. Interviewees acquired their knowledge through their elders, most often grandparents and parents, and from other relatives or friends. A lot of their knowledge was also self-taught, gained while spending time traveling or hunting on the land.

Most of the study participants had travelled extensively over the Richardson Mountains and had detailed knowledge of the mountains, rivers, creeks, and other landscape features. Nineteen interviewees had hunted Dall sheep (eight regularly); 13 had hunted grizzly bears (three regularly); and 14 had hunted or trapped wolves (five regularly). All interviewees pursued hunting, trapping or fishing activities, and some had worked in the study area (e.g., as monitors or wildlife officers). Other harvested species were, in decreasing order of mention: caribou, moose, fish (various species), marten (*Martes americana*), wolverine (*Gulo gulo*), snowshoe hare (*Lepus americanus*), muskrat (*Ondatra zibethicus*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), mink (*Neovison vison*), short-tailed weasel (*Mustela erminea*), Arctic ground squirrel (*Spermophilus parryii*), and porcupine (*Erethizon dorsatum*).

6.3.2. Dall sheep ecology

Historical and recent population trends

The oldest report on Dall sheep abundance dated approximately 200 years ago and was shared by Woodie Elias. He described a once abundant population in the Southern Richardson Mountains, ranging from Rock River to the Rat River, which was extirpated after over-harvest by local hunters (23 July 2008). More recent estimates of Dall sheep abundance shared by other interviewees corroborated to build the following chronology: in the 1950s and 1960s, abundance was low, probably due to a high hunting pressure. Until 1979, Dall sheep were considered quite rare in the Richardson Mountains, but it increased until it reached a peak between the late 1980s to early 2000s. The population then declined steadily to the current levels, which were deemed fairly stable by most interviewees. Two interviewees however stated that what is interpreted as changes in abundance may be due to Dall sheep migrating to other areas:

> Some years they disappear from the area, the Black Mountain area… And then they reappear. I guess they go; they must migrate in some other areas. (Freddie Greenland, 5 August 2008)

> It depends on the feed now. If there is no feed there, they move fast, they move away… You know, if it's good for food there, they will stay there… They go where there is good feeding and they stay there. (Abraham Peterson, 27 July 2008)

Habitat use & diet

When I asked where Dall sheep live in the Northern Richardson Mountains, participants mentioned, in decreasing frequency: Black Mountain area (including Black Mountain (also called Mount Goodenough), Tower Mountain, and Black Mountain Creek), Red Mountain (also called Mount Gifford) and all the front range adjacent to the Mackenzie Delta between Black and Red Mountains, Sheep Creek, Bear Creek, Fish Creek, Cache Creek (also called Little Fish Creek), Almstrom Creek, Willow River, Mt. Lang, Summit Lake, Horn Lake, Rat River, Millen Creek. Some interviewees in Fort McPherson indicated places in the Southern Richardson Mountains and tributaries of the Peel River like: Rock River, Doll Creek, Bell River, and Blackstone River.

Criteria of Dall sheep habitat selection mentioned by the interviewees can be divided in two fundamental categories: feeding and predator avoidance. Interviewees highlighted the need for ample feed, clean water, and mineral licks.

When I asked which vegetation Dall sheep consume, answers included lichens, grasses, mosses, some shrubs, and a variety of small plants. Five interviewees stated the need for minerals like salt, calcium, and sulphur. Three interviewees indicated that the diet of Dall sheep was most likely similar to that of caribou and muskoxen (*Ovibos moschatus*). Criteria mentioned in regard with predator avoidance included the need for: high mountains, steep terrain and elevation drops, escape routes, and good view, to help detect predators.

> You could tell that it's a good country for sheep because of the drops and the elevation. The sheep, they hang on the edges of the cliffs. And they have what you call escape routes all along the side of the cliffs. (Glen Alexie, 28 July 2008)

According to ten interviewees, the Black Mountain area, characterized with grassy south-facing slopes and plateau adjacent to steep cliffs with creeks in the valley bottom, provides an ideal habitat for them. When asked why Dall sheep remained in large groups in the Black Mountain area, birth site fidelity was also invoked:

> Well, they'd born there. This is like their home. They're like us. We have home where we settle in. So that sheep stick around that Black Mountain. Except when they run out of food; as somebody, they move to a different place. (Alfred Semple, 8 August 2008)

Eleven interviewees discussed sexual segregation and eight talked of seasonal habitat selection. According to them, Dall sheep prefer wind-blown ridges during the winter, which facilitate feeding and reduce the need for digging in the snow to access plants. Rams, ewes and lambs appear to stay together in small groups during the autumn and winter.

> Most of the time, they are well scattered around but not too far apart. You know… the same bunch spreads around, and then meet back together. (John Carmichael, 6 August 2008)

During the spring and summer seasons, however, ewes and lambs stay together while rams may keep a distance.

> The females go in the steeper [areas] and the males just go all over. (Ian McLeod, 7 August 2008)

Six interviewees thought that rams venture in small bands during the summer and migrate to higher mountains, close to the Yukon border or on the Yukon side, before returning in autumn. One interviewee hypothesized that rams may go in higher country to avoid mosquitoes; others thought rams would get nutritional benefits from accessing ungrazed areas and licks offering minerals important to their horn growth. Six interviewees believed that habitat available to Dall sheep is of very good quality, mostly untouched, and remained unchanged during their lifetime. Two elders, Ernest Vittrekwa and Donald Aviugana, noted that shrubs (particularly willows (*Salix* ssp.)) have increased their coverage throughout the years (26 July and 7 August 2008).

<u>Limiting factors</u>

Interviewees noted that a combination of factors drive the dynamics of this population. Overall, the most influential factor mentioned by participants was predation, followed by senescence, harvest, and severe weather events (Figure 6.2). Predation by grizzly bears and wolves, the most frequently named predators, is discussed separately in section 6.3.5. Eagle predation (bald eagles (*Haliaeetus leucocephalus*) and golden eagles (*Aquila chrysaetos*)) may also be an important mortality factor for lambs, in late spring to early summer, shortly after they are born.

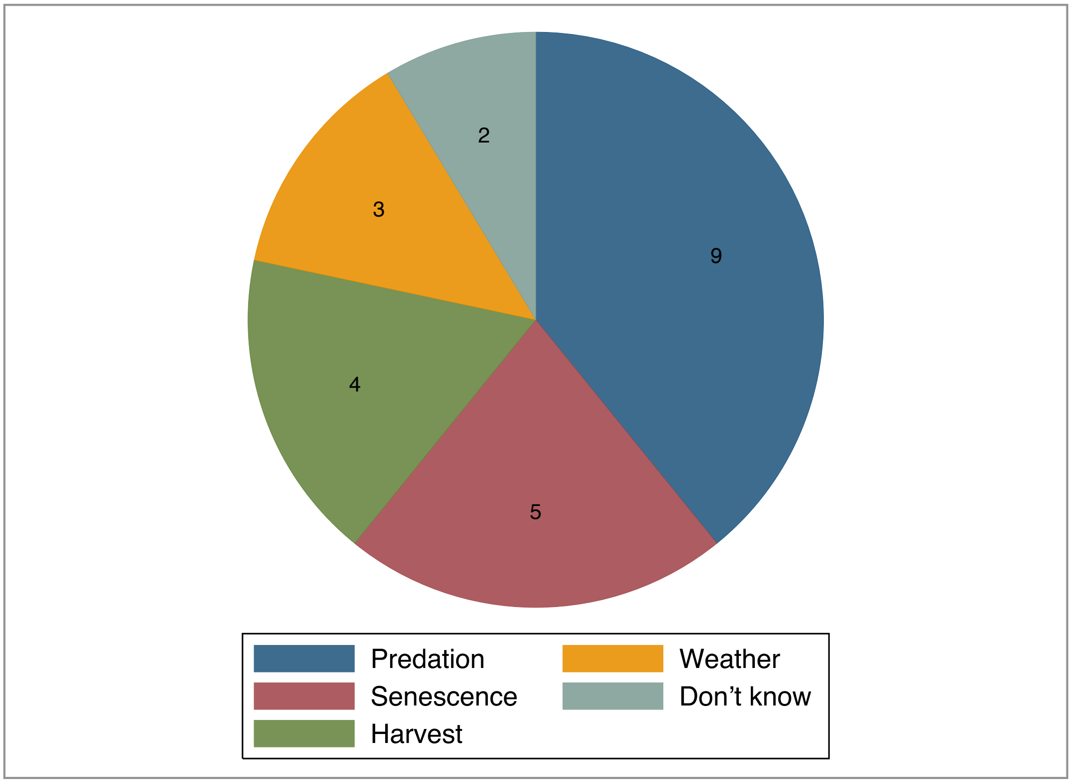

Figure 6.2. Single most limiting factor for Dall sheep in the Richardson Mountains, according to the interviewees. The chart shows how many interviewees cited each factor.

Interviewees identified other predators, such as lynx, red fox, and cougars (*Puma concolor*) occasionally preying on lambs. Cougars are uncommon in the area, but may be slowly expanding their range towards the Richardson Mountain (Jung and Merchant 2005) and were considered as a potential predator by four interviewees (also mentioned in Shaw *et al.* (2005)). Cougars were reported by three interviewees to have killed Dall sheep in the Black Mountain area, about 10 years ago:

> …there was one cougar that got around there and nobody knew where it came from. But I think it was running away from fire. (Mary Kendi, 5 August 2008)

> I know a cougar caught some [sheep], one year. I think it caught over ten. I think they are still around. Around Inuvik, Eight Miles – they're still around. (Johnnie Charlie, 25 July 2008)

Senescence would be the second most important limitation for this population:

> When they get too old, when they can't move around that much more. They just stay in the hills and just die in the hills. (Charlie Stewart, 6 August 2008)

As sheep get older, interviewees noted that they also become more vulnerable to predation, falls, and diseases. Nobody had witnessed Dall sheep falling off cliffs or victims of avalanches; however carcasses were occasionally found at the bottom of cliffs, which may have indicated a fall (or a predation event). In general, falling was believed to be relatively uncommon; however two interviewees noted that it may be relatively frequent, particularly after freezing rain.

> You know their hooves are made so that they stick to the rocks. It is pretty hard for them to fall unless you have a landslide or something. (Freddie Greenland, 5 August 2008)

In general, people in the communities focus on caribou, the most harvested large mammal species in the Gwich'in Settlement Area (GRRB 2009) and Inuvialuit Settlement Region (The Joint Secretariat 2003). Few of them hunt Dall sheep.

> I don't think that people really hunt sheep. I think they just get them as opportunistic hunts. If they're hunting something else and the sheep is easy to get, they will hunt it I think. (Ian McLeod, 7 August 2008)

> If there's no meat or anything, the sheep is there. Although most of the times, we go for caribou. (Patrick Gordon, 8 August 2008)

Harvest levels however increase when caribou are less abundant or further away from the communities or usual hunting routes, as stated by interviewees. Hunting pressure was deemed high in the 1950s and 60s compared to contemporary levels. One interviewee remembers hunting Dall sheep during that period:

> It is not a very easy animal to hunt. You always got to be sneaking up to it and keep away on the side of the wind… If he smells you, he is gone. They are hard animals to see, too. They are the same color as snow… You have to sneak to them, dressed in white. It's a lot of work to hunt that sheep. You got to do lots of good climbing and sometimes you climb up a steep place. (Abraham Peterson, 27 July 2008)

Some interviewees shared a concern regarding an emerging commercial harvest in recent years. Taxidermists from southern areas are known to contact hunters in the communities every year to request capes and horns, for which they offer between few hundreds to about a thousand dollars. This lucrative opportunity creates an incentive that may contribute to higher harvest pressure on Dall sheep, as three interviewees suggested. Nevertheless, current harvest levels were deemed within sustainable limits by 15 interviewees.

Weather, particularly snow and freezing rain, has an important effect on Dall sheep ability to feed and move in the mountains, which was often mentioned by the interviewees.

> Sometimes… if there's lot of snow on top the high hills… if they have frozen rain or something in the fall; it's hard to dig for them… they could starve from that. (Patrick Gordon, 8 August 2008)

Freezing rain may also make the terrain more slippery and render the cliff edges prone to falling. Deep snow increases their energy expenditure while feeding and moving (similarly to bighorn sheep (Goodson *et al.* 1991)) and may lead to higher predation risk, which was highlighted by six participants.

Most participants thought this Dall sheep population is very healthy. Four interviewees have reported sightings of sick or injured (limping) animals, but this was an exception rather than the norm. One interviewee reported one Dall sheep with abnormal horn growth:

> I've seen one… a female that its horn grew in some kind of a weird way and it started growing to its face. (Ryan McLeod, 5 August 2008)

Hunters assess Dall sheep health by looking at the general body condition and fat level of the animals. After the sheep is harvested, they examine the lungs and liver, and search for abnormalities:

> I look at the liver and the lungs to notice if it is sick or not. Sometimes we see blister on the liver or lungs, or something in the lung. And that sheep, when there is no fat, that sheep is poor. There was hardly any fat on them… Some of the sheep, I noticed there are blister on them (lungs)… So it must be sick or something. But a lot of sheep are healthy… They're good, healthy, and they're fat. (Alfred Semple, 8 August 2008)

No direct interactions between Dall sheep and other ungulates, like caribou, moose or muskoxen, were reported. However, they tend to avoid each other and may use different habitats:

> The sheep, they get around the caribou, maybe close to Black Mountain. Maybe they run into a sheep. But they don't look for one another… Because the sheep, they're different. They don't get mixed up with one another. They are not enemies with the moose, neither. (Alfred Semple, 8 August 2008)

> Old timers claim that when the sheep were hanging back here and the caribou coming behind here, that's when they go down here... They don't mix with caribou. (John Carmichael, 6 August 2008)

Several interviewees observed that moose select habitats of lower elevation and interferes little interference with Dall sheep, which corroborates a 2006 aerial survey that revealed higher concentration of moose in the valleys of the Richardson Mountains (Lambert Koizumi 2006). Donald Aviugana however noted that the moose seem to be getting higher in the mountains in recent years (7 August 2008). Opinions on muskoxen were more ambiguous. Approximately 150 years ago, muskoxen were extirpated from the region due to over-harvest. A herd was reintroduced from Greenland into Alaska in the 1930s and descendents were relocated to the north coastal plain in 1969-70 (Reynolds 1998). This herd has since expanded eastward, and muskoxen are increasingly present in the Richardson Mountains (Wishart 2004).

> Muskox did increase over the years… From single numbers up to maybe 200. (Eddie Greenland, 9 August 2008)

Five interviewees suspected muskoxen to have a deterrent effect on both caribou and Dall sheep.

6.3.3. Grizzly bear ecology

All animals, but especially grizzly bears, instilled much respect from the interviewees. Elders mentioned that grizzly bears sense when people talk about them and care has to be taken not to offend them:

> He's listening to us. Even though he's sleeping, he knows we talk about him… As long as you don't bother this grizzly, it won't bother you, you know… That's one animal you can't play with. (Abe Stewart, Sr., 29 July 2008)

> Grizzly bears, they are animals that you're not supposed to talk smart about… He knows it. Like if… you are talking smart about a bear, somewhere in the country he will come up to you and chase you because he knows that you talk smart about him. So… if he bothers your cabin, …don't talk smart about it. *Well, I will get you some day*. Never say that. Just let it go. Just replace your window and your door again. [Laughs] Just don't mind him… If you get smart and say: *well, I will kill you someday for it*, he'll know it and he'll destroy your cabin again, or else some way or another he'll chase you. (Abraham Peterson, 27 July 2008)

<u>Historical and recent population trends</u>

Oldest report on grizzly bear abundance goes back to 1927, when grizzly bears were remembered as being numerous and could be found nearly everywhere. Afterward, many participants mentioned there were very few grizzly bears in the Richardson Mountains in the late 1940s, the '50s and '60s.

> You know in 1947, people used to make dry rats for dogs during the summer. So, they hanged them up in their fish house… around Rat River, or any place in the whole Delta. They cleaned them, they dried them and they hanged them the whole summer there, because there were no black bears or no grizzly bears. (Peter Francis, 25 July 2008)

The rarity of grizzly bears seems to have continued in the 1970s and early 1980s, perhaps due to overhunting, according to interviewees. One participant mentioned that there were fewer grizzly bears after the arrival of the snowmobile. In 1992, many grizzly bears were killed in the mountains near Aklavik, which led to a moratorium on grizzly bear hunting –that was followed by the establishment of a tag system (GRRB 2000). The harvest tag system seemed to have helped the population recover. Ten interviewees thought the population was currently increasing; six thought it was stable; and two believed it was slowly declining. Perhaps due to a recent interest of hunters for larger, trophy-sized grizzly bears, two interviewees noticed that they are getting smaller in body size.

Habitat use, diet, and denning

Interviewees reported that grizzly bears were widely distributed throughout the Richardson Mountains. Many grizzly bears are known to be in vicinity of the Black Mountain area.

> Within less than a mile radius, there were seven bears… All in this range here… in front of the mountains. (Dale Semple, 10 August 2008)

Abe Stewart, Sr. also reported seeing 11 grizzly bears in this particular location, from John Carmichael's cabin (29 July 2008).

Others mentioned observing bears in Bear Creek, Big Eddy, Cache Creek, Mt. Lang, Rat River, Timber Creek, Willow River, and close to the Dempster Highway in the Southern Richardson Mountains; but they mostly were reported to be “all over”. Interviewees observed grizzly bears in higher mountains, foothills, in valley bottoms. They stay in the willows and shrubs, but also in the barren grounds; they can easily cross rivers and travel long distances. Few also go in the Mackenzie Delta, where people’s cabins (and the Aklavik dumpsite) sometimes attract them. Five interviewees complained of grizzly bears breaking into cabins and two noted that this is an increasingly common problem.

Most interviewees reported grizzly bear males and females sharing the same habitat, although three noted that they each have their own route and part at fall time to find a suitable den location. Eight participants also noted that females with their cubs keep a safe distance from the males, who may represent a danger for them –particularly in times of low food availability. Females may be constrained to use habitats that offer more protection, like higher mountains or tree-covered areas like the Mackenzie Delta, to protect their cubs from potentially infanticidal males. One interviewee, Johnnie Charlie mentioned one case of infanticide as he found small bear paws in the scats of an adult grizzly bear (25 July 2008). This phenomenon has also been documented in the scientific literature (Wielgus and Bunnell 1994). Two interviewees further noted that mothers and cubs remain together and share the same den for two to three years before separating.

According to interviewees, the major factor driving grizzly bears habitat selection appears to be food availability. Areas rich in ground squirrels and berries are likely to attract grizzly bears. Three interviewees noted that they also follow caribou in their migration, and are in larger numbers where people hunt caribou, since they feed on the guts and remains left by hunters. They may even steal caribou from hunters:

> I know that when we go hunting in the fall, sometimes we don't take the caribou out because there are grizzly bears. I see grizzly bears sitting on caribou… If I shoot caribou, they are there the next day, eating the guts and all. You got to get your meat and get out of there. (Johnnie Charlie, 25 July 2008)

Grizzly bears eat a variety of food. Berries, followed by caribou and ground squirrels, were the most often named items eaten by grizzly bears (Figure 6.3). Several types of berries were mentioned: blueberries (*Vaccinium uliginosum*), cloudberries (*Rubus chamaemorus*), cranberries (*Vaccinium vitis-idaea*), and bearberries (*Arctostaphylos uva-ursi*). Other foods identified included fish (Dolly Varden charr (*Salvelinus malma*)), roots, Dall sheep, vegetation (shrubs, willows, other plants), remains of caribou killed by hunters, grass, carrion, moose, muskoxen, and snowshoe hares.

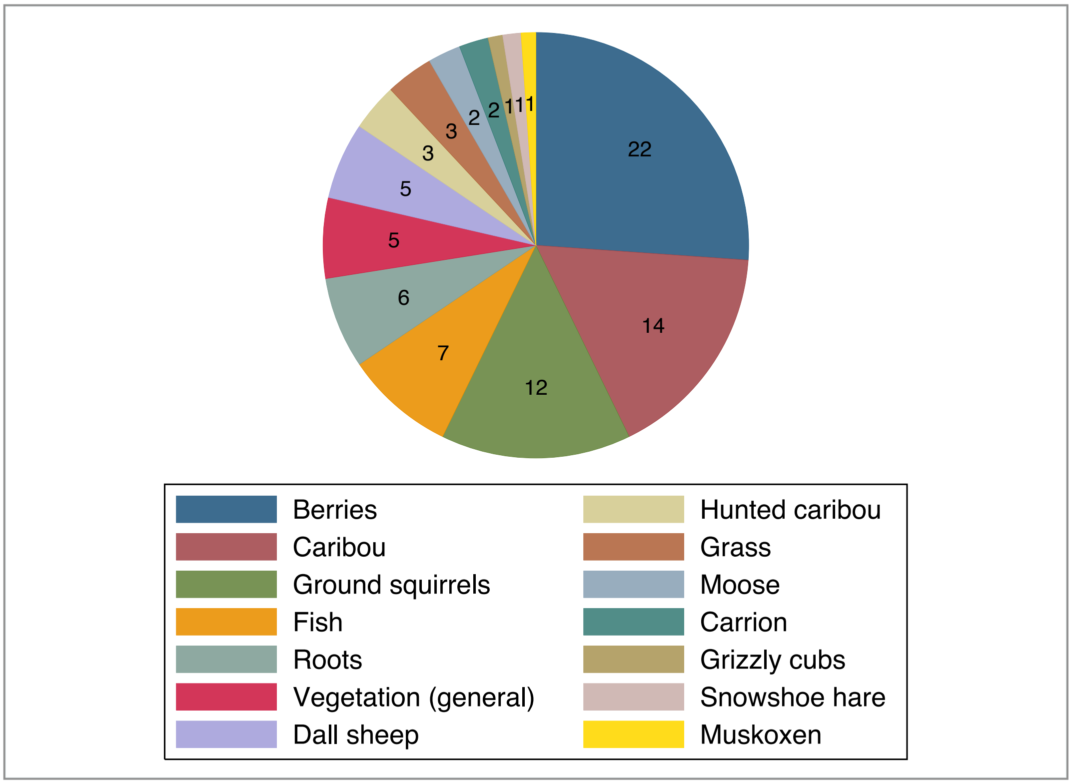

Figure 6.3. Food items constituting the grizzly bear diet in the Richardson Mountains. The chart shows how many interviewees named the item as being part of the grizzly bear diet.

The time when grizzly bears enter and emerge from their den, as well as the length of denning period, are highly influenced by weather and may vary from year to year, as stated by interviewees. Typically, grizzly bears enter their den in October to early November; but may enter anytime between September and December, depending on the weather. They generally emerge in April, but could do so anytime between late March to early June. Mary Kendi connected grizzly bear den emergence with snowmelt:

> They go to sleep. Then around January, when the sun starts coming up, they turn over, to sleep on the other side again until April. While they're sleeping, they hear water dripping at their doorway and that's when they wake up. Spring is here! (5 August 2008)

Ian McLeod mentioned that large males enter their den later, sometimes even as late as mid-November, and emerge earlier, often in early April, compared to females which may enter their den in October and emerge in May, when the weather gets warmer (7 August 2008). In some winters, milder weather may cause the temporary emergence of bears from their den for a few days, after which they return inside. Den site location was not discussed with the interviewees.

Limiting factors

Harvest and senescence were identified as the two most important factors limiting this grizzly bear population, with seven interviewees naming each as the principal cause. Fights with other bears, starvation, and wounds from shotguns were also mentioned as potential causes of mortality. Interviewees were aware that grizzly bears live several years and have a low reproductive rate, which make them especially vulnerable to harvest mortality. Traditionally, people did not bother grizzly bears unless they had to. They harvested them for subsistence only or to protect themselves, their children, and their property. How grizzly bear parts are used was not discussed, however Mary Kendi shared that the taste of grizzly bear meat is stronger than that of black bear (*Ursus americanus*) (5 August 2008). Grizzly bear fat may also be used in several ways and provides high quality lard, particularly when the animal is harvested in autumn, as noted by Robert Alexie, Sr. (25 July 2008). Two participants reported that since people started selling the hides, which may be worth few thousands dollars (about $5000 for a large bear), harvest levels have increased. The early 1990s were marked by a high harvest pressure on the population, which was deplored by a few participants, as exemplified by Freddie Greeland's comments:

> I can tell you years ago that some of these hunters found out about the kind of money they're paying for bears. At one spring, in the month of April, I'll never forget because I never saw anything like this before… All these hunters came back from the mountains up there. They got 27 bears… I was sick like, you know. Why are they doing that, you know? And that's why the bear population at that time went down for a while. (5 August 2008)

Shortly after this increase in grizzly bear harvest, a quota system was introduced in the communities, which limited the harvest and helped the population recover (GRRB 2000). Current harvest levels were considered sustainable by seven interviewees, who believed the actual tag system is effective.

Having few enemies beside human, the other main cause of grizzly bear mortality would be senescence. Old bears become unable to feed themselves and starve; some may even become blind. Bears also fight amongst themselves. Grizzly bears were observed to chase and fight one another to protect certain food (carcasses), although they may generally tolerate other bears if a safe distance is kept. They may be less tolerant of black bears. Three interviewees mentioned grizzlies chasing or killing black bears.

> See, if this big bear is hungry, he will kill this black bear here. I've seen it done. (Abraham Peterson, 27 July 2008)

Grizzly bears and wolves also tend to avoid each other, but may occasionally steal each other's prey. They may fight over a caribou carcass or other carrion. The winner of the contest often depends on the size of the bear and on the number of wolves in the pack, noted one participant. Four interviewees reported incidents of grizzly bears chased by wolves, and two talked of bears actually killed by wolves:

> One pack of wolves, they killed that grizzly bear. When they're hungry, they do that. That was long, long ago. (Peter Francis, 25 July 2008)

> Two wolves… one wolf [was] right on the sand bar, where there is like a hole; he was hiding in there. The bear doesn't know it. The bear was behind, [one wolf] chased him down. When he got to the other [wolf], [wolves] grabbed it in the nose. It was so awful. [Wolves] just went away and killed it. (Woodie Elias, 23 July 2008)

Nobody shared information related to diseases or sickness affecting grizzly bears.

6.3.4. Wolf ecology

Population trends and pack size

Interviewees reported that wolves have always been around but that their numbers fluctuate. Long ago, during the dog-team days, wolves were scarce. Interviewees reported that between the 1950s and the 1980s, and also in 2000, wolf abundance was low. Wolves were seen mostly when caribou were migrating. In recent years, however, ten interviewees believed the wolf population increased, and three mentioned it was stable. The increase in wolves appears to be linked to a recent increase in the moose population, which is particularly evident in the Mackenzie Delta and the Richardson Mountains (Lambert Koizumi 2006). Current wolf numbers appear to be greater than in the 1980s; however four participants estimated that wolves may now be declining compared to two-three years ago, possibly because of a high harvest pressure.

Interviewees reported that a typical wolf pack may have five to 15 members, but wolves may also be solitary or form larger groups. The most wolves reported to have been seen together by the interviewees themselves include up to 40-50 individuals, but the maximum seen by most participants was between eight to 30 wolves. Stories from elders or relatives however recount witnessing much larger packs. Eight interviewees mentioned stories of 50, 60, close to a hundred wolves; and three reported tales of 150, 500, and up to a thousand wolves together. In general, wolves concentrated in greater numbers around the caribou herd.

> I've heard of close to a hundred maybe… That was like long time ago. My grandma phoned me about it. It was a really cold winter… All the wolves seemed to hang out together for some reason. (Ryan McLeod, 5 August 2008)

<u>Habitat use</u>

Interviewees did observe wolves nearly everywhere, but most often in association with caribou or moose. Places named where wolves may be found include: the Black Mountain area, the front range of the mountains, Bear Creek, Husky River, Mackenzie Delta; and just about anywhere the caribou are. One participant, Lloyd Nerysoo, mentioned wolves appear to prefer places with clean water (27 July 2008). Wolves are considered smart animals that can travel long distances in short time periods.

Most wolves follow caribou in their migration, according to 15 interviewees. Five participants however noted that some packs reside all year within the same territory and focus on moose and other prey like Dall sheep, snowshoe hares, muskoxen, and beavers (*Castor canadensis*). High mountains and foothills seem like an optimal habitat for wolves, although they can also be seen in the Mackenzie Delta:

> When we traveled in the mountains, that's when we used to hear wolves crying. But when we stayed in the Delta, we never heard them… [Wolves are] high up on the mountain. But maybe at night, they travel around the river… We see their tracks in the river. (Mary Kendi, 5 August 2008)

Diet

The two main prey identified by interviewees were caribou and moose (Figure 6.4), followed by Dall sheep, snowshoe hares, fish, beavers, ground squirrels, small mammals like voles, muskoxen, and ptarmigan (*Lagopus* sp.). Wolf predation on Dall sheep is discussed in section 6.3.5.

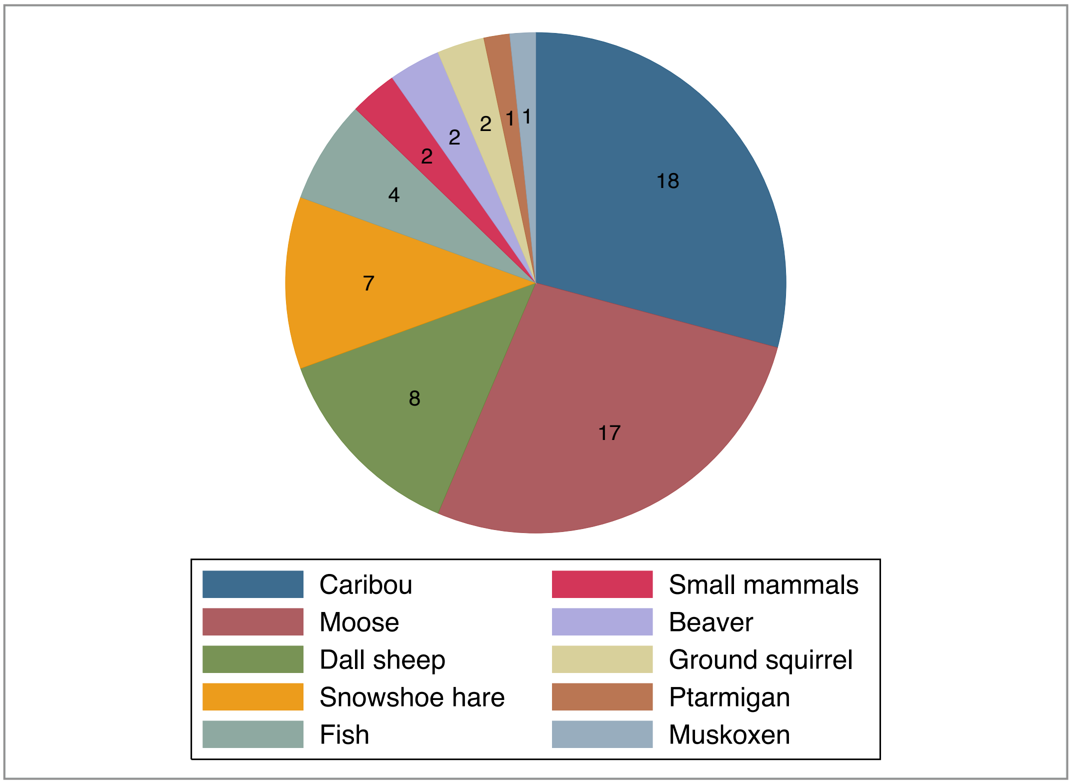

Figure 6.4. Food items constituting wolf diet in the Richardson Mountains. The chart shows how many interviewees named the item as being part of the wolf diet.

Limiting factors

According to 14 interviewees, the main limiting factor for wolves in the Richardson Mountains would be senescence. Old individuals become more susceptible to die from starvation or fights with other wolves.

> The only time… they die off is when they're really old. They can't kill anything for themselves. (Peter Francis, 25 July 2008)

> Sometimes they get so old that they can't eat. They just drop there… One slow wolf in a wolf pack; they would turn around and kill it. They kill him right there and leave him right there. (Abraham Peterson, 27 July 2008)

When starving, to protect their food or territory, wolves may kill each other. They however more often challenge each other, not to the point of killing:

> You know the wolves – they're like you and me. When they grow up, after they're born, they start walking. Maybe you have a sister around and you want to fight with your sister, eh? Like me, when I was a little boy you know, I wanted to fight with my brother… Wolves [do] the same thing. When they play, they get one another mad, and many times end up fighting, I think… But they don't mean to kill one another. (Alfred Semple, 8 August 2008)

Hunting would be the second most important cause of mortality for wolves, as mentioned by seven interviewees. Although the hunting and trapping levels were considered less than 20 years ago, modern snowmobiles are fast and powerful, which may increase the success of modern wolf hunters.

> Every time skidoo get faster; people get better at hunting wolves. (Ian McLeod, 7 August 2008)

Wolves are hard to trap, and most people hunt rather than trap wolves these days, reported the interviewees. Ten participants believed hunters do not overkill the population, but there seems to be renewed interest in younger hunters for catching wolves. Overall, wolf hunters appear to have two motives: those who hunt opportunistically if they encounter them while hunting caribou or other species; and those who target wolves, either for the bounty, for their nice fur, and perhaps also because they compete with humans for caribou.

> I think people try to shoot them because they kill a lot of caribou too. (Johnnie Charlie, 25 July 2008)

> A long time ago, in the '50s, there used to be hardly any moose and hardly any caribou. I remember wolves used to be bad… travelling on people's trap lines and taking people's baits, marten baits. When [people] caught marten or something, the wolf took it -it made a lot of people angry… There used to be no fur too, no

> marten... [Wolves] take their bait and if [people] catch marten, they take the marten too. (Robert Alexie, Sr., 25 July 2008)

Wolves in the Richardson Mountains seem to be healthy and do not seem to often suffer from sickness or diseases. Charlie Stewart and Donald Aviugana mentioned rabies as a potential limiting factor (6 and 7 August 2008) and Johnnie Charlie noted the presence of tapeworms in wolf excrements (25 July 2008). Starvation, on the other hand, may be more common. Abraham Peterson mentioned that wolves, like dogs, might survive several days, up to almost a month, without eating (27 July 2008).

6.3.5. Dall sheep predation by grizzly bears and wolves

<u>Dall sheep predation avoidance strategies</u>

Because Dall sheep are very fast and can jump down steep paths with extreme agility, several interviewees mentioned that grizzly bears and wolves have a hard time catching them. When questioned on predator avoidance strategies of Dall sheep, interviewees responded that cliffs and steep terrain of their habitat are a sanctuary from predators, and Dall sheep can navigate in rocky and rough terrain with unequaled ease. When chased by predators, Dall sheep will immediately reach for their escape route in steep terrain, where few predators are able to follow. Within the cliffs, they find ledges where they may hide and wait until the danger is gone. They also have good eyesight and are very vigilant when predators approach them.

> They jump from one cliff to another and if they see any danger, they just jump over the cliff. They slide down to a good spot where no wolves can get down to them. (Charlie Stewart, 6 August 2008)

It is when Dall sheep venture far from escape terrain, for example when crossing streams or creeks (noted by ten interviewees), traveling or feeding out in the open or flat land (noted by eight), or going to mineral licks (noted by one), that they are most vulnerable to predation. Three interviewees reported carcasses found in such areas, and two cases of predation were observed. Dall sheep exhibit greater vigilance in those areas of higher predation risk.

> Sheep don't cross creeks for a day. They go up and they stand up on top of this, you know, the highest point. Then they watch the whole creek itself before they cross –then they'll cross the next day. (Dale Semple, 10 August 2008)

Although they may be attacked anytime of the year, the wintertime appears to be when most attacks occur, since the snow cover impedes their movements and deep snow increases the chance for wolves to catch them, as described by two interviewees. In late spring and early summer, shortly after the lambs are born, the population probably also suffers higher predation rates, particularly by grizzly bears, as noted by Ernest Vittrekwa (26 July 2008) and Ryan McLeod (5 August 2008).

Predation by grizzly bears

Grizzly bears are good runners and most interviewees believed them to be capable of attacking large prey like Dall sheep. Only two interviewees did not think so, and two others were uncertain.

> They're big, powerful animals. They can bring anything down. (Peter James Kay, 23 July 2008)

While they also rely on other food sources, grizzly bears will attack Dall sheep when given the opportunity. Young lambs may be particularly vulnerable to grizzlies. Johnnie Charlie quantified the success rate as such:

> Probably once in every twenty tries; because the sheep can run pretty fast. (25 July 2008)

A grizzly bear sow with cubs may have greater chances of success, as participants suggested:

> And she used them for crawling up the hill. Once it scared the sheep, she went around this mountain and she killed one over there… She used her young ones to distract them. (Dale Semple, 10 August 2008)

> You find bones and that of sheep. Where they cross the creek there are grizzly bears tracks… In the springtime you see a lot of grizzly bears there [around Tower Mountain]. Mother and cubs, they're feeding and waiting for sheep too. (Eddie Greenland, 9 August 2008)

Grizzly bears are also known to constantly watch Dall sheep when within close distance and are prepared to attack if the opportunity arises. Grizzly bear predation may be more successful in valley bottoms when Dall sheep cross between mountains.

> One time I saw one got killed by a grizzly bear. Right in the mountain creek - in that Black Mountain Creek … That's when the grizzlies, they cross at 6

> o'clock in the morning... I've seen big grizzly bears gather and seen they already killed one. (Ernest Vittrekwa, 26 July 2008)

Ernest Vittrekwa also mentioned mosquitoes in the summer may also alter the lambs' eyesight and reduce their vigilance:

> There are some mosquitoes, mosquitoes chew their eyes, the [lambs]. They can't see good. And they can't go as fast as they're supposed to. [] Grizzly bears just pick them up on the [lambing] grounds. (26 July 2008)

<u>Predation by wolves</u>

Predation by wolves seems to follow similar patterns, except that wolves most often chase them in packs and can attack Dall sheep year round. However, if given the choice, wolves may select prey species like caribou and moose (kill rates were documented by Hayes and Russell (1998) and Hayes and Harestad (2000a)), which have greater body mass and do not frequent habitats potentially dangerous to them, two interviewees highlighted.

Wolves take advantage of their pack structure to chase Dall sheep from different directions:

> Some [wolves] scare them over. If there's a bunch of sheep, then some wolves scare them from the top and there's probably another bunch who's in the bottom. [Wolves] are pretty smart. (Patrick Gordon, 8 August 2008)

Wolves may ambush Dall sheep in areas with trees or shrubs (mostly valley bottoms and crossing points). In the wintertime, they may also lead them into deep snow where they can surround them:

> Like sometimes, when they cross these places, there are trees, you know. There are trees in the side, where there is snow. And they have their own trails

> there so the wolves get behind. They frighten them and surround them. (John Carmichael, 6 August 2008)

> I saw it two years ago. The sheep were crossing from one mountain over to the other side, and it was pretty deep snow. Four wolves just came out and they started chasing them. (Eddie Greenland, 9 August 2008)

But wolves are not always successful. As mentioned before, Dall sheep are fast and have a unique capability of going in very steep and rocky areas:

> …I was going to hunt sheep. And I've seen seven sheep running down the hill. And then they were running back up; some wolves were chasing them. There was a bunch down there waiting… [Dall sheep] actually outran wolves. They got back up in the high mountains. (Johnnie Charlie, 25 July 2008)

6.3.6. Climate change, development, and management recommendations

The Richardson Mountains, a remote location with no road access or industrial activity, are amongst the most pristine ecosystems of this planet. However, the area is impacted by climate change (Hinzman *et al.* 2005, Post *et al.* 2009), holds potential for mineral and fossil fuel development (Gwich'in Land Use Planning Board 2003, North Yukon Planning Commission 2009) and also grounds researchers of various fields (e.g., ecology, geology, archaeology). Interviewees discussed their views of climate change and development, and also shared recommendations for the management of Dall sheep, grizzly bears and wolves in this unique ecosystem.

Climate change may have a myriad of effects on Dall sheep, grizzly bears and wolves in the Richardson Mountains; these are complex and the ultimate outcome is hard to predict. Ten interviewees cited landslides in the mountains, caused by the melt of permafrost. Landslides or slumping affect the topography and may destroy precious escape terrain for Dall sheep. This land modification might increase Dall sheep's vulnerability to predation, as mentioned by three interviewees. Three other participants also noted permafrost melt augments the fragility of cliff edges, increasing the chances of sheep to fall down. More frequent landslides also increase the risk for hunters to travel on the land.

Interviewees mentioned climate change could modify biodiversity, species composition, population movements and habitat use. It may also affect the fire and precipitation regime. Range expansion species, like cougars (Jung and Merchant 2005), may colonize the north and become a common predator if trends in climate warming persist. New diseases and parasites (Kutz *et al.* 2004) could equally affect Dall sheep, grizzly bears, wolves, and other species of this ecosystem, as noted by Ian McLeod (7 August 2008). Other species, like caribou and migratory birds, may change their migration routes and therefore affect the whole food web. More trees and shrubs in the mountains may create better hideouts for predators to ambush Dall sheep, as suggested by Glen Alexie (28 July 2008) and Ian McLeod (7 August 2008). Warmer weather might mean increased frequency of freezing rain in autumn, which could create an ice layer over ground vegetation and make it harder for Dall sheep to feed during the winter. Longer growing season could however also benefit Dall sheep, since there would be more feed available to them throughout a longer period. Ernest Vittrekwa stated:

> I think it will be good if it gets warmer. When it's cold they have a hard time… Hard to go on Black Mountain when it's cold. Everything gets iced up, blizzards, and all that. And sheep have hard time to dig for food. (26 July 2008)

For grizzly bears, climate warming makes the hibernation period shorter and less predictable than before:

> The weather is changing... It's getting warmer. It's taking longer to freeze, it's thawing earlier… So they're out and about early, more months than usual. (Billy Wilson, 26 July 2008)

Potential effects of development on these species vary in magnitude. In their recommendations, five interviewees categorically rejected any development whatsoever in the region. They claimed that any kind of development would alter the life of the animals and plants in the mountains. Other participants strongly recommended to keep development and other human-related disturbances to a minimum, while recognizing the potential for wildlife to adapt to certain disturbances and be resilient to some habitat modifications. For example, two interviewees stated that animals may get used to the noise and become less wary of vehicles, snowmobiles or airplanes as years go by. Along the Dempster Highway, which crosses the Southern Richardson Mountains, caribou and grizzly bears have become used to the traffic. Occasional snowmobile traffic, for instance, appears to create only minimal effects on wildlife, as deemed by Archie Jerome (28 July 2008).

Habitat modifications like seismic lines or pipelines can also change how wildlife use their habitat. Animals may select newly created paths or modify their migration route to avoid them. Two interviewees have also recognized that hunters and trappers tend to travel on seismic lines, which may change their harvesting patterns. New roads increase accessibility and may lead to more harvest (McLellan and Shackleton 1988) or facilitate wolf predation (James and Stuart-Smith 2000). Interviewees also noted that some activities related to the oil and gas industry can lead to deleterious effects on water quality and species abundance. Peter Francis linked offshore drilling in the Arctic Ocean with the disappearance of charr and sardine cisco (herring) (*Coregonus autumnalis* and *C. sardinella*) from rivers in the Richardson Mountains, which could reduce the food available to grizzly bears and wolves:

> Once they hit the ocean out to that Shallow Bay… down towards that Herschel Island, Shingle Point. They drill way out on the ocean, you know. Deepest cases way out is 17 feet, 12 feet towards shore. Lots of seismics around… They just blast around there, blast around there. I noticed that since that time, hardly any Arctic charr come up. You notice that? Boy, they just blast all that area, you know, right down to Herschel River towards Aklavik River, way out. There used to be lot of herring, no herring now too. They must kill lots of fish around that. (25 July 2008).

Similar concerns were reported in relation with the proposed Mackenzie Gas Project (Salokangas 2005). Two interviewees however believed seismic lines or drilling have no adverse effects on wildlife.

If development must occur, interviewees expressed management recommendations to minimize negative impacts on wildlife and habitat. The list is non-exhaustive, but recommendations included: hire local monitors to ensure environmental policies are enforced; adopt a better monitoring system of aircraft over the region; set a limit below which aircraft would not be allowed to fly; protect Dall sheep critical habitats, particularly during lambing season; create a protected conservation area in the Richardson Mountains (a conservation zone is already established through the Gwich'in Land Use Plan (Gwich'in Land Use Planning Board 2003); when necessary, limit harvest with a quota system to help wildlife populations recover. Scientific research on wildlife may benefit the populations by providing important information and lead to better management policies, which was acknowledged by one interviewee. Research may also benefit the communities, since field guides, monitors or assistants are often hired by researchers, thereby stimulating the local economy. However, Woodie Elias firmly chastised invasive research like radio-collaring and helicopter captures due to the inflicted stress to wildlife. He affirmed that animals can die from collaring and instead recommended using more on-the-ground, less invasive methods (23 July 2008).

Respect of the land and the animals was unanimous during the interviews. Wildlife is intrinsically part of the Gwich'in and Inuvialuit culture and way of life. Harvest should be limited to the people's needs and conducted with dignity and respect.

> You want to take an animal, you know you got to respect it. When you're hunting, treat it with dignity and respect. Please don't show it around and do a good job at cutting and cleaning… As long as they're there, we're going to be hunting them and eating them. (Johnnie Charlie, 25 July 2008)

Interviewees concluded with thoughts regarding the younger generation and future of this ecosystem. Here is a small token of the wisdom they shared:

> Just listen to your elders. And if you are interested in the elders, they will explain everything to you. Other than that… always watch what you are killing and don't over-harvest any animal… You have to understand that when populations go

> down… just put a limit, or slow down or something. (John Carmichael, 6 August 2008)
>
> Take what you got to take, don't just overkill. Respect the land, mostly, I think is a good think to do. Just learn your country. (Patrick Gordon, 8 August 2008)
>
> Don't over-kill it. Each one of the animals. Caribou, moose, anything. Just take what you need out of them… Look after them, you know. Skin them right. Not for money… Make every bit of use of it. (Alfred Semple, 8 August 2008)

Education was considered crucial in transmitting TEK to the younger generation. Because of the modern educational system, today's children spend their days in institutional schools and little time on the land with their families, as they did traditionally (Milloy 1999). To help the passage of TEK down to younger generations, field camps in the mountains, where elders teach their skills and knowledge, are necessary.

> I think programs that take the kids hunting through [the government]; I think those are good. There should be more of that. I think most young people now don't know very much about the land. So any chance they get where someone is teaching them is good for them. I think it's good for the future of our animals too. (Ryan McLeod, 5 August 2008)

Five interviewees suggested ecotourism (through the establishment of a protected area) or guided sport hunting may be viable alternatives to industrial development. Such activities would have a much smaller ecological footprint, promote the Gwich'in or Inuvialuit way of life and TEK, and contribute to the conservation of Dall sheep, grizzly bear and wolves in the Richardson Mountains.

6.4. Discussion

Gwich'in and Inuvialuit TEK on Dall sheep, grizzly bears and wolves is multifaceted and concerns various elements of the ecology of these three species. Information shared by the interviewees often corroborated and complemented itself. Sometimes contradictions emerged, depending on the interviewees' personal experience, unique background and education, and transmitted values and knowledge.

When analyzing aboriginal knowledge, it is tempting, but not necessarily advisable, to fall into a pattern that has been called the *scientization* of TEK (Agrawal 1995, Ellis 2005). It is the practice of giving greater value to TEK statements that fit into the typical scientific model, perhaps to the detriment of stories and contextual knowledge that are the reflection of a life and culture intertwined with wildlife and the environment. Scientization happens when TEK is filtered to distinguish the analytical from the descriptive, the factual from the mythics; selecting only statements that fulfill criteria like rigour, replicability, and universality (Ellis 2005).

In this report, I tried to include not only statements that fit into the conventional scientific approach, but also some stories and statements illustrating the relationship and vision held by interviewees about this ecosystem. I tried to present a wholistic view of the documented TEK, even if, due to space constraints, I could not include all hunting stories, anecdotes, legends, and political views shared during the interviews. At the same time, as a wildlife biologist, my main research interests admittedly centered on the basic and quantifiable facts shared about these species and their interactions. Luckily, many such facts were documented throughout the interviews. For example, Dall sheep abundance estimates, at least since the 1970s –when aerial monitoring started, remarkably concurred with results of aerial censuses. Information pertaining to previous years, and also trends in grizzly bear and wolf populations, contained knowledge that has not otherwise been documented. Such information may become useful in the future to understand population dynamics and abundance cycles. Criteria of habitat use, seasonal preferences, sexual segregation, and spatial overlap between the ranges of Dall sheep, grizzly bears and wolves identified in this study also relate to findings from satellite telemetry (Lambert Koizumi and Derocher 2010). Moreover, descriptions of Dall sheep predation avoidance strategies as well as grizzly bears and wolves predation patterns substantially enrich results of the behavioural field trip conducted in June 2007 (Chapter 5). As a conclusion, Ryan McLeod summarized the relationship between Dall sheep, grizzly bears and wolves:

> I think the bears and wolves kind of depend on the sheep. Not a whole lot I think, but, when there's no caribou around and [other prey], I'm sure the wolves really hunt sheep. And they all seem to use the same, pretty much the same habitat. So I'm sure they run into each other a lot. (5 August 2008)

Overall, information shared regarding the three species habitat, diet, limiting factors and interactions revealed a detailed knowledge and appreciation of these species and their environment by the interviewees. The depth of the TEK documented may be linked to the significant time each of them have spent in the

Richardson Mountains, their strong relationship with wildlife, and also to the rich oral tradition inherent to their culture. Some answers may also have been influenced by scientific information exchanged with researchers in other circumstances, a consequence of living in dynamic communities subject to several studies. Their recommendations and concerns related to climate change, development and anthropogenic disturbances also reflect a deep care and respect for wildlife and nature. Gwich'in and Inuvialuit TEK documented here provide a solid contextual base to analyze results from other scientific methods and deepen our understanding of Dall sheep, grizzly bears and wolves ecology and interactions, particularly at the predator-prey level. It also has the potential to serving the conservation and guide the management of these three species in the Richardson Mountains, for example in the context of management planning or environmental impact assessments.

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APPENDIX A

Consent form used in the Traditional Knowledge Study

Traditional Knowledge Study of Dall Sheep, Grizzly Bear and Wolf Interactions in the Richardson Mountains: Informed Consent Statement

Main investigator: Catherine Lambert Koizumi
Affiliation: Gwich'in Renewable Resource Board & University of Alberta

Interviewer: ____________________ Date: ____________________
Interviewee: ____________________ Community: ____________________

Location of the interview: ______________________________

The following information will be read to, or by, the interviewee. Any unclear matter will be explained. The interview will not proceed unless the participant signs this form or confirmation of consent has been otherwise documented.

Project Information

The goal of this research is to document local and Traditional Knowledge (TK) about Dall sheep, grizzly bears, and wolves in the Richardson Mountains. These interviews will integrate and complement a larger-scale research involving other research techniques. The information will be used to increase our general knowledge about these species, to assist in reviewing the Dall sheep Management for the Northern Richardson Mountains and Grizzly Bear Management Agreement in the Gwich'in Settlement Area, to increase capacity building and promote traditional knowledge in the communities.

The results will be organized into a plain language document to be distributed within the communities to share the Gwich'in Traditional Knowledge and value the wildlife species inhabiting the Richardson Mountains. Results from the interviews will also be submitted for publication in a peer-reviewed journal and will be part of the main investigator's PhD thesis at the University of Alberta.

The raw data will be stored with the Gwich'in Renewable Resource Board and copies will be deposited at the Gwich'in Social and Cultural Institute. Interviewee may request access to their own information after the completion of the interviews, but the information provided by other interviewees will remain confidential and will not be released.

If the interviewees are comfortable being filmed, an audio-visual documentary may be produced. The interviewee may stop the interview at any time if they do not feel comfortable.

Interview procedures

To ensure a proper transcription of the interviews and a better analysis/publication, we would like to record the interview on audio and video tape.

- Can we record the interview with a sound recorder? ☐ Yes ☐ No
- Can we film the interview with a camcorder? ☐ Yes ☐ No

- Can we take a photo of you during or after the interview (to be used in report, newsletters or poster)? Yes No
- Would you prefer to be interviewed in another language than English? Yes No
- If so, please specify which language and which dialect: ____________________

Credit

- Would you like to be cited or credited for any information shared during this interview? Yes No
- Can we cite you specifically (at the end of all quotes)? Yes No
- If no, can we cite your name as one participant of the project? Yes No
- If no, would you prefer us to use a pseudonym? Which one? _______________

Confidentiality of the interviewee will be respected accordingly.

Draft and final report

A draft of the information collected will be presented before publication for verification, either personally or in a community forum. Any suggestions at that time will be considered to be incorporated into the final report.

Copies of the annual and final reports will be forwarded to your Renewable Resource Council, and will also be available on the Gwich'in Renewable Resource Board website (www.grrb.nt.ca)

Compensation

We will offer you 50$/hour for your participation to this interview.

PARTICIPANT DECLARATION

I have read, or have been read, and understand the information presented on this document. I have been explained any matter that remained unclear regarding this project. By signing this form, I fully accept to participate to this interview, in agreement with the terms established on this form. I also understand that I can withdraw from the interview at any time and that I am not obligated to answer any particular question.

____________________________	____________________________
Interviewee name	Signature

APPENDIX B

Questionnaire used in the Traditional Ecological Knowledge Study

Traditional Ecological Knowledge Study on Dall Sheep, Grizzly Bears and Wolves in the Richardson Mountains

Date:____________________ Community:___________________________

Interviewer:___________________ Coordinator:___________________________

Interviewee: ________________________ Start time: _________

Introduction

Describe the scope and objectives of the project, and how this Traditional Knowledge Study fits into the large picture. Explain the interview process, and request the interviewee to sign the consent form. A cheque will be provided to them at the end of the interview.

Has the interviewee signed the consent form? ☐ Yes ☐ No
(if no, do not proceed!)
Has she/he approved to film the interview? ☐ Yes ☐ No
Has she/he approved to take photos? ☐ Yes ☐ No

1. Experience of the Interviewee

Show a map and explain the location of the Northern Richardson Mountains.

A. Have you been in the Northern Richardson Mountains? ☐ Yes ☐ No

- If so, how often? ____
- When? *Which years and time of the year*
- What was your travel route? *Identify routes, camps and travel locations on a map*
- What did you go to the Northern Richardson Mountains for?
  - Hunting *Species hunted:* ________________________________
  - Fishing *Species fished:* __________________________________
  - Travelling
  - Other: ____

Where does your knowledge of the area come from?

B. How familiar are you with Dall sheep? Where does your knowledge come from?
C. How familiar are you with grizzly bears? Where does your knowledge come from?
D. How familiar are you with wolves? Where does your knowledge come from?
E. Have you hunted Dall sheep, grizzly bear or wolf in the past? If so, how often and when?

	Hunted? (Y / N)	**How many animals and when?**
Dall sheep		
Grizzly bear		
Wolf		

Additional comments:

2. Dall Sheep Ecology

Population trends
- Do you remember times when there were no or very few sheep? When was that? Why do you think this was?
- Do you remember times when there were more sheep than usual? When was that? Why do you think this was?
- What can you tell about the current density/abundance of Dall sheep in the Richardson Mountains (increasing, declining, stable)?

Habitat use (*identify sheep range, licks and lambing areas on map*)
- What kinds of habitats are more important for Dall sheep for eating, lambing, licks, etc.?
- Have you noticed differences in where the males and females go?

Diet
- What kind of plants are the sheep eating?
- Do you think that the sheep are limited by the quantity/quality of food? Do you remember times when the sheep had no food to eat?
- Is the status of the range the same as before? If not, how did it change?

Limiting factors
- We are very interested to learn about Dall sheep predation. Which species do you think are the most likely to prey on sheep?
- Have you ever seen any sheep killed by predators?
- Is the effect of predation the same as before? If not, how did it change?
- Do people hunt sheep as much as before? If not, what changes did you notice?
- Are there special places where the sheep are more open to be killed by predators or hunters?
- How do sheep escape from predators or hunters?
- Have you ever seen any sick sheep?
- How do the sheep interact with Caribou? Moose? Muskox?
- What in your sense is the most important limiting factor for sheep (diseases, competition, predation, hunting)?
- Does the importance of those limiting factors vary through time? How?
- How often have you seen one female with two lambs (twins)?
- Have you noticed anything unusual about Dall sheep over the course of your life?
- Is there any Dall sheep story you would like to share with us?

3. Grizzly Bear Ecology

Population trends
- Do you remember times when there were no or very few grizzly bears? When was that? Why do you think this was?
- Do you remember times when there were more grizzlies than usual? When was that? Why do you think this was?
- What can you tell about the current density/abundance of the bears in the Richardson Mountains (increasing, declining or stable)?

Habitat use (*identify grizzly bear range, feeding and denning areas on map*)
- What kind of habitats do grizzly bears need?

- Have you noticed differences about where the males and females with cubs go?

Diet
- Bears can eat both plants and animals. In the Richardson Mountains, what do they feed mostly on?
- Do they feed on sheep? If so, how often, and which bears would do it?
- When and where would the bears mostly prey on Dall sheep?
- Do you think the bears are limited by the quantity or quality of the food? Why?

Limiting factors
- Have you ever seen any sick bear?
- Do you think grizzly bears compete with other species for food or space (wolves, wolverines, black bears, polar bears, etc.)?
- Can you tell us about the impact of hunting on the bears?
- Do people hunt bears as much as before? If not, what changes did you notice?
- What in your sense are the most important limiting factors for the grizzly bears (diseases, competition, infanticide, hunting)?
- Does the importance of those limiting factors vary through time? How?
- When do the bears start their hibernation, and when do they go out of their den? Did you see changes through the years?
- Have you noticed anything unusual about grizzly bears over the course of your life?
- Is there any Grizzly bear story you would like to share with us?

4. Wolf Ecology

Population trends
- Do you remember times when there were no or very few wolves? When was that? Why do you think this was?
- Do you remember times when there were more wolves than usual? When was that? Why do you think this was?
- What can you tell about the current density/abundance of wolves in the Richardson Mountains (declining, increasing or stable)?

Habitat use (*identify wolf habitat on the map*)
- What kinds of habitats are more important to wolves?
- How large was the largest pack of wolves you have seen / heard about? What is the typical size of a wolf pack?

Diet
- What is the wolves' main prey species in the Richardson Mountains? Do they feed on sheep? If so, how often, and which wolves would do it?
- When and where would the wolves mostly prey on Dall sheep?
- Do you think the wolves are limited by the availability of prey?

Limiting factors
- Have you ever seen any sick wolf?
- Do you think wolves compete with other species for food or space?
- Can you tell us about the impact of hunting on wolves?
- Do people hunt or trap wolves as much as before?

- What in your sense are the most important limiting factors for wolves (food, diseases, competition, harvest)?
- Does the importance of those limiting factors vary through time? How?
- Have you noticed anything unusual about wolves over the course of your life?
- Is there any wolf story you would like to share with us?

5. Development and Climate Change

- If there is development in the Richardson Mountains (i.e., mines, Mackenzie Gas
- Project), how do you think the species would be affected?
- How would the sheep, bears and wolves be affected from climate change?
- What is your idea of sustainability? How can we ensure that the ecosystem stays wild for future generations?

6. Closing Remarks

- Is there anything you would like to add regarding the relationship between Dall sheep, grizzly bears and wolves?
- Is there anything we did not ask that you would like to mention?

[End of interview] End time: ________

7. General conclusion

This doctoral thesis provides an updated knowledge about Dall sheep in the Northern Richardson Mountains, examines factors driving their habitat selection and sexual segregation, and characterizes their interactions with grizzly bears and wolves based on spatial associations, the predators' assimilated diet, Dall sheep behaviour patterns, and traditional ecological knowledge. My main research contributions and their broader implications are summarized in this concluding chapter.

Beforehand, however, I will discuss one more matter particularly relevant to the management of this population: the role of predation and other limiting factors in driving its abundance. Are grizzly bears and wolves threatening the viability of this population? What are the main factors responsible for the wide fluctuations recorded in past decades? Do predators need to be controlled to help Dall sheep thrive in the Northern Richardson Mountains? Or are Dall sheep mostly limited by climate, habitat capacity (density dependence), or harvest?

Due to the remoteness and inaccessibility of the Northern Richardson Mountains, which is typical of other northern locations, this population's management is challenged by irregular survey intervals, unknown demographic rates, unknown predation rate (and little known predator populations), and poorly monitored harvest. Despite the prevalence of missing data, identifying the processes driving a population is critical to properly assess its viability and set sustainable management strategies (Boyce 1992, Morris and Doak 2002, Possingham *et al.* 2007). As such, one former objective of my doctoral research was to understand how various factors interact to drive the abundance of Dall sheep in the Northern Richardson Mountains. Although I could not collect the data required for quantifying the direct effects of predation (e.g., kill rates and functional response), there is little evidence that predation could have been directly linked to precedent abundance fluctuations recorded in this population. As highlighted throughout this thesis, Dall sheep have evolved with several strategies to avoid predation, including vigilance behaviour and the frequentation of rugged habitats. To gain additional insights about this population, I share in the following section my attempts in disentangling three other potentially important (and better documented) factors: harvest, climate variables, and density dependence.

7.1. Identifying limiting factors despite missing data

Because Dall sheep aerial survey estimates are characterized by irregular timing, missing data, and varying geographical coverage, disentangling the main driving factors prove to be challenging. As reviewed in Lambert Koizumi *et al.* (2011) and to reiterate Simmons' concern (1973), harvest appeared to act as a major limiting force during the 1970s and early 1980s, a period marked by low abundance estimates and high harvest rates (between 8 and 60% of the population). Lower harvest rates (less than 1%) then coincided with an increase in the population until the mid 1990s, and recent harvest rates, which are more moderate(about 2% in the 2000s), seem to be keeping this population near stability. Clearly, despite several years with missing data, there is a strong inverse correlation between minimal reported harvest and survey abundance estimates (r = -0.78, Figure 7.1), which emphasizes the vulnerability of this population to overharvest. In contrast, no clear relationship was found between population size or growth rate and other variables.

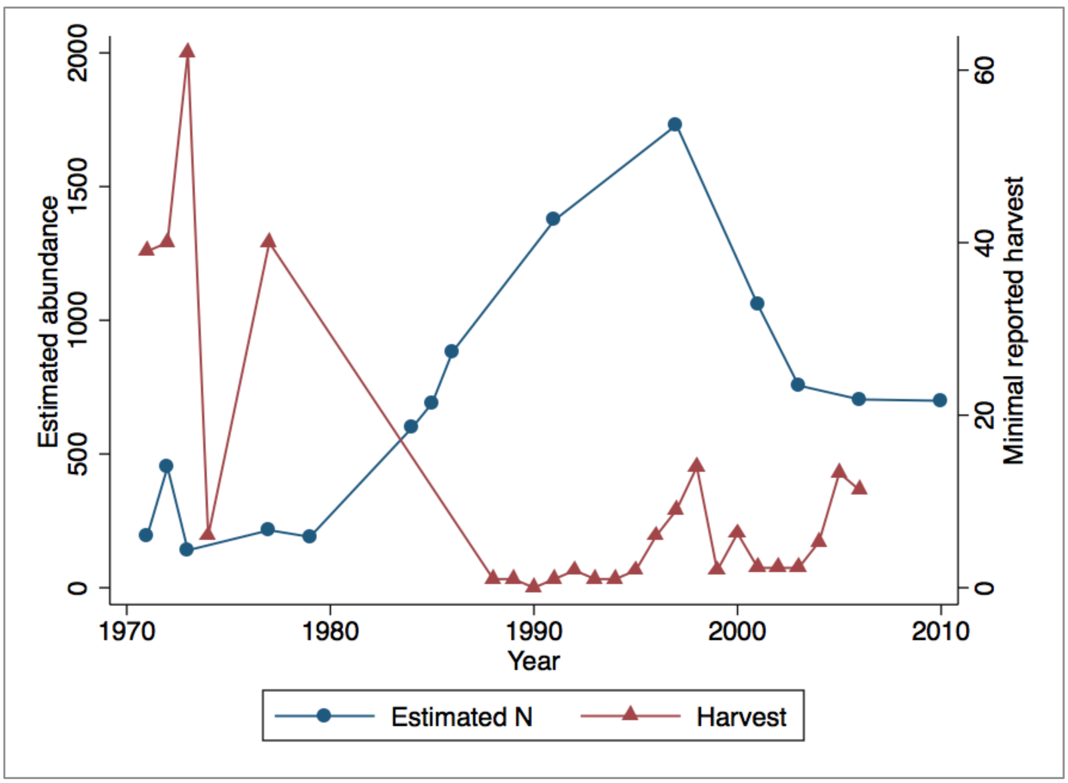

Figure 7.1. Relationship between estimated abundance and minimal reported harvest of Dall sheep in the Northern Richardson Mountains (r = -0.78).

To evaluate the effect of climate variables and density dependence after accounting for the impact of harvest, I used a stochastic version of the Ricker model, modified from Dennis and Taper (1994), that incorporated effects related to density-dependence and climatic covariates, corrected with harvest records (following methods of Taper and Gogan 2002). I was privileged to collaborate with Dr. Mark Taper (Montana State University), who accepted leading the modeling part of this analysis. We constrained the model so that growth rates greater than maximum physiologically possible were not allowed. The observation error variance was estimated based on the replicate surveys of Barichello *et al.* (1987) and Stenhouse and Kutney (1987). Missing years were dealt with using data cloning procedures. Data cloning is a statistical approach that calculates maximum likelihood estimates and standard errors for complex ecological models (Lele *et al.* 2007, Ponciano *et al.* 2009). It has the particularity of being based on a Bayesian framework and exploiting the Markov Chain Monte Carlo (MCMC) algorithms.

For our time series, we used abundance estimates of surveys that covered the 11 main survey blocks (years 1972, 1977, 1984, 1985, 1986, 1991, 2001, 2003, 2006, and 2010). To maximize use of available data, we also included surveys that had limited geographical coverage (1971, 1973, 1987, 1997) (see Chapter 2, section 2.3.2) and adjusted them accordingly. Adjustments were made using a linear regression of log of total abundance ($\log(N_{total})$) against the log of abundance in observed blocks ($\log(N_{observed\ blocks})$) for years with complete data.

For the years with missing data, $\log(N_{total})$ was predicted from $\log(N_{observed\ blocks})$ using the regression equation. Measurement error for the adjusted observations corresponded to the prediction error standard deviation for those points in the regression. Because the period between 1978 and 1983 (inclusive) had neither observations nor covariates, those years were removed of the analyses. In total, we used data collected in 14 surveys over 33 years of monitoring (missing years = 19, or 58% of the dataset). The climatic covariates considered in these models were spring precipitation, lagged spring precipitation, NAO (North Atlantic Oscillation), winter temperature, and snowfall. Because harvest records were not always available or sometimes incomplete, adjusting the abundance estimates accordingly was not straightforward. Furthermore, this approach did not specifically test the effect of harvest on this population.

After testing various models, two emerged as significant: the best model with lagged spring precipitation and snowfall covariates, the second with lagged spring precipitation only. Density-dependence itself was not significant in the absence of climatic covariates. The best model suggested that the growth rate of this population is positively related to snowfall and negatively related to previous spring precipitation. However, to validate this model, we had to verify how tolerant it is to missing data. To address this question, we simulated a complete time series using the best model, then progressively removed observations and re-estimated the model parameters from these new time-series, twice. In both cases, estimates appeared reasonably stable until a threshold of 11 or 12 observations, or about 33% of the dataset, were missing. More missing observations lead to a dramatic increase in both bias and uncertainty when estimating model parameters (Figures 7.2 and 7.3).

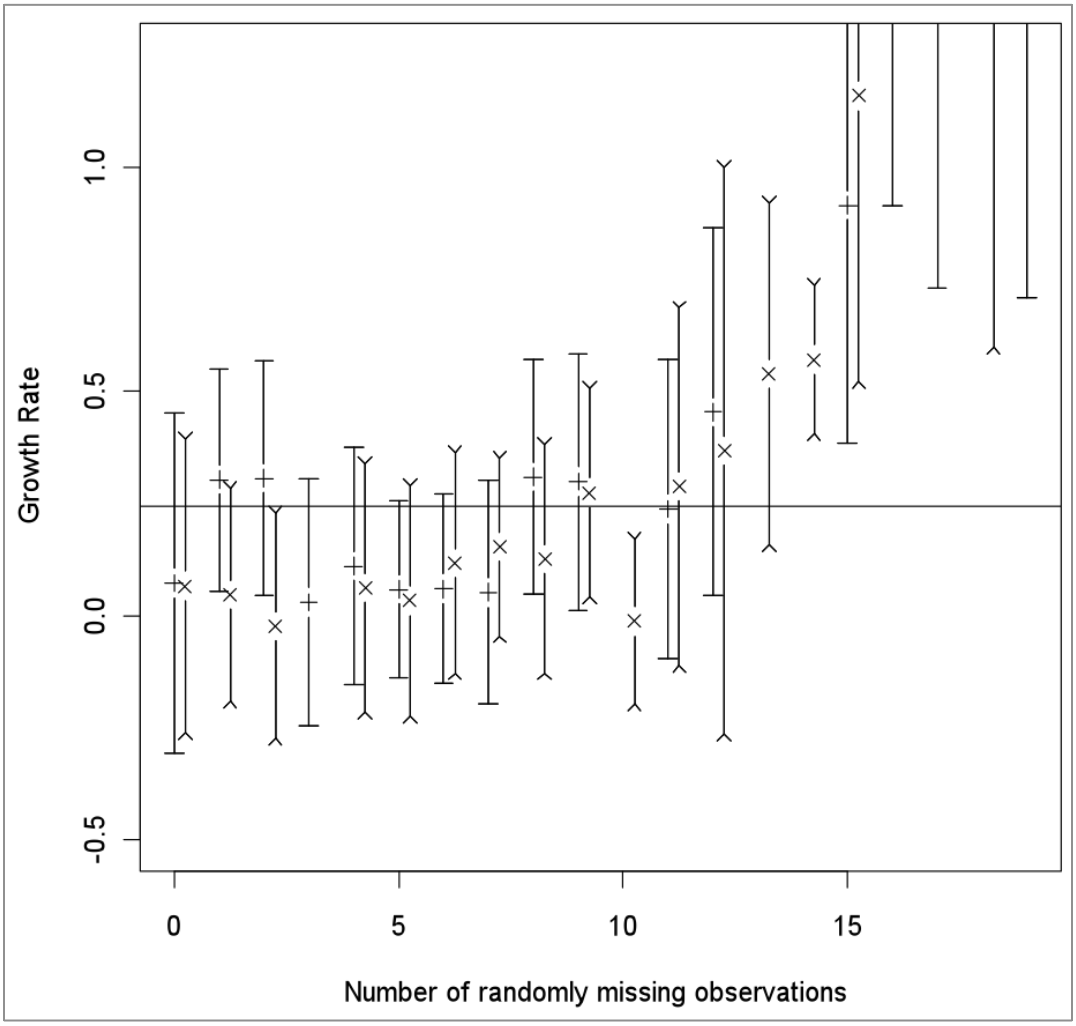

Figure 7.2. Estimates of growth rates with 95% confidence intervals versus the number of missing observations. Two different time series, marked with × and +, were created with randomly different locations in the time series for the missing observations. The slight variation between the two estimates for the 0 missing observation case is related to the stochastic nature of MCMC estimation. Breakdown occurs around 12 missing observations.

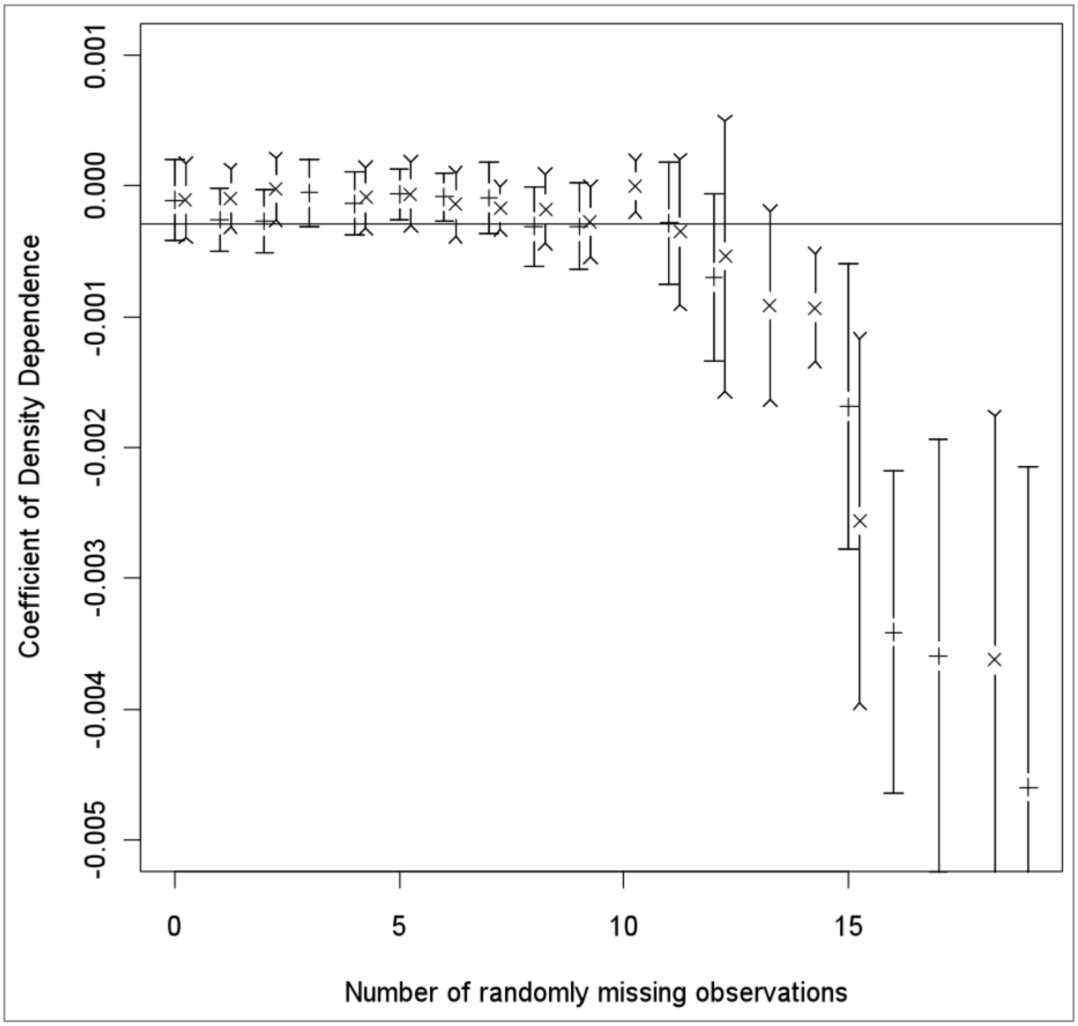

Figure 7.3. Estimated coefficients of density dependence with 95% confidence intervals versus the number of missing observations. Two different time series, marked with × and +, were created with randomly different locations in the time series for the missing observations. The slight variation between the two estimates for the 0 missing observations case is related to the stochastic nature of MCMC estimation. Breakdown occurs around 12 missing observations.

Although our modeling approach was tolerant to a high proportion of missing data, the time series of Dall sheep in the Northern Richardson Mountains suffered from a number of missing observations considerably surpassing the threshold that we had identified. Therefore, our model conclusions were likely afflicted by high bias and uncertainty. We concluded that, unfortunately, little can actually be said using this dataset about the role of climate and density dependence in driving this Dall sheep population. A higher frequency of monitoring would be necessary to investigate those factors. These analyses emphasize the paramount importance of regular monitoring to understand the dynamics and fluctuations of populations.

7.2. Contributions

The status report in Chapter 2 summarized the information available on Dall sheep in the Northern Richardson Mountains and highlighted several gaps in knowledge. As pointed out in the preceeding section (7.1), more frequent monitoring paired with complete and unbiased harvest records are needed before we can evaluate the effects of density dependence, climate and harvest on this population. Admittedly, aerial surveys are costly, particularly in such remote areas. However, as revealed in Chapter 6, the population trends reported in the traditional ecological knowledge study concurred relatively well with aerial surveys estimates. As such, ground monitoring could be thoughtfully integrated with local knowledge to provide estimates during those years when no aerial survey is conducted. Such monitoring plan would have to be designed carefully, but could fulfill monitoring needs and help reinforce the cooperative spirit among stakeholders of this population.

In Chapter 3, I demonstrated that in areas of core utilization, Dall sheep were exposed to greater spatial overlap with grizzly bears than with wolves. However, throughout their full range –when areas of lesser utilization were also considered, wolves were more likely to be present. Holders of traditional ecological knowledge have also highlighted the prevalence of grizzly bears in areas highly used by this Dall sheep population (Chapter 6), particularly in vicinity of Black Mountain, at the eastern limit of the Northern Richardson Mountains.

Not all grizzly bears or wolves have the same patterns of associations with Dall sheep, however. When examining the overlap of individual monitored in this study, in Chapter 4, important variations emerged among the members of each species. After considering other prey present in this range, both with stable isotopes analyses and traditional ecological knowledge, the diet of grizzly bears and wolves in the Northern Richardson Mountains manifested themselves as remarkably diversified. For both predators, Dall sheep did incorporate their diet, although in various proportions and not as a predominant food source. The carbon and nitrogen stable isotope analyses were not capable of adequately distinguishing between Dall sheep, caribou, and arctic ground squirrels, which I merged together in the mountain mammals group. This limitation highlighted the need to develop alternative methods to investigate the diet of generalist predators consuming several prey species. My results nevertheless showed that animal sources composed most of the grizzly bear diet, with vegetation and aquatic browsers (including moose and/or beavers) constituting the two most important groups, followed by mountain mammals. Aquatic browsers constituted the wolves' principal food, seconded closely by mountain mammals. Even if Dall sheep did not emerge as the most important prey of both grizzly bears and wolves, a few individual predators targeting Dall sheep could suffice to provoke a population decline (Ross *et al.* 1997, Festa-Bianchet *et al.* 2006). As such, the continued monitoring of these three species is advised.

In Chapters 4 and 5, I examined the question of sexual segregation in Dall sheep, based on patterns of habitat use and behavioural activity under grizzly bear and wolf predation risk. Multiple hypotheses have been proposed to explain sexual segregation in ungulates, but I focused my attention on two specific ones. First, I considered the "predation risk hypothesis" (Main and Coblentz 1996, Corti and Shackleton 2002, Hamel and Côté 2007), stating that females increase their reproductive success through the survival of their young, leading them to prioritize safe environments. In turn, the males' reproductive success depends on their ability to breed with females and compete with other males, leading males to select habitats based on available forage, even if those habitats expose them to higher predation risk. Second, I considered the "activity budget hypothesis", stating that, because males and females have varying nutritional needs and movement rates, their activity budgets differ and naturally lead to the formation of groups with similar activity budgets, (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2000, Ruckstuhl and Neuhaus 2002).

I discovered distinctive patterns of seasonal habitat use both for ewes and rams. Habitat utilization of rams were linked to the barren lands, water features, and southerly aspects, suggesting choices of habitat primarily lead by foraging needs. In contrast, habitat patterns of ewes were predominantly associated with steepness and ruggedness, suggesting that safety was a greater concern to them. During summer, rams were also exposed to higher levels of grizzly bear risk compared to ewes. Overall, these habitat use patterns were supportive of the predation risk hypothesis to explain sexual segregation. The traditional ecological knowledge also highlighted the importance of predator avoidance, in combination with foraging needs, water, and mineral licks, in Dall sheep habitat selection.

In Chapter 5, my investigations of Dall sheep behaviour during early summer revealed that ewes foraged longer, were more vigilant, rested less, and exhibited less dominance behaviour than rams. Also, rams were subject to higher exposure to wolf predation risk and stayed in smaller groups. This particularity, combined with the increased vigilance in ewes, further supported the "predation risk hypothesis". However, by providing evidence of differential activity budgets between ewes and rams, my results also validated some predictions of the "activity budget hypothesis", thereby testifying that these two hypotheses are not mutually exclusive.

In Chapter 6, I documented the traditional ecological knowledge of Gwich'in and Inuvialuit elders and land users who were familiar with Dall sheep, grizzly bears and wolves in the study area. The information they shared revealed population trends that had previously not been documented (e.g., important Dall sheep population crash over 200 years ago, low Dall sheep abundance in the 1950s and before the start of aerial surveys, population trends of grizzly bears and wolves). Moreover, traditional ecological knowledge admirably complemented findings from scientific methods, with varying levels of details. Notably, interviewees have highlighted the importance of predator avoidance and foraging in Dall sheep habitat selection; sexual segregation, particularly during lambing and summer, with a tendency for ewes to stay in steeper terrain and protect their lambs; the grizzly bear's diet diversity and their vulnerability to harvest. They also provided various management recommendations for the three study populations and their habitat in the Northern Richardson Mountains.

7.3. Concluding remarks

In communities near the Northern Richardson Mountains, harvesters primarily rely on caribou, fish, waterfowl and small game for subsistence. Typically, Dall sheep represents only a small portion of their harvest (The Joint Secretariat 2003, GRRB 2009). Dall sheep meat is nevertheless considered a delicacy, and the non-consumptive value of this population is cherished throughout the region. The increasing export of horns and capes, however, combined with interest for commercial sport hunting, potential industrial development, and climatic changes, prompt for an effective monitoring of Dall sheep and their limiting factors in this region. The preoccupying low population abundance recorded in the 1970s and 80s, which were likely related to the heavy harvest pressure (see Figure 7.1), combined with the drastic decline observed in early 2000s, have promoted a series of collaborative efforts; notably periodic aerial surveys and the 2008-2013 draft management plan. My research, designed in concert with the local Gwich'in renewable resources councils, is a testament of the importance of Dall sheep, but also grizzly bears and wolves, to those communities.

Using a series of complementary methods, my thesis contributes to raise the available knowledge on the ecology of Dall sheep, grizzly bears and wolves in the Northern Richardson Mountains. My research provides a concrete example of how aboriginal traditional ecological knowledge and other scientific methods can be integrated to improve our understanding of ecological systems, even in presence of missing or irregular data. Although my analyses mostly focused on aspects of Dall sheep ecology, the data I collected throughout this project may also help understanding the spatial ecology of grizzly bears and wolves in future investigations. Likewise, this research provides a starting ground to analyze interactions with more species of this northern ecosystem, which might help detect ecological processes like trophic cascades (Schmitz *et al.* 2004). Finally, in the event of upcoming environmental impact assessments or land use development, findings presented in this thesis may prove valuable to assist the management and conservation of wildlife in the remote, pristine, and yet vulnerable, Northern Richardson Mountains.

7.5. Literature cited

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