SPATIO-TEMPORAL RECRUITMENT DYNAMICS OF MOUNTAIN-DWELLING CARIBOU IN THE YUKON TERRITORY, CANADA

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A

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Abstract

Understanding processes and mechanisms resulting in observed ecological patterns is critical information for biologists charged with effectively managing and conserving wildlife populations. In many areas across North America woodland caribou (*Rangifer tarandus caribou* Gmelin) populations are declining, as are caribou and reindeer populations globally. Why these declines are occurring is a key research question of biologists and managers.

I investigated factors influencing recruitment of mountain-dwelling woodland caribou using long-term time series from ten herds (populations) in the Yukon Territory, Canada (Yukon). Recruitment was indexed by the calf:cow ratio observed during the fall breeding season using data collected during aerial monitoring surveys.

I first examined the seasonal effects of the Pacific Decadal Oscillation (PDO), on observed recruitment in these herds. The PDO was positively related to recruitment and had its strongest effect during the winter preceding birth and immediately before calving. These results indicate that female body condition, and hence conception rates, were not affecting observed recruitment patterns. Rather, parturition and/or early calf survival were the most likely vital rates affecting the number of calves being recruited into the breeding population.

I next examined the interacting effect of large-scale climate (PDO) and predation [wolf (*Canis lupus* L.) density] on recruitment in the Finlayson herd of east-central Yukon. A large-scale wolf control program in the 1980s allowed me to assess recruitment over a range of wolf densities and climatic conditions. The effect of the PDO immediately before calving was negligible when wolf numbers were significantly reduced indicating the climatic effect was modified by wolf density. Additionally, as springtime climate improved (i.e. increasing PDO) the difference in recruitment between years with and without wolf removals was reduced.

Finally, I examined the degree of spatial synchrony in recruitment across ten herds and modeled inter-herd synchrony by differences in their landscape characteristics. Spatial synchrony in recruitment was generally low and much less than spatial synchrony in snow depth measurements across the Yukon. The only landscape characteristic influencing the correlation (synchrony) in recruitment between herds was the difference in elevation variability of calving locations.

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CHAPTER 1 GENERAL INTRODUCTION

1.1 Introduction

Across their range, many woodland caribou (*Rangifer tarandus caribou* Gmelin) populations (or herds[1]) in North America (Fig. 1.1) have or are experiencing declines (Bergerud 1974; Thomas & Gray 2002), in line with *Rangifer* declines globally (Vors & Boyce 2009). In southern British Columbia and northern Alberta, some herds are at drastically low levels (Wittmer *et al.* 2005a) and are at risk of extirpation (McLoughlin *et al.* 2003; Schneider *et al.* 2010; Wittmer, Ahrens & McLellan 2010). Some herds in northern regions, such as the Yukon Territory (Yukon), have also experienced declines (e.g. Farnell *et al.* 1998; Hayes *et al.* 2003). Many of these declines have been linked to anthropogenic factors including habitat loss, human harvest, and altered predator-prey relationships (Sorenson *et al.* 2008; Wittmer, Sinclair & McLellan 2005b; Wittmer *et al.* 2010). As human activity increases in caribou ranges, effective management and conservation of caribou will require sound information on demographic processes to mitigate or reverse declining trends (Gordon, Hester & Festa-Bianchet 2004).

In addition to direct anthropogenic impacts, climatic factors also have a strong influence on caribou population dynamics (Sæther 1997). For example, the Chisana herd in southwest Yukon and east-central Alaska (Fig. 1.2) experienced dramatic declines over the past decade (Farnell & Gardner 2002). These declines, brought on by poor calf recruitment, resulted in a drop in estimated herd size from > 1000 in 1989 to below 500 in 2001. These years of low recruitment were initiated by a series of years with severe winters (e.g. deeper snow). Climate can influence population dynamics through a number of

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[1] In keeping with the nomenclature typically used to describe caribou, the term *herd* (e.g., Chisana herd) is used to define a discrete "local population" and the term *population* (e.g., Northern Mountain Population) is used to define a collection of local populations (Thomas and Gray 2002).

mechanisms. Hebblewhite (2005) reported that climate played a strong role in wolf (*Canis lupus* L.) predation on elk (*Cervus elaphus* L.) in the Rocky Mountains of Alberta primarily through changes in snow depth. Poor winter weather (e.g. deep snow) may reduce female energy reserves leading to lower calf weights (Adams 2005; Weladji & Holand 2003) thus reducing calf survival (Cook *et al.* 2004). Poor summer weather (e.g. short growing season) may limit the nutritional quality of forage thus limiting body mass gain during the summer and leaving animals (calves and adults) in a more vulnerable state for winter (Cook *et al.* 2004; Pettorelli *et al.* 2005a, b).

The influence of large-scale climate indices on a variety of ungulates has been well-documented elsewhere (e.g. Post & Stenseth 1999; Weladji *et al.* 2002), and includes, for example, the relationship between the Arctic Oscillation (AO) and the Porcupine caribou herd (Griffith *et al.* 2002) and the influence of the North Atlantic Oscillation (NAO) on caribou and muskoxen (*Ovibus moschatus* Zimmermann) in Greenland (Forchhammer *et al.* 2002), Soay sheep (*Ovis aries* L.) on St. Kilda, Scotland (Coulson *et al.* 2001), and elk in Yellowstone National Park (Garrott *et al.* 2003). In addition to its direct effect on vital rates, climate has also been shown to influence population dynamics through its effect on spatial synchrony among populations (Aanes *et al.* 2003; Grøtan *et al.* 2005; Post & Forchhammer 2004), offspring sex ratios (Mysterud *et al.* 2000; Post *et al.* 1999), density-dependent processes (Forchhammer *et al.* 1998), and harvest rates (Mysterud *et al.* 2000).

Interest in resource development in the Yukon is increasing (e.g. Yukon Oil and Gas Branch 2005) and includes mining, forestry, oil/gas exploration, agriculture, and pipeline construction. Given observed global caribou declines, increasing development on the landscape, and the observed effects of development on caribou from southern regions (Dyer *et al.* 2001), an understanding of processes that affect population dynamics is needed to guide land-use management to sustain caribou populations. However, efforts to project future population dynamics that consider only landscape effects may be flawed and overly optimistic without a consideration of climatic variability. Climate change will have varying influences on caribou (e.g. Porcupine herd; Inkley *et al.* 2004) through changes in long-term average climatic conditions and increased climatic variability and extreme events (Drake 2005; Stenseth *et al.* 2002; Walther *et al.* 2002), such as rain on snow events causing icing. Indeed, these effects may occur regardless of any direct anthropogenic factors.

To investigate how climatic factors influence population dynamics, long-term studies incorporating sufficient temporal climatic variability are necessary (Gaillard *et al.* 2000). Models that forecast how populations will respond to changes in climatic conditions should be based on how populations have responded to climatic variability in the past. Furthermore, individual populations may have localized responses to climatic variability possibly through differential climatological downscaling (Pettorelli *et al.* 2005b; Joly *et al.* In Press) across ranges. Therefore, to obtain a robust and generalizable understanding of climatic influences on population dynamics multiple populations should, ideally, be considered to account for this inter-population (i.e. spatial) variability (Boyce, Irwin & Barker 2005; Frederiksen, Harris & Wanless 2005).

Mountain-dwelling caribou are an opportune species to investigate climatic patterns because they are distributed in discrete herds with substantial habitat variability. Using population data from multiple years provides a source of temporal variability. By including multiple herds in the analysis spatial variability is incorporated, allowing results and inferences to be generalized across herds (Gelman & Hill 2007). Examining this variation in population dynamics among herds provides more robust results and a greater understanding of the population dynamics of mountain-dwelling caribou.

Wildlife managers commonly collect information such as age ratios for monitoring ungulate populations (e.g. Bender 2006). While this information is useful for assessing the status of a population, it may also be valuable for assessing processes affecting population dynamics. As part of annual monitoring activities for mountain-dwelling caribou in the Yukon, fall composition surveys, conducted during breeding, are routinely carried out to collect information on the age and sex composition of surveyed herds. Recruitment is represented by the fall calf:cow ratio (e.g. Garrott *et al.* 2003; Grøtan *et al.* 2009). These surveys have been conducted in the Yukon since the early 1980s (Farnell *et al.* 1998) providing a rich dataset of time series from a number of herds (Fig. 1.2) with which to investigate processes affecting herd dynamics.

For mountain-dwelling caribou, the majority of calf mortality occurs within the first month of life (Adams, Singer & Dale 1995; Gustine *et al.* 2006) and thus these age ratios are deemed an adequate measure of the number of calves "entering" the herd (i.e. recruitment). Pregnancy rates in mountain-dwelling caribou are typically high and generally show low annual variability (Wittmer *et al.* 2005a, b) and thus fall calf:cow ratios can be considered a useful proxy for calf survival (e.g. Harris, Kauffman & Mills 2008) to approximately 4-5 months of age. Variation in large herbivore population growth rate is often best explained by variability in juvenile survival (Gaillard, Festa-Bianchet & Yoccoz 1998). Therefore, obtaining an understanding of the processes influencing caribou population dynamics will benefit from investigating mechanisms affecting juvenile survival (i.e. calf:cow ratio).

1.2 Research Objectives

The primary goals of this research are two-fold. First is to contribute to the broader body of knowledge of ungulate population dynamics. Second is to investigate mechanisms influencing recruitment of mountain-dwelling caribou in the Yukon. To allow for findings to be applicable to populations and species beyond mountain-dwelling woodland caribou in the Yukon, a process-oriented (i.e. mechanistic) approach is used rather than simply describing patterns of the observed data (Krebs & Berteaux 2006). Within these broader goals are 5 specific research objectives.

First, I examined the seasonal effects of Pacific-based climate on recruitment in mountain-dwelling caribou herds in the Yukon (Objective 1). These herds are commonly assumed to be predator-limited (Bergerud & Elliot 1986; Hayes *et al.* 2003; Seip 1992), and ungulate populations occurring in areas with predator-prey communities often exhibit weak, if any, density-dependent regulation of population growth (Wang *et al.* 2009). While the influence of Atlantic-based climate has been well-studied in ungulate populations in western Europe and eastern North America (e.g. Patterson & Power 2002; Post & Stenseth 1998, 1999; Vucetich & Peterson 2004), there are relatively few reports of the effects of Pacific-based climate on ungulate populations or on ungulate populations coexisting with predators (but see Hebblewhite 2005). Climatic effects on ungulate populations co-existing with large predators may differ than those found in predator-free environments. For example, ungulate populations near carrying capacity may be strongly influenced by winter weather affecting female body condition and subsequent fecundity (e.g. Post & Stenseth 1999). Alternatively, ungulate populations exposed to predation may be more strongly influenced by climatic conditions during different seasons through climate's influence on predation rates (Hebblewhite 2005).

Due to the relative scarcity of research on Pacific-based climatic effects on animal populations and the variety of Pacific-based climate indices available, I compared two previously used indices to model recruitment in Yukon mountain-dwelling caribou (Objective 2). Hebblewhite (2005) used the North Pacific Index (Trenberth & Hurrell 1994) in a study of elk population dynamics in the Canadian Rocky Mountains and both Hik & Carey (2000) and Morrison & Hik (2007) used the Pacific Decadal Oscillation (Mantua & Hare 2002) in assessing population parameters of Dall's sheep (*Ovis dalli dalli* Nelson) and collared pika (*Ochotona collaris* Nelson), respectively.

Additionally, Hallett *et al.* (2004) noted that large-scale climate indices may better predict ecological processes than local weather measurements (e.g. snowfall, temperature). This may be due to the ability of large-scale indices to incorporate broader spatio-temporal heterogeneity into one metric (Stenseth & Mysterud 2005). However, in some systems, local weather proved a better predictor than large-scale climate indices (Mysterud *et al.* 2007; Ogutu & Owen-Smith 2003). Thus, in addition to comparing Pacific-based climate indices, I also compared the strength of large-scale climate and local weather metrics in modeling Yukon caribou recruitment (Objective 3).

Most research on the influence of large-scale climate on ungulate populations has focused on “bottom-up” effects (e.g. Forchhammer *et al.* 1998; Pettorelli *et al.* 2005b); largely as many of these populations occur in predator-free environments. However, climate also influences “top-down” processes (Hebblewhite 2005; Krebs 2009; Wilmers *et al.* 2006). During the 1980s, a large-scale predator removal program (i.e. wolf control) occurred in the range of the Finlayson caribou herd of east-central Yukon (Fig. 1.2; Hayes & Harestad 2000). Wolf and caribou population data were collected during this time providing a “natural” experiment to assess the influence of climate on recruitment across a gradient of wolf densities (Objective 4).

Spatial variability in the effect(s) of climate on populations are in part due to the differential downscaling of climate to observed local weather patterns (Pettorelli *et al.* 2005b). In the heterogeneous landscapes of the Yukon, mountain-dwelling caribou herds occur over a range of landscape conditions. These conditions likely result in differing local weather patterns. Thus, to better understand processes by which climatic conditions affect caribou population dynamics, investigating the role of landscape conditions may prove useful. Understanding factors affecting spatial synchrony in population dynamics is a valuable approach for identifying mechanisms of population dynamics (Ranta *et al.* 1995). To accomplish this, I estimated the degree of spatial synchrony in recruitment among these caribou herds (Fig. 1.2) and subsequently examined how landscape similarity was related to recruitment synchrony between herds (Objective 5).

1.3 Study Area

Mountain-dwelling woodland caribou in the Yukon belong to the Northern Mountain Population of woodland caribou in Canada (Thomas & Gray 2002) and are nationally designated as a species of special concern (COSEWIC 2002) under Canada's Species at Risk Act (SARA). This designation was primarily due to increasing levels of anthropogenic activity within Northern Mountain caribou range (Thomas & Gray 2002). The Northern Mountain Population represents a caribou ecotype. This ecotype is characterized by animals that typically forage on terrestrial lichen (e.g. *Cladina mitis* Sandst.) during winter and which migrate between seasonal ranges, although these migrations are substantially smaller than those observed in tundra-dwelling caribou (e.g. *R. t. groenlandicus* Borowski). Woodland caribou elsewhere in Canada belong to the Southern Mountain Population and the Boreal Population (Fig. 1.1) which are both designated as threatened under SARA. SARA defines a threatened species as one that is likely to become endangered if limiting factors are not reversed while a species of special concern is one which has characteristics making it particularly sensitive to anthropogenic effects or natural events. Endangered status implies a species faces imminent extirpation or extinction.

Mountain-dwelling caribou in the Yukon are distributed over roughly the southern half of the territory. Twenty-six distinct herds have at least some portion of their annual range within the Yukon (Fig. 1.2). With a few exceptions, these herds occupy habitats with minimal human footprints, in comparison to caribou herds in southern British Columbia and Alberta (Sorensen *et al.* 2008; Wittmer *et al.* 2010), and generally exist within intact multi-predator multi-prey systems with varying levels of human harvest. These herds occur in both the Boreal Cordillera and Taiga Cordillera ecoregions (Marshall & Schut 1999) and are found across a range of terrain variability (Table 4A.1). Environmental conditions are highly seasonal sub-arctic climate represented by typically long, cool winters and relatively short, mild summers.

Data from 10 herds (Fig. 1.2) were used for the research in this dissertation because they had time series of data longer than five years. These herds are well distributed across the Yukon and exist across a range of habitat conditions. This includes, for example, those with a relatively high human footprint in their range, such as the Carcross herd found adjacent to Whitehorse (Florkiewicz *et al.* 2007), and those with virtually no human footprint such as the Chisana herd (Farnell & Gardner 2002). The status of these herds represents a range of states including increasing, decreasing and stable trajectories, with population estimates ranging from < 200 to > 3000 (Table 1.1).

1.4 Management Implications

Knowledge of which Pacific-based climate index influences recruitment in these herds is useful as it provides a temporal variable potentially that may be useful for assessing annual recruitment in areas where local weather measurements are unknown. Further, having a generalizable model of recruitment incorporating this index, coupled with an estimate of the degree of spatial synchrony of recruitment, will assist managers in predicting annual recruitment in herds that are not monitored. Ultimately, linking recruitment to large-scale processes occurring in the Pacific Ocean may be valuable in assessing the effects of global climate change on these herds as it provides a direct linkage to oceanic conditions that driver global climate.

Environmental conditions during different seasons have differing effects on caribou population parameters (e.g. calf survival, fecundity). Knowledge of which seasonal climatic conditions most strongly explain variability in recruitment is valuable for understanding how population growth is limited. For example, if climate preceding conception (i.e. affecting female body condition at breeding) is most influential, this would indicate that fecundity may be limiting recruitment. However, if environmental conditions at, or shortly after, calving are most influential, this may indicate that calf survival is limiting recruitment. This information is important for management as it allows for informed decisions to be made regarding mechanisms affecting recruitment.

Mountain-dwelling woodland caribou in the Yukon exist in generally intact ecosystems with both top-down and bottom-up forces acting on population dynamics. Predation is commonly assumed to be the primary limiting factor of these herds. Therefore, understanding how predation and climate interact to influence recruitment is valuable information to evaluate management options (e.g. predator control) related to caribou management as it may be used to assess the likelihood of meeting management objectives.

Finally, investigating how broad-scale landscape factors affect the synchrony in recruitment between herds can be used to identify those features influencing population dynamics. Those factors influencing spatial synchrony can then be considered for future research into their direct effects on recruitment, which may subsequently be useful for assessing environmental impacts on caribou herds.

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Table 1.1. Status of the ten mountain-dwelling woodland caribou herds in the Yukon Territory, Canada, included in this research (Environment Yukon, unpublished data).

Herd	Population Estimate	Last Surveyed	Estimated Trend[a]
Aishihik	2044	2009	Increasing
Burwash[b]	181	2003	Decreasing
Carcross	775	2008	Stable
Chisana	766	2007	Stable
Ethel Lake	300	1993	Stable
Finlayson	3100	2007	Decreasing
Ibex	850	2008	Increasing
Klaza	650	2000	Increasing
Tatchun	500	2000	Stable
Wolf Lake	1400	1998	Stable

a: Estimated trends based on empirical population estimates or local knowledge of Environment Yukon biologists; b:Also referred to as the Kluane herd.

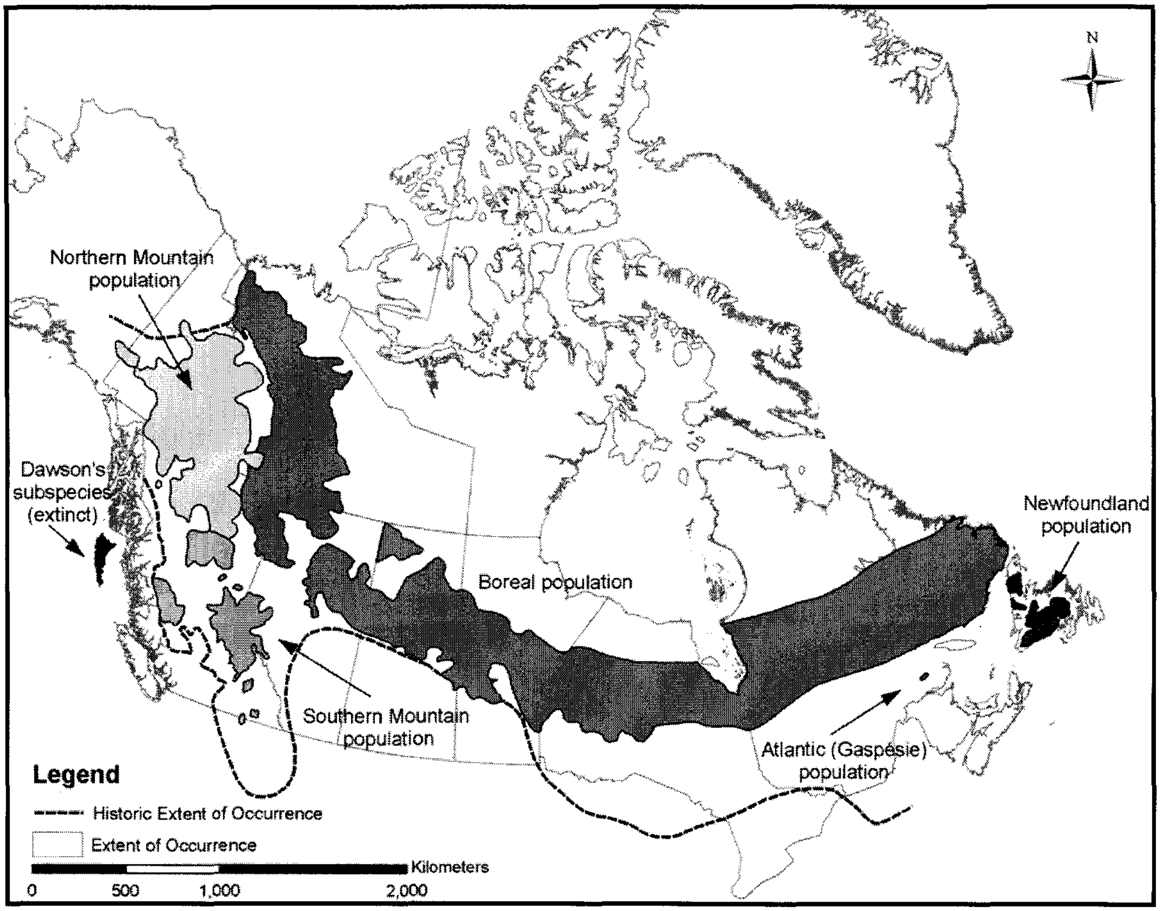

Figure 1.1. Distribution of woodland caribou in North America (from Thomas & Gray 2002).

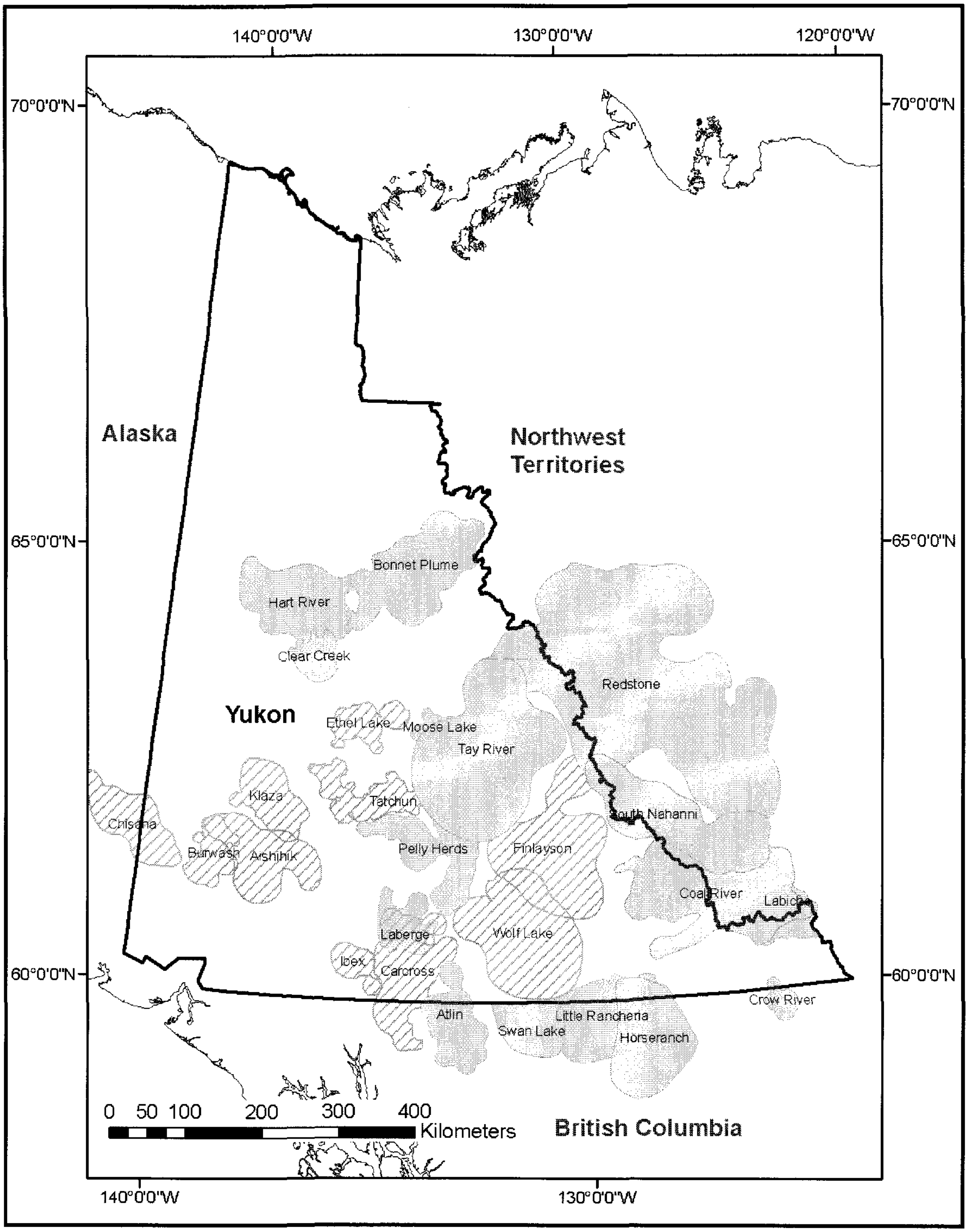

Figure 1.2. Mountain-dwelling woodland caribou herds found in the Yukon Territory, Canada. Hatched ranges indicate those herds included in this research. Herds with solid grey ranges were excluded from the analysis due to insufficient data.

CHAPTER 2 SEASONAL EFFECTS OF PACIFIC-BASED CLIMATE ON RECRUITMENT IN A PREDATOR-LIMITED LARGE HERBIVORE[1]

2.1 Introduction

The influence of climate on ungulate population dynamics and life-history traits is well documented in western Europe (e.g. Post & Stenseth 1999; Coulson *et al.* 2001; Mysterud *et al.* 2001) and eastern North America (e.g. Post & Stenseth 1998, 1999; Patterson & Power 2002; Vucetich & Peterson 2004) where the ecological effects of the North Atlantic Oscillation (NAO) are strong (Stenseth *et al.* 2002, 2003; Mysterud *et al.* 2003). Research on the influence of climate on ungulates in western North America is sparse (Griffith *et al.* 2002), and few studies have explicitly examined the role of Pacific-based climate (Hebblewhite 2005). Further, much of the research relating large-scale climate to large herbivore populations has been assessed on forage-limited populations with few or no natural predators. Climate influences herbivore population dynamics through its effect on forage characteristics (Forchhammer *et al.* 1998; Vucetich & Peterson 2004); however, in predator-limited populations climate may also affect population dynamics through its effect on predation rates (Hebblewhite 2005). Here we investigated the seasonal influence of climate on population recruitment patterns of northern mountain-dwelling caribou in the Yukon Territory (Yukon), Canada, using the Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997) as a climate index.

Mountain-dwelling caribou populations in northwest North America are considered predator-limited (Gauthier & Theberge 1986; Hayes *et al.* 2003) and typically occur at low density. They are generally characterized by high pregnancy rates (Wittmer, Sinclair & McLellan 2005; Gustine *et al.* 2006), variable parturition rates (Adams & Dale 1998; Gustine *et al.* 2006), and low

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[1] Hegel, T.M., Mysterud, A., Ergon, T., Loe, L.E., Huettmann, F. & Stenseth, N.C. (2010) Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. *Journal of Animal Ecology*, **79**, 471-482.

juvenile survival (Seip 1992; Hayes *et al.* 2003) in which predation on neonates is often the primary mortality source (Adams, Dale & Mech 1995a; Adams, Singer & Dale 1995b; Gustine *et al.* 2006). Density plays a weak role in the dynamics of these populations as predators keep numbers sufficiently low to limit density-dependent forces (Crête 1999; Wang *et al.* 2009). Recruitment (i.e. the joint contribution of fecundity and calf survival), indexed here by the fall calf:cow ratio, is highly variable and often < 0.3 (Hayes *et al.* 2003). Age ratios such as this are effective at tracking population growth rates and trajectories (Harris, Kauffman & Mills 2008), yet the role of climate on recruitment in these populations is currently not well understood.

Mechanistically, climate may be related to recruitment through its influence on fecundity and/or calf survival (Table 2.1). We hypothesized (H1) that because of high neonatal calf losses from predation, seasonal climate during winter preceding birth (in utero) and in springtime should have a strong influence on recruitment through its effect on snow depth during the neonatal period. Due to high neonate losses, the majority of females are unburdened of providing energetic resources to offspring, thus allowing them to allocate all acquired resources to self-maintenance. However, given the highly seasonal conditions in the Yukon, female fecundity may be influenced by pre-conception climate (Table 2.1) as a result of an insufficient time window to restore body reserves prior to breeding, resulting in a stronger influence of these climate conditions (H2). H1 and H2 are not mutually exclusive.

2.2 Methods

2.2.1 Study Populations

Recruitment data are from 10 northern mountain caribou herds (i.e. populations; Fig. 2.1), representing nearly half of the 22 herds residing at least partially in the Yukon (Farnell *et al.* 1998). They represent the northern mountain ecotype of woodland caribou in Canada (Thomas & Gray 2002) and are federally designated as a species of special concern under Canada's Species at Risk Act (COSEWIC 2002). Densities ranged from approximately 0.03 to 0.20 individuals/km^2 (Thomas & Gray 2002) and are much lower than those reported for forest-dwelling reindeer in, for instance, the mountainous regions of Norway with much fewer natural predators (e.g. 1.03 to 1.41 individuals/km^2: Reimers *et al.* 1983). All herds reside within relatively intact multi-predator (e.g. black bear *Ursus americanus* Pallus, grizzly bear *U. arctos* L., wolf *Canis lupus* L.), multi-prey (e.g. Dall's sheep, moose *Alces alces* L.) systems (Hayes *et al.* 2003). Mountain caribou are seasonal migrants moving relatively short distances between seasonal ranges. Terrain within herd ranges was mountainous with substantial topographic relief. Mean elevation varied from approximately 1000 to 1500 m above sea level. Herds were distributed in the southern portion of the Yukon (approximately 60° – 63°N, 129° – 141°W) in the boreal cordillera ecozone (Marshall & Schut 1999) with highly seasonal sub-arctic climate characterized by long, cold winters and relatively short, mild summers.

2.2.2 Caribou Recruitment Data

Herds were aerially surveyed from a rotary aircraft to estimate recruitment from 1980 to 2007 as part of monitoring activities in the Yukon (Farnell *et al.* 1998). Following a standardized protocol, surveys occurred during the fall breeding season from the last week of September through mid-October. Groups of animals were classified and the ratio of total numbers of calves to cows used as an index of recruitment at the population (i.e. herd) level. Calves were identified by their small size and females distinguished from immature males by the presence of a black vulva patch. During breeding, animals aggregate on high alpine plateaus devoid of trees, thus making sightability of animals, particularly calves, much greater than in forested habitats. A comparison of calf:cow ratios based on aerial survey data, as used here, with temporally concurrent calf:cow ratios based on sampled adult females, captured for radio-collaring, indicated no significant difference (T. Hegel, unpublished data). Data on recruitment rates represented 165 herd-years from 10 herds during the period 1980 – 2007 (Fig. 2.2). The total number of annual recruitment rates estimated per herd ranged from nine to 26. The average number of animals classified to estimate an annual recruitment rate, across all herds and years, was 516.9 (SE = 42.5).

2.2.3 Population Recovery Activities

A number of management programs aimed at increasing low population sizes have occurred in the Yukon (Farnell *et al.* 1998). During 1983 – 1989, wolves were annually removed from the Finlayson herd range (Fig. 2.1) to < 20% of pre-removal numbers (Farnell & McDonald 1987; Hayes & Harestad 2000). During 1993 – 1997, a wolf removal and sterilization program occurred in the Aishihik herd range, with some actions overlapping onto the ranges of the adjacent Burwash and Klaza herds (Fig. 2.1; Hayes *et al.* 2003). During 2003 – 2006 a captive-rearing program was undertaken for the Chisana herd (Fig. 2.1) to enhance low recruitment. During late winter, parturient females were captured and transferred to a predator-free facility where they calved and were subsequently released in early June. To avoid potential bias associated with increased survival and recruitment due to the Chisana recovery program, we censored captured females and their surviving captive-born calves (Yukon Fish and Wildlife Branch, unpublished data) from the data.

2.2.4 Climate Data

The PDO is a measure of climatic variability in the north Pacific region characterized by shifts between warm and cool phases on an interdecadal time scale (Mantua *et al.* 1997; Mantua & Hare 2002). It is measured as the leading principal component of monthly sea surface temperatures (SST) in the north Pacific from 20°N poleward. Positive (warm phase) PDO values are characterized by cool SST in the central Pacific and warm SST along coastal areas. The PDO is related to sea level pressure (SLP) such that warm phase PDO values (i.e. cool SST) generally coincide with below average north Pacific SLP (Stenseth *et al.* 2003). The PDO is also related to terrestrial weather patterns (Mantua *et al.* 1997; Papineau 2001) and ecological processes such as forest fires (Duffy *et al.* 2005) in western North America. The PDO likely also influences population dynamics in other vertebrate taxa in the Yukon (Hik & Carey 2000; Morrison & Hik 2007).

We used summarized PDO values (data available at http://jisao.washington.edu/pdo) in seasons with biological significance for caribou recruitment: Winter (November to April), Summer (June to August), Fall (September to November), and Spring (March to May) or calving (April, May, and June). We used four time windows from March through June, representing the springtime/calving seasons, as each could have a different mechanistic effect on caribou. March to May (early Spring) PDO values represent conditions of the three months immediately preceding calving when most fetal mass is deposited in utero (Barboza & Parker 2006). April represents conditions immediately prior to calving. May climate summarizes conditions during peak calving season (mid to late May; Yukon Fish and Wildlife Branch, unpublished data) and June represents conditions for lactation when the need for highly nutritious forage is strong.

In the Yukon, the PDO is positively correlated with mean air temperature across all seasons (Table 2.A-1). Winter-PDO is negatively correlated with total precipitation (Table 2.A-1), and there is a negative relationship between both springtime and Winter-PDO and the Julian date of the first snow-free day of the year (Morrison & Hik 2007, Table 2.A-2) and snow depth (Table 2.A-3). The relationship between Summer- and Fall-PDO and precipitation is generally weak (Table 2.A-1).

2.2.5 Statistical Analysis

We used generalized linear mixed-effects models (GLMM; Skrondal & Rabe-Hesketh 2004; Gelman & Hill 2007) with a binomial distribution and logit link function to model recruitment (calf:cow ratio) as a function of seasonal PDO, and other covariates. Since female caribou typically do not produce twins, limiting the response to the unit scale (0, 1) was deemed appropriate. We included "Herd" and "Year" as crossed (i.e. non-hierarchical) random effects. We treated them as random effects because we assumed they contained unobserved heterogeneity we could not model and to account for pseudo-replication. Further, one of our aims was to estimate a global (i.e. population-averaged or marginal) model of the effect of PDO on recruitment which could be used to generalize beyond these years and herds (Skrondal & Rabe-Hesketh 2004), and our data were unbalanced across herds and years which could bias parameter estimates (Gillies *et al.* 2006). We included a "Trend" variable to account for possible long-term trend in recruitment which could potentially mask a climate effect. The effects of seasonal PDO and Trend were modeled as random coefficients varying among herds because we could not assume a constant effect across all herds. Since binomial count data, such as used here, often contain extra-binomial variation (i.e. are overdispersed) which may bias precision estimates (Gelman & Hill 2007), we fitted models using a quasi-GLMM approach whereby this extra variation (ϕ), or dispersion parameter, was also modeled. We used the package 'lme4' (Bates & Maechler 2009) in the statistical program R 2.9.1 (R Development Core Team 2009).

We compared models using a quasi-Akaike information criterion (QAIC) adjusted for small sample sizes (QAIC*c*; Burnham & Anderson 2002). Within the candidate set, the model with the lowest QAIC*c* was selected as best, with models having ΔQAIC*c* < 2 compared to the best model interpreted as having strong support (Burnham & Anderson 2002). A current challenge for model selection among competing random-effects models is the calculation of degrees of freedom (df). For any random effect (e.g. year), the number of effective parameters may range between 1 and N-1, where N is the number of levels within the random effect (Bolker *et al.* 2009). As our level of inference was not focused on the specific herds or years, per se, we counted one df for each fixed-effect, one for each random coefficient and intercept, and one for ø (Vaida & Blanchard 2005).

While our objective was not to estimate the effect of wolf control on recruitment per se, accounting for its effect was necessary in order to adequately separate climatic effects from recruitment changes due to reduced wolf numbers. A description of how this effect was modeled is provided in Appendix 2B. Following the identification of models to account for wolf control, we specified models including single- and multi-season PDO variables (seasons identified in Table 2.1). Correlated seasons ($r > 0.6$; Table 2.A-6) were not specified in the same model. For models including PDO values from >1 season, springtime (calving season) was represented by the season/month (Spring, April, May or June) having the lowest QAIC*c* among these four single-season models.

2.3 Results

The effect of wolf removal was represented by a constant effect during the years of active removal for the Treatment herds (Aishihik and Finlayson) followed by a five-year declining effect (Table 2.A-4). For the Adjacent herds (Burwash and Klaza), a two-year lag followed by a constant effect during the remaining years of active removal (Table 2.A-5) best represented the wolf removal effect on recruitment. In years of active wolf removal the average increase in recruitment rate for the treatment and adjacent herds was 0.20 and 0.11, respectively.

Of the candidate models, the most supported model included Winter- and May-PDO (Table 2.2), supporting H1. Coefficients for both climate variables were significant, with the effect size of Winter-PDO ($\beta = 0.110$, SE = 0.007) being substantially greater than that for May-PDO ($\beta = 0.013$, SE = 0.006) (Table 2.3).

Standardized estimates were calculated, on the scale of two standard deviation units (Gelman 2008), to allow for easier comparison between them and were 0.171 and 0.024 for Winter- and May-PDO respectively. Recruitment rose with increasing Winter- and May-PDO, corresponding to increasing temperature and decreasing precipitation during these periods (Tables 2.A-1 to 2.A-3). The most supported model also indicated a declining trend in recruitment ($\beta = -0.023$, SE = 0.001).

The estimated dispersion parameter ($\o$) was 0.045 for the top model in Table 2.2, indicating underdispersion. This underdispersion may be due to increased variability in the data being modeled through the random components of the model. For example, $\o$ estimated from the data in the absence of any random effects, but with the same fixed effects as the top model, was 17.011. This indicates that in the absence of these random effects accounting for unobserved heterogeneity, substantial overdispersion was present. There is a lack of consensus on whether or not QAIC*c* should be used in the presence of underdispersion (Cooch & White 2009). Model rankings were insensitive to the use of either AIC*c* or QAIC*c* and thus we report only AIC*c* (Table 2.2). For comparison, results for the top model fitted without adjusting for underdispersion are provided in Table 2.A-7. Coefficients were unchanged; however standard errors and deviations of the fixed and random effects, respectively, were increased by a factor of $\o^{-1}$.

There was considerable variability in the herd-specific responses to both Winter- and May-PDO (Fig. 2.3, Table 2.A-8) and Trend (Table 2.A-8). In all cases a random-coefficient model was more supported than only a random-intercept model. For comparison, ΔAIC*c* of the Winter- and May-PDO model without random coefficients was 384, and the most supported model with no random coefficients included Winter_{t-1}- and Fall_{t-1}-PDO and had ΔAIC*c* = 379. Residuals were assessed using a Shapiro-Wilk test and were normally distributed when pooled across Herd and Year ($W = 0.99$, $P = 0.50$). When assessed by Herd and Year individually, residuals were normally distributed for all levels with the exception of 1993 ($W = 0.78$, $P = 0.01$). We also assessed residuals, by Herd, for any remaining autocorrelation not accounted for in the model structure. There was indication of remaining autocorrelation for the Tatchun herd [$AR(1) = -0.51$, $P = 0.024$].

The model fit the pooled data well (Fig. 2.4), with predicted and observed recruitment rates highly correlated ($r = 0.86$, $P < 0.001$). The degree of model fit varied by herd (Fig. 2.5) and the correlation between predicted and observed recruitment ranged from $r = 0.97$ to $r = 0.07$. Generally, model fit was adequate for all herds except Tatchun and Wolf Lake.

From the most supported model (Table 2.3), we compared predicted to observed recruitment from an external dataset of 13 recruitment rates estimated on eight herds (two of which were not included in the training dataset) over six years (one of which was not included in the training dataset). The mean percent error of predicted recruitment values was 15.7% (Fig. 2.6). The two herds not included in the training dataset, Nahanni and Coal River (Weaver 2008), are both distributed along the eastern Yukon border with the Northwest Territories and are located directly east and southeast of the Finlayson herd (Fig. 2.1) respectively.

2.4 Discussion

Recruitment is a valuable indicator of population productivity as it represents the joint contribution of fecundity and calf survival. It is the most variable parameter in ungulate populations and thus a key factor influencing observed variation in population growth rates (Gaillard, Festa-Bianchet & Yoccoz 1998). We have provided a comprehensive analysis, in terms of numbers of populations and years, on the influence of large-scale climate on recruitment in a predator-limited large herbivore. Our work also adds to the sparse body of literature on the effects of Pacific-based climate on large herbivore population dynamics.

Seasonal climate affecting environmental conditions at calving (see Table 2.1) were much more supported than those affecting fecundity (i.e. pre-conception) in mountain-dwelling caribou in the Yukon (Table 2.2), supporting H1. Recruitment was positively related to both Winter- and May-PDO. There was weak support for H2, that seasonal climate affected fecundity in these populations. Higher Winter- and May-PDO represents decreased precipitation and increased temperature through the winter and May respectively, a reduced snowpack at calving, and an earlier onset of the first snowfree day of the year.

Consistent with the view that wolf predation plays a major role on recruitment in these populations there was a marked effect (Table 2.3) of the wolf removal programs as earlier reported (Hayes *et al.* 2003). There was a strong, and spatially variable, relationship between the PDO and local environmental conditions (e.g. snow depth). Wang *et al.* (2009) reported that density dependence was weak for northern ungulates coexisting with large carnivores. Our results confirm that in these relatively small populations with intact predator communities, top-down forces play a greater role on recruitment than bottom-up factors. Prevailing weather conditions such as snow depth are known to influence predation rates on neonatal ungulates (Bergerud & Page 1987; Adams *et al.* 1995b). Winter-PDO was negatively related to both the amount of snowfall in the spring (Table 2.A-3) and the first snow-free day of the year (Table 2.A-2). Both of these environmental factors could influence the degree of predation on newborn caribou calves by limiting the ability of parturient caribou to move away from predators and other calving females (Bergerud & Page 1987), and possibly on the ability of post-parturient caribou and their calves to move away from calving locations (Gustine *et al.* 2006). Skogland (1991) commented that the spatial relationship between predator and prey may be a large factor affecting predator-prey dynamics. The inability of parturient caribou to move away from predators due to environmental conditions at calving, following a low Winter-PDO, supports this assertion. Given this strong mechanistic link between snow depth at calving and neonatal calf survival, the strong effect of Winter-PDO was expected.

The effect of climate at calving (May-PDO), while smaller than for winter (Table 2.3), was nevertheless sufficiently influential to be present in the most highly supported model (Table 2.2). One would anticipate climate at calving to influence calf survival given the high degree of mortality shortly after birth. Indeed, an extremely warm spring (high PDO) could negate the effect of a high winter snowfall, or a very poor spring (e.g. heavy spring snowfall) could result in higher calf mortality regardless of in utero winter conditions. Thus, extreme springtime climate (above or below average) may be influencing recruitment in these herds where extremely warm and dry springs result in a reduced snowpack and earlier snowmelt, thus reducing predation rates on neonates. Conversely, a strongly below average spring characterized lower temperatures and/or increased precipitation in the form of snow, may limit parturient female's movements to safe calving grounds. Extremely poor weather at calving (e.g. cold and wet) may also have a direct influence on neonate survival (Gauthier & Theberge 1986). Extreme climate events are influential in the population dynamics of numerous species (Parmesan, Root & Willig 2000). For example, an extreme icing event in winter coated forage with thick layer of ice and resulted in the 80% decline of a reindeer population on Svalbard (Chan *et al.* 2005).

The positive effect of the PDO on caribou recruitment in the Yukon is consistent with Hebblewhite's (2005) finding of a negative effect of the North Pacific Oscillation (NP) on elk population growth rates in Alberta, Canada, given the negative relationship between the PDO and NP (Yang *et al.* 2005). Hebblewhite (2005) also reported variability across populations in their growth rate response to the NP. Elk density and the NP were more influential when wolves were rare, while predation and its interaction with the NP became more influential when wolf numbers were greater. We regarded our index of a wolf removal effect on recruitment as too coarse, and the absence of wolf population data across herds insufficient to warrant inclusion of wolf abundance as an interaction with the PDO.

Calf body mass in ungulates is related to climate (Weladji & Holand 2003; Adams 2005), maternal condition during gestation (Thorne, Dean & Hepworth 1978; Keech *et al.* 2000), and maternal body mass at breeding (Kojola 1993; Adams 2005). Subsequent calf development is also related to pre-parturition conditions (Kojola 1993; Adams 2003). Lighter-born calves and those with reduced growth and developmental capabilities early in life may be subject to increased mortality from birth throughout the summer (Guiness, Clutton-Brock & Albon 1978; Mech, Nelson & McRoberts1991). Winter-PDO and winter snowfall were positively and negatively correlated, respectively, with average annual birth mass of Denali calves (from Adams 2005; Fig. 2.7). Thus, winter climate may affect calf survival throughout the first summer of life, in addition to early mortality due to predation. Our index of recruitment measured during the fall could not separate mortality occurring during different periods after birth.

Since our results were only suggestive of an effect on calf survival, we related seasonal PDO to calf mortality over different time periods shortly after birth using mortality hazard rates from radio-collared neonates in Denali (from Adams *et al.* 1995a, b). For comparative purposes, we included seasonal climate both pre- and post-conception. As expected (Table 2.1), climate affecting environmental conditions at calving (i.e. Winter-PDO, May-PDO) was negatively correlated with early calf mortality, while the relationship with mortality later through summer became weaker (Table 2.4). Conversely, seasonal climate affecting female condition at breeding (i.e. Winter-PDO$_{t-1}$, Summer-PDO$_{t-1}$, and Fall-PDO$_{t-1}$) was more strongly related to later calf mortality. While the correlation between pre-conception climate and later calf mortality was strong and significant for the Denali herd, these relationships, if present, were not influential enough to result in pre-conception climate being supported in our candidate models of Yukon caribou recruitment.

For both of the climate predictors there was considerable variability in their herd-specific effects on recruitment (Fig. 2.3, Table 2.A-8). This variability is consistent with Martínez-Jauregui *et al.* (2009) who found a lack of a general climatic effect on red deer weights across Europe. While the average effects of Winter- and May-PDO were positive and significant in our model, local characteristics of individual herds and their ranges (e.g. terrain features, latitude) may result in the downscaled effect of the PDO resulting in different localized weather conditions (Mysterud *et al.* 2000; Pettorelli *et al.* 2005). The spatial variability in the correlation between local weather and large-scale climate (Tables 2.A-1, 2.A-3), such as the PDO, may also lead to variability in its effect on herd population parameters (Ginnett & Young 2000). Additionally, intrinsic characteristics of these herds may also affect the role of climate on recruitment. For example, the effect of climate may be more pronounced at higher population density (Wilmers *et al.* 2006), and may affect age classes differentially (Coulson *et al.* 2001). Information on age-structure for the herds considered here was unavailable. However, herds with greater proportions of young and/or older females may be expected to respond to winter climate more strongly as smaller (e.g. younger) females or those with reduced body conditions (e.g. senescent animals) may not be able to fully carry a calf to term under more severe winter weather.

Given the strong effect of predation on recruitment in these herds, predator and alternate prey density may also play an important role in influencing the effect of climate. Wolf numbers may also be influenced by climate indirectly through the direct influence on their prey base (Post & Forchhammer 2001). This may result in a lag effect as wolves numerically respond to changes in prey density (Fuller, Mech & Cochrane 2003). In systems where moose and caribou coexist with wolves, and other predators, caribou are often a secondary prey species with wolf density being most strongly affected by moose density (Seip 1992). Thus, climate effects on moose may also play a large part in predation rates on caribou, heightening the complexity by which climate affects wolf populations and hence caribou numbers. Further, climate may affect wolves behaviorally by altering characteristics such as pack size which in turn may increase predation rates (Post *et al.* 1999). Incorporating annual variability in predator and/or alternate prey density across herds could strengthen our understanding of climate's effect on recruitment. The influence of calving season climate may also best be understood in terms of its interaction with predator density, since it is environmental conditions at calving that can have a strong influence on predation rates. Hence, a multiplicative rather than additive effect of calving season climate may be warranted. Predator data were unavailable for the majority of years and herds considered here, precluding the incorporation of such an interactive effect in this study.

Overall, our model fit the pooled and herd-specific data well (Fig. 2.4, 2.5). However, two herds, Tatchun and Wolf Lake, were poorly fitted. These herds had the fewest data points among all the herds considered (Fig. 2.2) which could have affected their modeled relationship with the PDO. The external data used to evaluate the model also indicated relatively good predictive ability (Fig. 2.6). As should be expected, since our model did not incorporate herd-specific characteristics, it generally predicted recruitment better for those herds included in model training (e.g. Finlayson, Aishihik). The incorporation of herd-specific variables may enhance our understanding of the environment-climate mechanisms (e.g. Pettorelli *et al.* 2005) shaping recruitment patterns.

Our goal was not to compare the PDO with local weather variables in their ability to explain recruitment patterns. Indeed, given the remoteness of some of the herds used in this analysis, weather stations at relevant locations were not available. This fact demonstrates the utility of using large-scale climate indices. Additionally, weather variables measured at one location may not be relevant for a highly mobile species such as caribou (Stenseth & Mysterud 2005). Elsewhere in a direct comparison of local weather and the PDO, the PDO proved to be a more highly supported predictor of caribou population parameters than local weather (Hegel *et al.* In Press). Rather, our goal was to compare the effect of different seasons on recruitment in these herds using the PDO to facilitate that comparison. We acknowledge that there are limitations in using a large-scale climate index across seasons. For example, the relationship between the PDO and local weather may not be consistent across seasons. In the Yukon, the PDO-local weather relationship appears strongest during winter and spring, with a weaker relationship in summer, thus reducing our power to detect a relationship between the PDO and recruitment at this time. However, this would not have affected our ability to detect a difference between in utero winter climate (Winter-PDO) and pre-conception winter climate (Winter_{t-1}-PDO). The PDO may also not be related to a specific local weather variable important to recruitment. However, this issue is present in any observational study in that the proper variable(s) must be selected for analysis. Finally, the PDO-local weather relationship may also vary spatially. Such a spatially varying relationship could confound a general relationship between the PDO and recruitment, however, the inclusion of random-coefficients across herds would aid in accounting for this spatial variability.

This is one of the first studies to explicitly examine the influence of the PDO on large herbivore populations. Hik & Carey (2000) reported an oscillatory pattern of horn growth in Dall sheep rams with a suggested relationship to the PDO. In northern Yukon and Alaska, phase-shifts in the PDO was suggested as a factor influencing changing trends in population growth of the Porcupine caribou herd (Griffith *et al.* 2002). A phase-shift of the Winter-PDO from -1.5 to +1.5, for example, would result in an average increase in recruitment of approximately 25% in Yukon mountain caribou. The PDO has previously been shown to be a factor in the population dynamics of, for example, Pacific salmon (*Oncorhynchus* spp.; Mantua *et al.* 1997), songbirds (Ballard *et al.* 2003), and small herbivores (*Ochotona collaris* Nelson; Morrison & Hik 2007). At broader scales the PDO influences freshwater (Winder & Schindler 2004), marine (Field, Francis & Aydin 2006), and terrestrial (Loik *et al.* 2004) ecosystem dynamics.

Recent future climate scenarios indicate that while temperatures are expected to increase over the next century across the Yukon, precipitation will also rise, as will the frequency of extreme climatic events (Carter *et al.* 2007) such as rain-on-snow icing events, which can have a substantial negative effect on ungulate populations (Chan *et al.* 2005; Helle & Kojola 2008). Climate projection models suggest increases in winter precipitation in the Yukon ranging from approximately 5 to +30% (Canadian Climate Change Scenarios Network: www.cccsn.ca). Increases in snowfall of this magnitude could have significant impacts on recruitment; however, given an increase in temperature both in spring and fall it is uncertain how this would affect the length of the summer growing season. Further, in multi-predator multi-prey systems such as the Yukon, the interactions across trophic levels (Post & Forchhammer 2001) coupled with individual species' responses to changes in climatic conditions are complex and difficult to predict (Stenseth *et al.* 2002; Walther *et al.* 2002).

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Table 2.1. Potential mechanisms relating seasonal climate to fall recruitment in northern mountain-dwelling caribou through effects on a) fecundity and b) calf survival. The subscript *t*-1 indicates a pre-conception season. Variables without a subscript represent seasons post-conception. We treated fall climate during breeding as occurring prior to conception. Based on PDO – local weather relationships (see Tables 2.A-1 – 2.A-3) we expect the relationship between each season and recruitment to be non-negative.

Season[a]	Mechanism	Reference
a) Fecundity		
Winter$_{t-1}$	Harsh conditions in the winter prior to conception may result in females being in sufficiently poor condition that they may be unable to regain adequate body mass to reproduce the subsequent year.	Adams & Dale (1998)
Summer$_{t-1}$ Fall$_{t-1}$	Fecundity is strongly related to female body condition at breeding. Poor forage conditions prior to breeding may limit successful reproduction by females unable to obtain sufficient resources during summer and fall.	Cameron *et al.* (1993); Crête & Hout (1993); Cook *et al.* (2001, 2004)
b) Calf survival		
Spring	Increased snow depth due to either cool temperatures and/or spring snowfall may prevent parturient females from moving up in elevation (i.e. dispersing) to calving sites away from predators.	Bergerud & Elliot (1986); Bergerud & Page (1987)
April May June	Climatic conditions leading to poorer forage quality and/or quantity can result in reduced calf development and survival. Nutritional requirements at this time are high as it is the period of peak lactation.	Albon, Guinness & Clutton-Brock (1983); Griffith *et al.* (2002); Pettorelli *et al.* (2005, 2007)
Summer	Temperature may influence insect harassment levels thus affecting energetic demands, through avoidance behavior, and subsequently calf growth and survival.	Helle & Tarvainen (1984)
	Climatic effects on summer forage conditions may influence calf growth and development.	Reimers, Klein & Sørumgård (1983); Crête & Hout (1993); Lenart *et al.* (2002)
Winter	Calf birth mass and development negatively related to winter severity during gestation.	Adams *et al.* (1995a); Adams (2003, 2005)
	Increased snowfall that persists late into the spring may prevent parturient females from moving up in elevation away from predators.	Bergerud & Elliot (1986); Bergerud & Page (1987); Adams *et al.* (1995a,b)
Winter$_{t-1}$ Fall$_{t-1}$ Summer$_{t-1}$	Calf birth mass positively correlated to maternal mass at breeding, which is subsequently influenced by climatic conditions prior to conception (see above).	Reimers *et al.* (1983); Adams (2005)

a: Seasons defined in the text (see Methods).

Table 2.2. Models of the effect of seasonal PDO on calf recruitment (*n* = 165). Models include the seasonal PDO values modeled as random coefficients, trend, two variables representing the effects of wolf removal (see Table 2.A-5), and random intercepts for both Herd and Year. A null model with no PDO variables is included for comparative purposes.

Number	Model	Log-Likelihood	K^a	AICc	ΔAIC*c*
1	Winter + May	-487.6	11	998.93	0.00
2	Summer + Winter	-506.3	11	1036.33	37.40
3	May + Winter$_{t-1}$	-520.0	11	1063.73	64.80
4	Summer + Winter$_{t-1}$	-522.1	11	1067.93	69.00
5	Winter + Winter$_{t-1}$	-524.6	11	1072.93	74.00
6	Fall$_{t-1}$ + May	-528.0	11	1079.73	80.80
7	Summer$_{t-1}$ + May	-530.1	11	1083.93	85.00
8	Summer$_{t-1}$ + Summer	-531.3	11	1086.33	87.40
9	Summer + Fall$_{t-1}$	-531.5	11	1086.73	87.80
10	Summer	-538.6	9	1096.36	97.44
11	May	-539.0	9	1097.16	98.24
12	Winter	-546.4	9	1111.96	113.04
13	June	-547.8	9	1114.76	115.84
14	Fall$_{t-1}$ + Winter$_{t-1}$	-546.5	11	1116.73	117.80
15	Summer$_{t-1}$ + Winter$_{t-1}$	-549.0	11	1121.73	122.80
16	April	-554.5	9	1128.16	129.24
17	Spring	-556.4	9	1131.96	133.04
18	Winter$_{t-1}$	-556.9	9	1132.96	134.04
19	Fall$_{t-1}$	-565.4	9	1149.96	151.04
20	Summer$_{t-1}$	-566.2	9	1151.56	152.64
21	Null	-574.1	7	1162.91	163.99

a: Number of estimated parameters.

Table 2.3. Parameter estimates (logit scale) and standard errors for the top-ranked model (Table 2.2) relating seasonal PDO and wolf control effects on recruitment.

Variable	Parameter	SE
Winter-PDO	0.110	0.007
May-PDO	0.013	0.006
Trend	-0.023	0.001
Treatment	0.824	0.003
Adjacent	0.489	0.006
Constant	-0.742	0.019
σ^a (Winter-PDO Random Coefficient)	0.012	
σ (May-PDO Random Coefficient)	0.011	
σ (Trend Random Coefficient)	0.002	
σ (Year Random Intercept)	0.019	
σ (Herd Random Intercept)	0.053	
$\emptyset^b$	0.045	

a: Standard deviation; b: Dispersion parameter.

Table 2.4. Correlation between seasonal PDO and mortality hazard rate[a] over various ages and time periods for caribou calves in Denali National Park, Alaska (1984 – 1991).

	Mortality time period			
Season	Birth to 15 days[b]	Birth to 30 days[b]	Birth to 120 days[c]	30 to 120 days[c]
Winter-PDO	**-0.90**[d]	**-0.80**	-0.81	-0.78
Winter-PDO$_{t-1}$	-0.58	**-0.86**	**-0.92**	**-0.91**
Summer-PDO$_{t-1}$	-0.65	-0.56	-0.69	-0.69
Fall-PDO$_{t-1}$	**-0.71**	-0.68	-0.80	-0.79
May-PDO	**-0.91**	**-0.77**	-0.86	-0.84
Years of Data	8	7	5	5

a: Mortality hazard rates were calculated as $-\log_e(S)$, where S is the percentage of calves alive at the beginning of the time period surviving to its end. Hazard rates were used instead of S as they make the correlations invariant of the time units; b: Source – Adams *et al.* (1995a, b); c: Source – Adams *et al.* (1995a); d: Significant correlations ($P < 0.05$) are bolded.

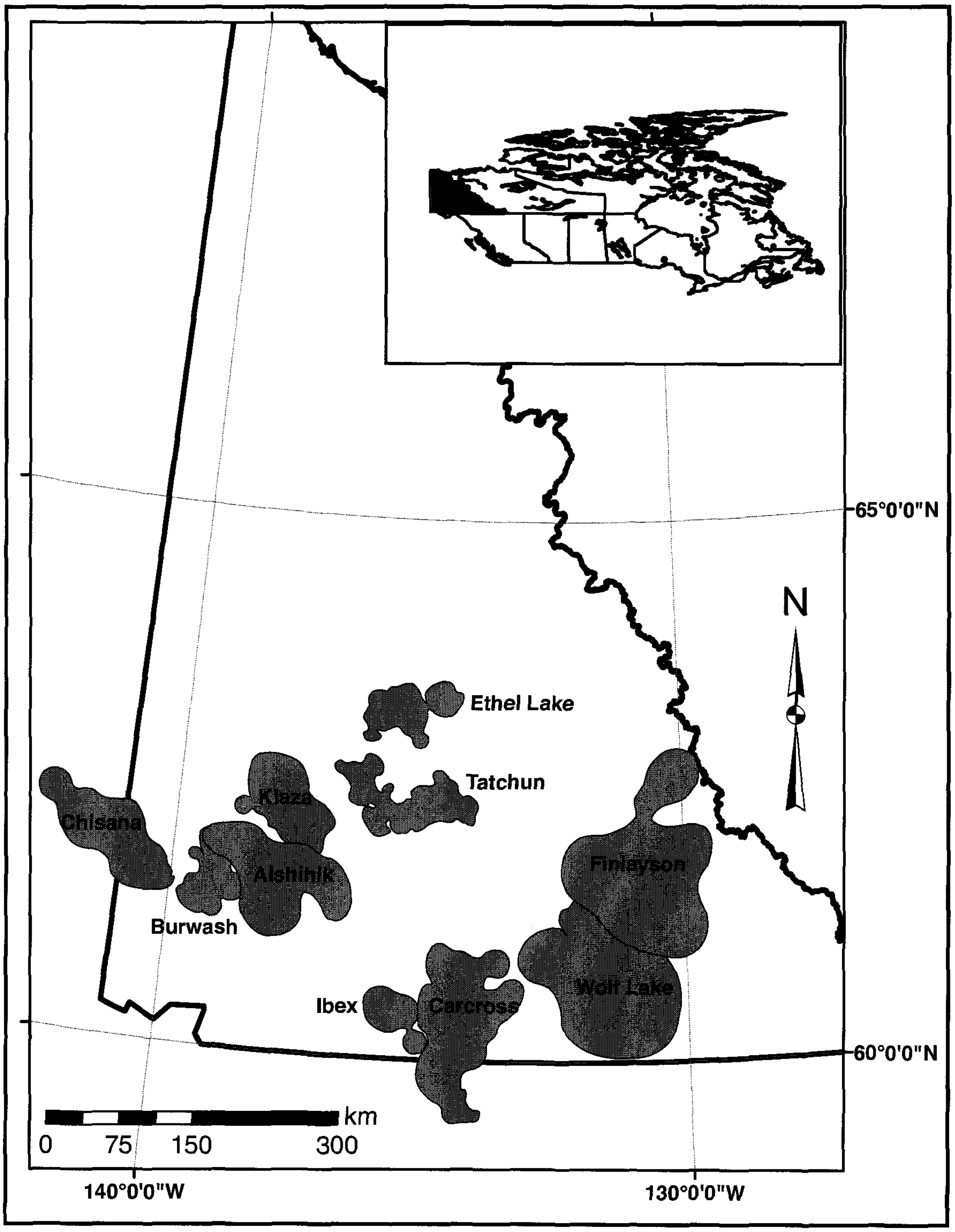

Figure 2.1. Locations of ten mountain-dwelling woodland caribou herds in the Yukon Territory, Canada, in which seasonal effects of the PDO on calf recruitment were assessed.

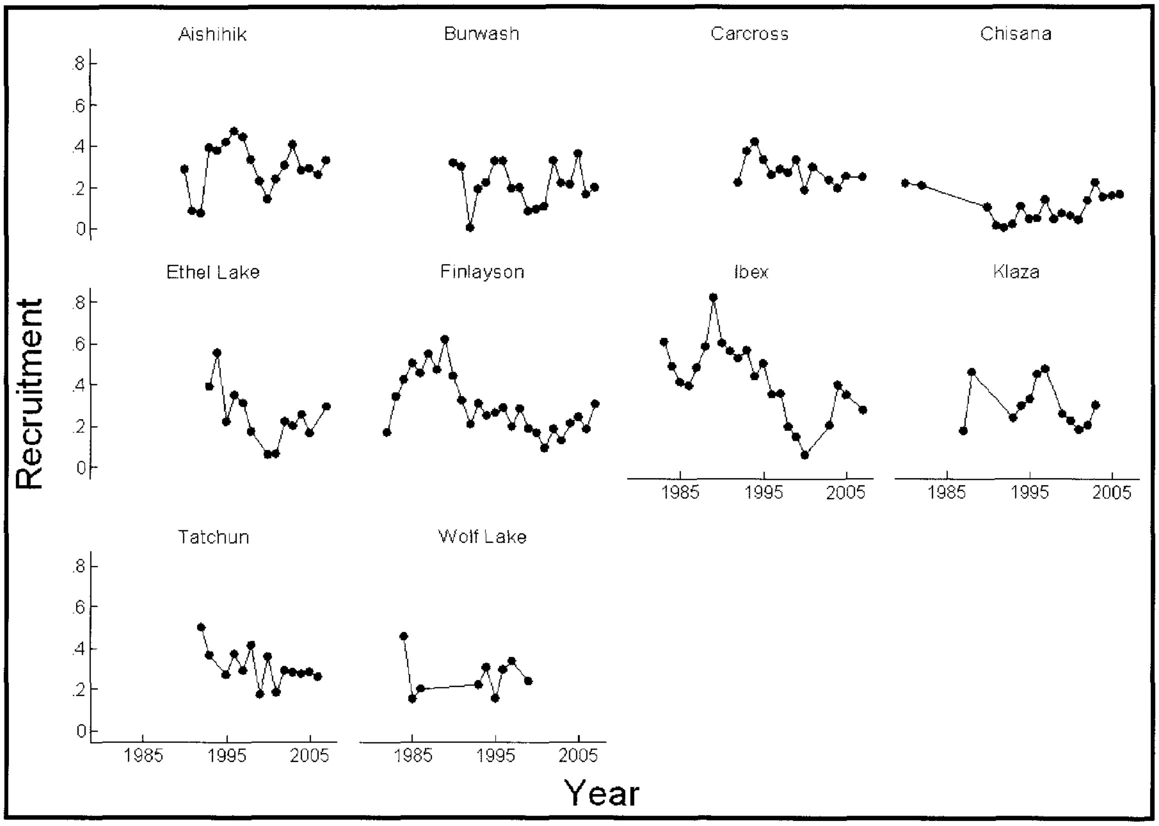

Figure 2.2. Annual recruitment rates (calf:cow ratio) for ten mountain-dwelling caribou herds in the Yukon Territory, Canada (1980-2007).

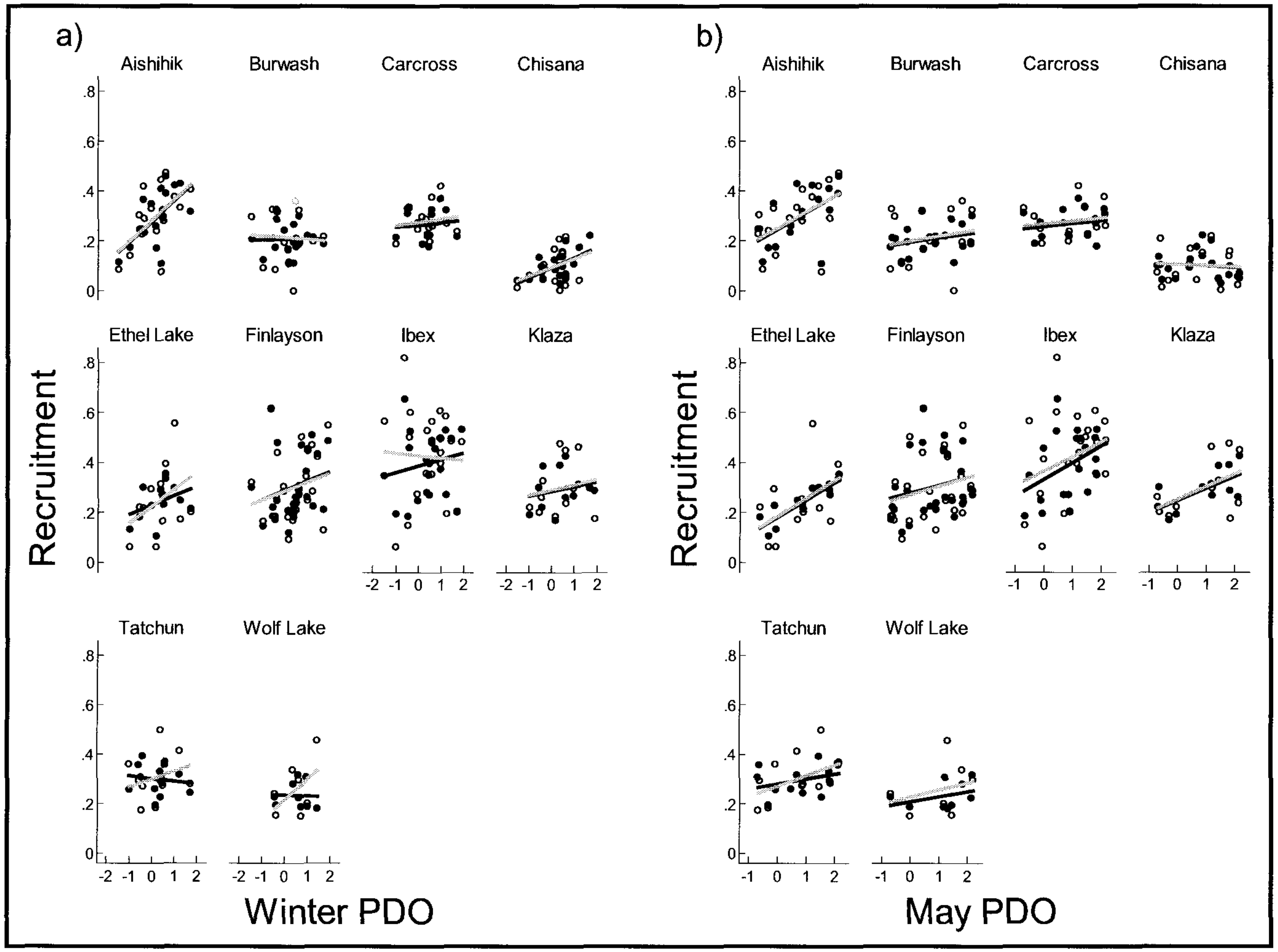

Figure 2.3. Relationship between recruitment (calf:cow ratio) and a) Winter-PDO and b) May-PDO. Black circles represent observed recruitment rates while open circles indicate model predictions of recruitment. Black and grey lines represent lines of best fit for observed and predicted recruitment respectively.

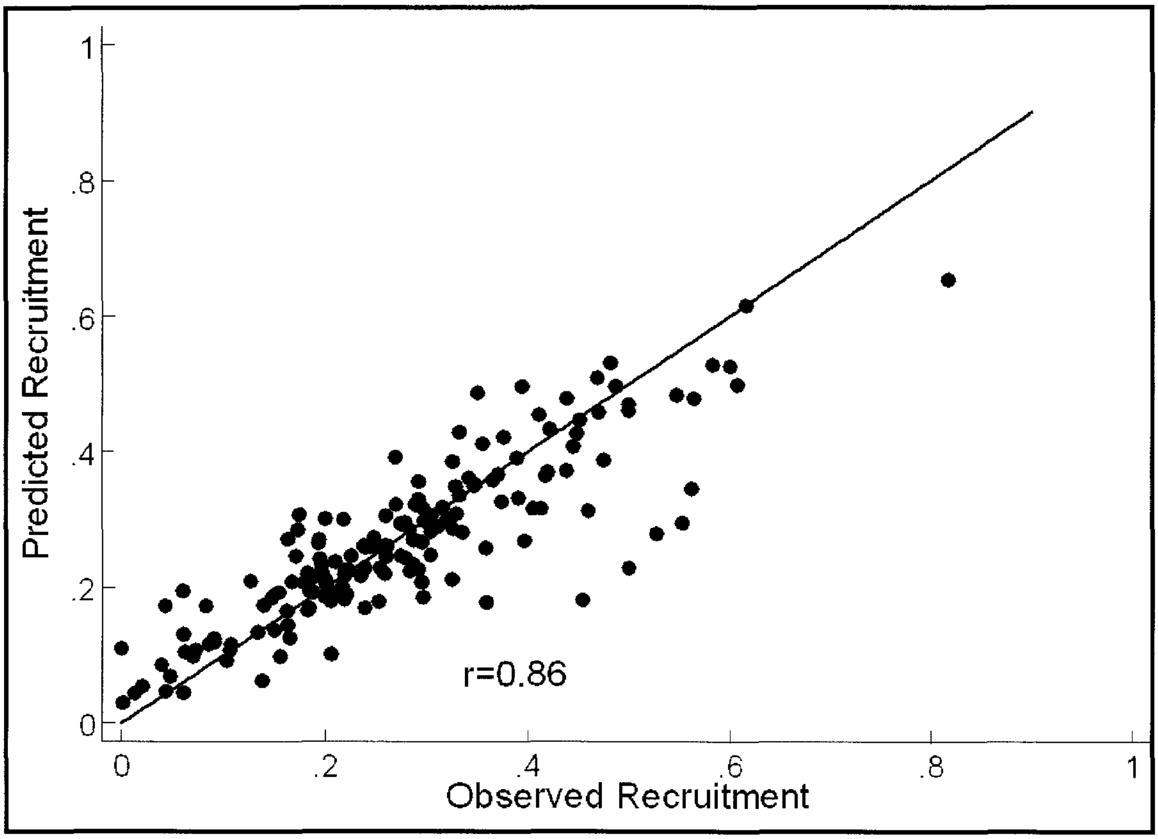

Figure 2.4. Relationship between observed and predicted recruitment rates pooled across all herds and years (*r* = 0.86, *P* < 0.001). The diagonal line represents perfect correlation (*r* = 1.0).

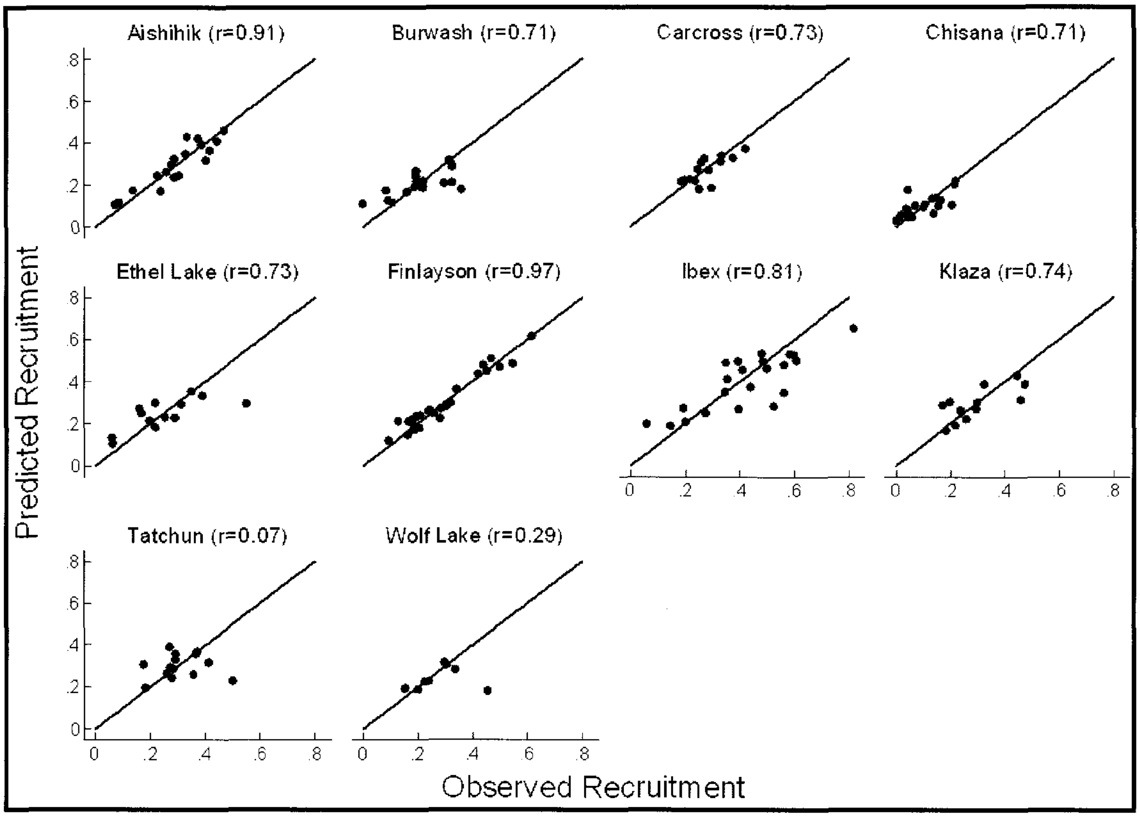

Figure 2.5. Relationship between observed and predicted recruitment rates by herd. All correlations reported are significant (*P* < 0.05) except for Tatchun (*P* = 0.82) and Wolf Lake (*P* = 0.45). The diagonal lines represent perfect correlation (*r* = 1.0).

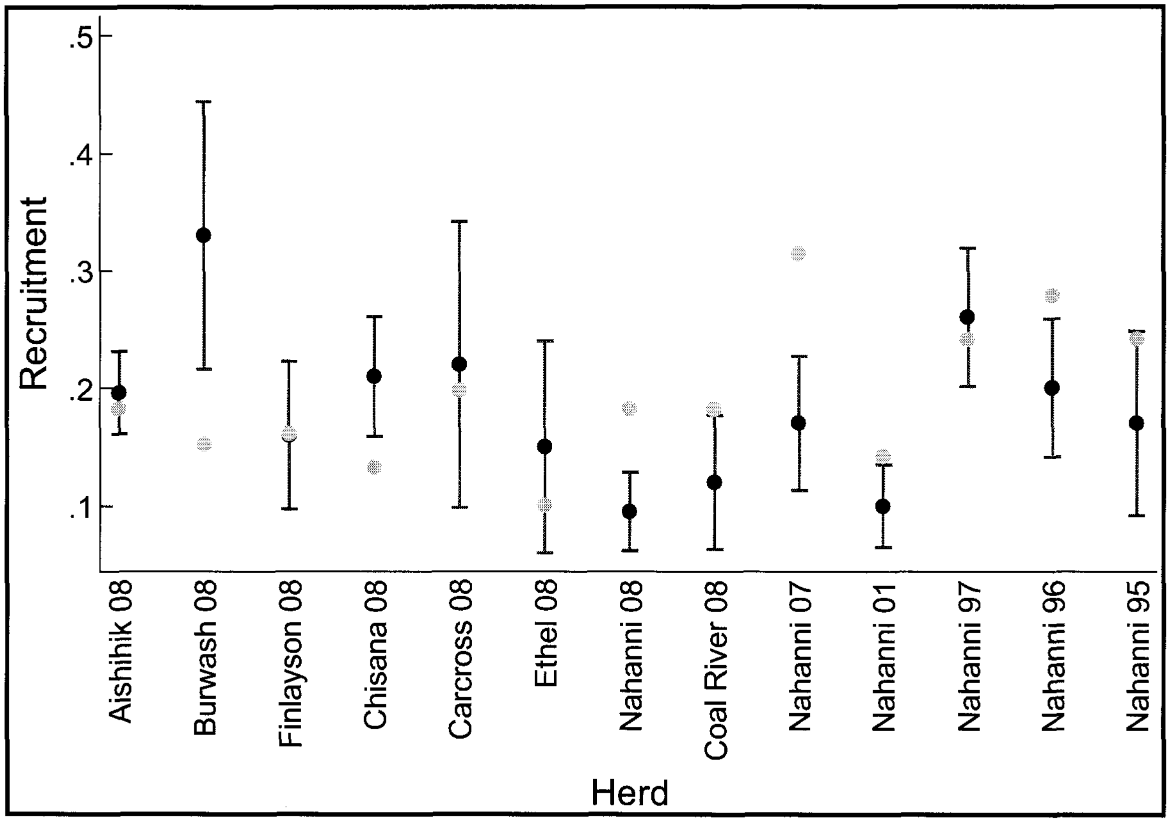

Figure 2.6. Predicted (grey circles) and observed (black circles) for 13 additional recruitment rates of mountain dwelling caribou in the Yukon Territory. Error bars represent 95% confidence intervals of the observed rates. Herd names are noted on the x-axis and are followed by the year of the recruitment estimate.

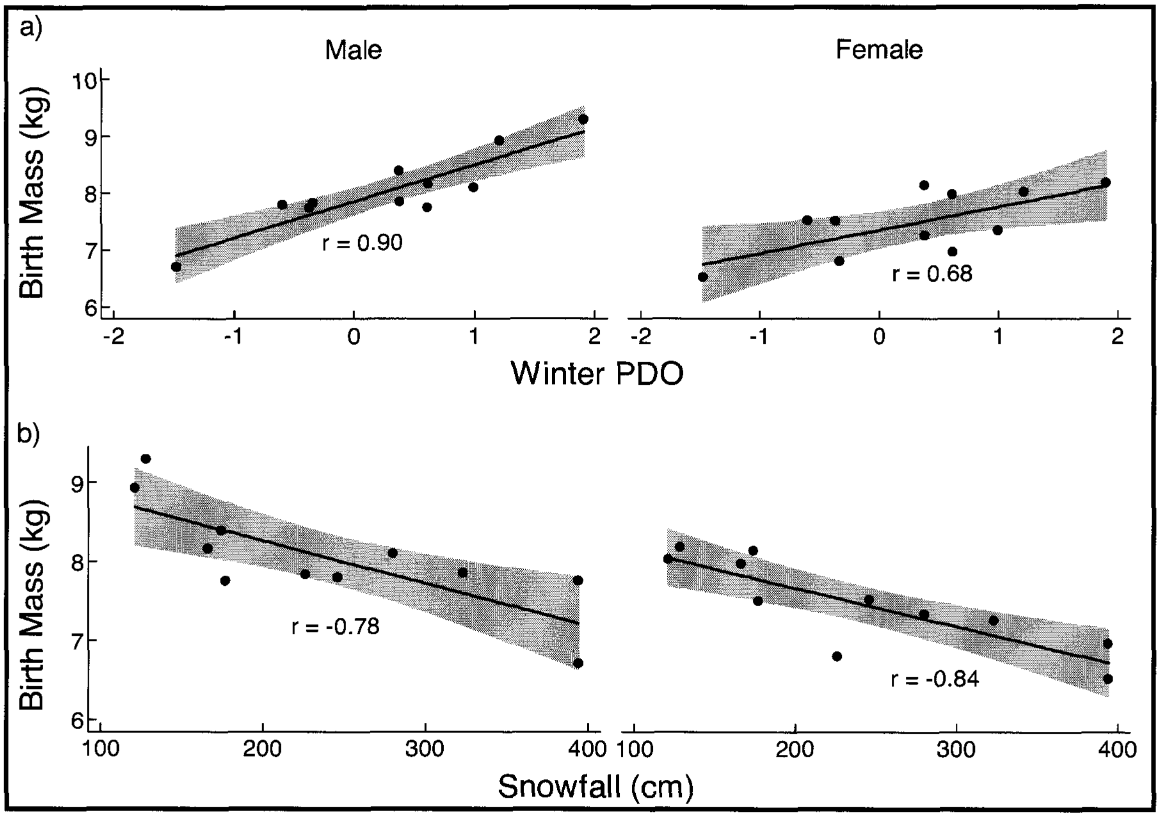

Figure 2.7. Relationship between average caribou calf birth mass by sex (1987 – 1997) from Denali National Park, Alaska (data from Adams 2005) and a) Winter-PDO and b) winter snowfall. Lines of best fit with 95% confidence intervals are shown. $P < 0.05$ for all reported correlations.

Appendix 2A. Chapter 2 Supplementary Tables

Table 2.A-1. Correlation between a) average temperature (°C) and b) precipitation (mm of water) and seasonal/monthly PDO from 8 weather stations (c) across the southern portion of the Yukon Territory, Canada (1980 - 2007). Weather data are available on-line from Environment Canada (www.climate.weatheroffice.ec.gc.ca).

	Weather Station							
	Anvil	Burwash	Dawson City	Faro	Haines Junction	Teslin	Watson Lake	Whitehorse
a) Temperature – PDO Correlation								
Fall	0.32	0.29	0.21	0.41	-0.74	0.27	0.25	0.10
Summer	-0.46	0.06	-0.03	-0.12	-0.55	-0.06	-0.08	-0.12
Winter	0.06	**0.50**[a]	0.35	0.14	-0.53	0.42	0.03	**0.43**
Spring	0.49	-0.12	0.20	0.36	-0.35	-0.25	0.06	0.27
April	-0.46	0.03	0.06	-0.04	0.40	0.11	0.11	0.10
May	0.10	0.33	0.36	0.33	0.51	0.30	0.30	**0.45**
June	-0.74	-0.04	-0.25	-0.22	-0.38	-0.17	-0.17	0.12
b) Precipitation – PDO Correlation								
Fall	0.30	-0.05	-0.06	-0.20	-0.04	0.24	0	-0.04
Summer	0.51	-0.01	0.09	0.23	-0.52	-0.17	0.09	0.01
Winter	-0.23	-0.29	-0.07	-0.34	0.09	0	0.08	-0.18
Spring	-0.60	-0.07	0	0.24	**-0.77**	-0.27	0.02	0.01
April	-0.07	0.12	0.13	0.03	**-0.93**	0.28	-0.10	0.02
May[b]	-0.18	0.15	-0.-6	0.19	-0.29	-0.05	-0.01	-0.16
	(-0.34)	(0.17)	(-0.03)	(0.14)	(0.32)	(-0.15)	(0.01)	(-0.13)
June	0.50	-0.32	0.37	0.09	0.45	0.18	0.15	0.20
c) Station Details								
Number of Years	8	26	26	26	11	20	26	25
Latitude	62°37'	61°22'	64°2'	62°12'	60°46'	60°10'	60°7'	60°42'
Longitude	133°38'	139°3'	139°7'	133°22'	137°34'	132°44'	128°50'	135°4'
Elevation (m a.s.l.)	1158	807	370	716	599	705	685	700

a: Significant correlations (*P* < 0.05) are bolded; b: Values in parentheses represent the correlation between PDO values and square-root transformed

Table 2.A-2. Correlation between the annual first snow-free day (measured as the Julian date) in the southwest Yukon Territory, Canada, (Morrison & Hik 2007) and Spring-, April-, May-, June-, and Winter-PDO values (1995-2001).

Season[a]/Month	*r*	*P*
Winter-PDO	-0.81	0.028
April-PDO	-0.74	0.060
May-PDO	-0.65	0.112
June-PDO	-0.60	0.155
Spring-PDO	-0.76	0.048

a: Seasons defined in the text (see Methods).

Table 2.A-3. Correlation between Winter-, Spring-, April-, and May-PDO values and snow depth (cm) data in the first week of a) March, b) April, and c) May from d) 15 snowcourse stations across the southern Yukon Territory and northern British Columbia, Canada (1980 – 2007). Data were provided by Environment Yukon (Water Resources Branch).

	Snowcourse Station														
	Aishihik	Atlin	Beaver	Finlayson	Hyland	MacIntosh	Meadow	Mt. Berdoe	Plata	Rackla	Summit	Tagish	Tintina	Watson	Whitehorse
a) Correlation With March Snow Depth (cm)															
Winter-PDO	-0.43	-0.27	**-0.51**[a]	-0.06	-0.21	**-0.41**	**-0.53**	-0.25	-0.01	-0.19	-0.26	-0.26	-0.19	-0.27	-0.37
Spring-PDO	-0.25	-0.18	**-0.45**	-0.08	-0.14	**-0.43**	**-0.47**	-0.22	0.12	0.08	-0.12	-0.12	-0.26	-0.29	-0.28
b) Correlation With April Snow Depth (cm)															
Winter-PDO	-0.48	-0.16	**-0.40**	-0.07	-0.21	**-0.45**	**-0.38**	-0.23	-0.04	-0.15	-0.31	-0.27	-0.27	-0.24	-0.37
Spring-PDO	-0.23	-0.12	**-0.41**	0.03	-0.08	**-0.40**	-0.36	-0.18	0.07	0.01	-0.17	-0.17	-0.26	-0.27	-0.22
April-PDO	-0.21	-0.11	**-0.48**	-0.04	-0.14	**-0.45**	**-0.41**	-0.25	-0.01	-0.05	-0.21	-0.21	-0.32	-0.30	-0.24
c) Correlation With May Snow Depth (cm)															
Winter-PDO	**-0.66**	0.12	0.05	-0.34	-0.19	-0.30	-0.15	-0.03	0.07	-0.06	-0.19	-0.07	-0.12	-0.21	-0.04
Spring-PDO	**-0.72**	-0.03	-0.16	-0.42	-0.21	**-0.43**	-0.17	-0.16	-0.05	0.09	-0.17	-0.14	-0.24	-0.21	-0.22
April-PDO	**-0.65**	0.01	-0.12	-0.37	-0.23	**-0.44**	-0.17	-0.19	-0.05	0.04	-0.17	-0.14	-0.24	-0.19	-0.20
May-PDO	**-0.60**	-0.15	-0.27	**-0.45**	-0.12	**-0.50**	-0.23	-0.32	-0.14	0.16	-0.24	-0.19	-0.33	-0.17	-0.33
d) Station Details															
Number of Years	14	28	28	21	28	28	28	28	28	19	28	28	27	28	28
Latitude	61°12'	59°34	62°25	61°42	61°31	61°43	60°35	62°2	63°31	64°17	60°51	60°17	61°5	60°7	60°42
Longitude	137°0'	133°2	140°5	130°4	128°1	137°2	133°5	136°1	132°3	133°1	137°4	134°1	131°1	128°5	135°4
Elevation (m a.s.l.)	945	730	655	988	855	1160	1235	1035	830	1040	1000	1080	1067	685	700

a: Significant correlations ($P < 0.05$) are bolded.

Table 2.A-4. Models representing the effect of wolf removal on calf recruitment on woodland caribou herds in the Yukon Territory, Canada, for herds in which wolf removal programs were directed (Aishihik and Finlayson herds). All models have 4 parameters (intercept, "Treatment" effect, year-level variance, herd-level variance). The "Treatment" coefficient represents the effect of wolf control on recruitment during the years of wolf removal and *k* years after removal ended, where *k* ranges from 1 to 6 and represents when the wolf control effect is not detected. ΔAIC*c* is also presented for ease of model comparison.

Model	Log-Likelihood	ΔAICc	"Treatment" coefficient (SE)
No effect after wolf removal ended (*k* = 1)	-1200.489	141.412	0.726 (0.053)
Declining effect for 1-year after wolf removal ended (*k* = 2)	-1183.060	106.554	0.762 (0.051)
Declining effect for 2-years after wolf removal ended (*k* = 3)	-1163.869	68.172	0.797 (0.049)
Declining effect for 3-years after wolf removal ended (*k* = 4)	-1151.719	43.872	0.806 (0.048)
Declining effect for 4-years after wolf removal ended (*k* = 5)	-1136.376	13.186	0.834 (0.047)
Declining effect for 5-years after wolf removal ended (*k* = 6)	-1129.783	0	0.848 (0.047)

Table 2.A-5. Models representing the effect of wolf removal on calf recruitment on woodland caribou herds in the Yukon Territory, Canada, for herds adjacent to those in which wolf removal programs were directed (Burwash and Klaza herds). All models have 5 parameters. In addition to those described in Table 2.A-4, the "Adjacent" coefficient represents the effect of wolf removal on recruitment in adjacent herds beginning *m* years after wolf removal began (lag effect), where *m* ranges from 0 to 4, and an effect from *k* = 1 to 6 years following cessation of wolf removal. ΔAIC*c* is also presented for ease of model comparison.

Model	Log-Likelihood	ΔAIC*c*	"Adjacent" coefficient (SE)
Effect during all wolf removal years (*m* = 0 , *k* = 1)	-1125.690	13.186	0.239 (0.083)
Effect 1-year after removal begins (*m* = 1 , *k* = 1)	-1122.023	5.852	0.348 (0.088)
Effect 2-years after removal begins (*m* = 2 , *k* = 1)[a]	-1119.097	0	0.441 (0.094)
Effect 3-years after removal begins (*m* = 3 , *k* = 1)	-1122.797	7.400	0.416 (0.110)
Effect 4-years after removal begins (*m* = 4 , *k* = 1)	-1127.568	16.942	0.328 (0.154)
Effect 2-years after removal begins and 1-year after control ends (*m* = 2 , *k* = 2)	-1119.657	1.120	0.430 (0.095)
Effect 2-years after removal begins and 2-years after control ends (*m* = 2 , *k* = 3)	-1120.753	3.312	0.407 (0.095)
Effect 2-years after removal begins and 3-years after control ends (*m* = 2 , *k* = 4)	-1120.611	3.028	0.415 (0.096)
Effect 2-years after removal begins and 4-years after control ends (*m* = 2 , *k* = 5)	-1120.245	2.296	0.427 (0.097)
Effect 2-years after removal begins and 5-years after control ends (*m* = 2 , *k* = 6)	-1120.517	2.840	0.427 (0.099)

a: This is the Null model (after adding a trend variable) reported in Table 2.2.

Table 2.A-6. Matrix of pairwise correlation coefficients between seasonal (monthly) PDO values (1980 – 2007).

	April-PDO	May-PDO	June-PDO	Spring-PDO	Summer-PDO	Summer-PDO$_{t-1}$	Winter-PDO	Winter-PDO$_{t-1}$	Fall-PDO$_{t-1}$
April-PDO	1	**0.86**[a]	**0.70**	**0.98**	**0.60**	**0.53**	**0.77**	0.08	**0.61**
May-PDO		1	**0.86**	**0.91**	**0.76**	**0.44**	**0.53**	0.05	**0.51**
June-PDO			1	**0.74**	**0.91**	**0.27**	**0.41**	0.03	**0.34**
Spring-PDO[b]				1	**0.63**	**0.51**	**0.75**	0.08	**0.62**
Summer-PDO					1	**0.18**	**0.37**	0.08	**0.36**
Summer-PDO$_{t-1}$						1	**0.58**	**0.39**	**0.79**
Winter-PDO							1	0.11	**0.82**
Winter-PDO$_{t-1}$								1	0.13
Fall-PDO$_{t-1}$									1

a: Significant correlations ($P < 0.05$) are bolded; b: Seasons defined in the text (see Methods).

Table 2.A-7. Parameter estimates (logit scale) and standard errors for the top-ranked model (Tables 2.2, 2.3) without adjustment for underdispersion.

Variable	Parameter	SE
Winter-PDO	0.110	0.156
May-PDO	0.013	0.138
Trend	-0.023	0.020
Treatment	0.824	0.062
Adjacent	0.489	0.139
Constant	-0.742	0.428
σ^a (Winter-PDO Random Coefficient)	0.273	
σ (May-PDO Random Coefficient)	0.239	
σ (Trend Random Coefficient)	0.054	
σ (Year Random Intercept)	0.422	
σ (Herd Random Intercept)	1.168	

a: Standard deviation.

Table 2.A-8. Herd-specific coefficients of the relationship between recruitment and May-PDO, Winter-PDO and Trend. Coefficients were calculated by adding each herd's empirical Bayes predicted random effect for a specific variable to the global parameter estimate from Table 2.3.

Herd	Intercept	Trend	Winter-PDO	May-PDO
Aishihik	-1.60	0.015	0.225	0.076
Burwash	-0.59	-0.040	0.072	-0.082
Carcross	1.24	-0.104	0.020	-0.213
Chisana	-2.37	0.017	0.623	-0.438
Ethel Lake	-0.40	-0.052	0.011	0.247
Finlayson	-0.91	-0.022	-0.020	0.102
Ibex	0.24	-0.070	-0.224	0.418
Klaza	-1.16	0.008	0.003	0.082
Tatchun	0.51	-0.062	-0.135	-0.015
Wolf Lake	-2.34	0.080	0.525	-0.045

Appendix 2B. Modeling the Effect of Wolf Removal on Recruitment

Hayes & Harestad (2000) reported that in Finlayson (Fig. 2.1), the wolf population recovered to pre-removal levels in six years. We therefore fit a series of models with a "Treatment" variable, indexing a potential linear decline in recruitment following wolf removal for the Aishihik and Finlayson herds (i.e. the wolf control treatment herds). Years with active wolf removal had a value of 1.0 and linearly decreased in value, on the logit scale, after wolf removals ceased. We compared models which differed in when the wolf removal effect became undetectable (k). This ranged from a lack of effect in the first year after wolf removal (k = 1) to a lack of effect at six years (k = 6). The value (V_i) of the Treatment variable was calculated by $V_i = 1 - i/k$, where $1 \leq k \geq 6$, and i = number of years after wolf removals ceased ($i \leq k$). All other years were valued at 0. The best value of k was chosen based on the model with the greatest log-likelihood.

Further, because the Aishihik wolf control area overlapped onto the ranges of the Burwash and Klaza herds (i.e. the herds adjacent to the treatment herds; Fig. 2.1) we accounted for a wolf removal effect in these herds, although we assumed this effect would be different than for the Aishihik or Finlayson (Treatment) herds because the proportion of the herd's ranges covered was substantially less (Hayes *et al.* 2003). Since wolf removals occurred on the periphery of these herds' ranges we were uncertain as to the nature of the response in recruitment. Therefore, we considered a number of possible response patterns following wolf removal in these two adjacent herds, specified as an "Adjacent" variable. These possible response patterns included a direct effect during all years of wolf removal, a lag effect in which the effect of wolf removal was not detected until 1 – 4 years (m) after removals began, and a possible linear decline in recruitment after wolf removal ceased for k number of years. The possible number of years for which a post-wolf removal effect was tested (k) depended upon results from the Treatment herds, since we regarded it implausible that a wolf removal effect could remain longer in the adjacent herds than the treatment herds. Therefore, to account for wolf removal in subsequent models, we included two variables: one for the Treatment herds and one for the Adjacent herds, which represented an index of wolf removal on recruitment. Overall, our results for the climatic effect on recruitment were insensitive to the detail on how wolf removal was modeled.

The effect of wolf removal on recruitment was confirmed for the "Treatment" herds, and represented a constant positive effect on recruitment during active removal followed by a post-removal six-year linear decline (Table 2.A-4; $k = 6$). For the "Adjacent" herds, a variable representing a two-year lag effect after wolf removal began, with no post-removal effect, was selected (Table 2.A-5; $m = 2$, $k = 1$).

CHAPTER 3 INTERACTING EFFECT OF WOLVES AND CLIMATE ON RECRUITMENT IN A NORTHERN MOUNTAIN CARIBOU POPULATION[1]

3.1 Introduction

The use of large-scale indices has proven successful in enhancing our understanding of climate's influence on ecological patterns (Stenseth et al. 2003). In western Europe and eastern North America, the North Atlantic Oscillation (NAO) index sometimes better predicts ecological processes (e.g. survival) than measures of local weather, as it captures variation across multiple months (i.e. time window), spatial scales (e.g. altitude, latitude), and incorporates variation and interactions from multiple weather variables (e.g. precipitation, temperature) into one parsimonious metric (Hallett et al. 2004, Stenseth and Mysterud 2005). For mobile and/or dispersed individuals in a population, one single weather metric may not represent conditions experienced by all individuals. However, in some continental areas of Europe far from the coast, the impact of the NAO is weaker and principal component-based indices of local weather parameters were better predictors (Mysterud et al. 2007). Additionally, an integrated climate index may represent more complexity than necessary if a single local weather variable is the primary factor affecting an ecological process (e.g. population growth). For example, ungulate population dynamics in South Africa are largely influenced by dry season rainfall limiting plant growth, rather than a large-scale climate index (Ogutu and Owen-Smith 2003).

Recently, two Pacific-based indices have been related to terrestrial vertebrate population dynamics in North America (Hebblewhite 2005, Morrison and Hik 2007, Hegel et al. 2010): the North Pacific Index (NPI) and the Pacific Decadal Oscillation (PDO). However, the identification of a "best" Pacific-based climate index in terms of influencing terrestrial vertebrate population dynamics over a broad geographical scope, akin to that of the NAO (Stenseth et al. 2003),

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[1] Hegel, T. M., Mysterud, A., Huettmann, F. and Stenseth, N. C. In Press. Interacting effect of wolves and climate on recruitment in a northern mountain caribou population. Oikos.

remains elusive and identification of such an index may enhance our understanding of ecological systems. The PDO is a measure of climatic variability in the north Pacific region characterized by shifts between warm and cool phases on an interdecadal time scale (Mantua et al. 1997, Mantua and Hare 2002). It is measured as the leading principal component of monthly sea surface temperatures (SST) in the north Pacific from 20°N poleward and 110°E-110W°. Positive (warm phase) PDO values are characterized by cool SST in the central Pacific and warm SST along coastal areas. The PDO is related to sea level pressure (SLP) such that warm phase PDO values generally coincide with below average north Pacific SLP (Mantua et al. 1997, Stenseth et al. 2003). The NPI is an area-weighted mean SLP index summarizing the north Pacific from 30°N-65°N and 160°E-140W° (Trenberth and Hurrell 1994). Due to the negative relationship between SST and SLP in the North Pacific region, relationships between the PDO and local weather variables (e.g. snowfall) are opposite in direction to NPI – local weather relationships.

Climate can have both direct and indirect effects operating through trophic interactions (Mysterud et al. 2008). Most research on trophic interactions has focused on bottom-up effects (Post and Stenseth 1999, Mysterud et al. 2001, but see Stenseth et al. 2004 for dynamics of Canada lynx *Lynx canadensis*); however, climate may also affect top-down interactions with predators (Hebblewhite 2005, Wilmers et al. 2006). For example, Hebblewhite (2005) reported that in elk populations exposed to wolf predation, snow depth explained more variation in population growth rate than the NPI, whereas in populations absent of wolves the NPI was a better predictor. Winter and spring PDO is also negatively correlated with snowmelt phenology (Morrison and Hik 2007, Hegel et al. 2010) such that high values indicate an earlier first snowfree day of the year.

Northern mountain-dwelling caribou in the Yukon Territory, Canada (Yukon; Farnell et al. 1998) are regarded as predator-limited (Hayes et al. 2003), primarily through predation on newborn calves (Adams et al. 1995, Gustine et al.

2006) which limits recruitment. As with most ungulate populations that occur with natural predators, density dependent factors regulating population growth are weak (Crête 1999, Wang et al. 2009). Previous research indicates that recruitment dynamics in these populations are influenced by climate affecting environmental conditions at calving (Hegel et al. 2010). However, there is variability in the relationship between climate and recruitment across populations (Grøtan et al. 2009), not unlike the variable response in red deer *C. elaphus* body weight to environmental conditions across Europe (Martínez-Jauregui et al. 2009). One possible explanation for this is that the effect of climate at calving is related to variable predator densities. At calving, parturient female caribou move up in elevation to separate themselves from predators and other parturient females (Bergerud and Page 1987). In years with high snow depth during the calving season, this upward movement may be limited, resulting in higher predation rates on neonates (Bergerud and Page 1987, Adams et al. 1995). Thus, the effect of climate on recruitment may be modified by the number of predators present on the landscape.

We used long-term recruitment data from the Finlayson caribou population (herd) in the Yukon to test three hypotheses regarding the influence of large-scale climate, local weather, and predator density on recruitment dynamics. Local weather and wolf abundance data were available for the Finlayson herd allowing us to focus explicitly on the influence of a predator-climate (local weather) interaction on recruitment. First (H1: regional climate vs. local weather hypothesis), we tested the prediction (H1a) that large-scale climate indices would better explain observed patterns in recruitment than local weather variables (Hallett et al. 2004) versus the prediction that local weather was a better explanatory variable (H1b). If local weather better explained observed recruitment patterns, we predicted that this would be most evident with respect to those weather variables related to environmental conditions at calving, such as winter snowfall, given the high predation on neonates in mountain caribou populations. Second (H2: PDO vs. NPI hypothesis), we tested the hypothesis that the PDO and NPI are equally supported in their ability to explain observed recruitment patterns. Due to the lack of direct comparative analyses between Pacific-based climate indices on ungulate population dynamics we had no a priori basis to assume one index would outperform the other. Finally (H3: climate-predation interaction hypothesis), we predicted that the influence of seasonal climate, or local weather, on caribou recruitment would change (Table 3.1) with reduced wolf densities following a large-scale predator removal program (Farnell and McDonald 1987, Hayes and Harestad 2000).

3.2 Methods

3.2.1 Study Area and Population Data

The Finlayson mountain-dwelling caribou herd (~ 62°N, 128°W), a member of the Northern Mountain ecotype of woodland caribou, is located in the east-central Yukon (Farnell et al. 1998) and is a part of a multi-predator (e.g. wolf, grizzly bear, black bear), multi-prey system (e.g. Dall's sheep, moose). Details regarding the environmental characteristics of its range are described by Farnell and McDonald (1987) and Hayes and Harestad (2000).

Aerial surveys were conducted during rutting (breeding) season (late September to mid-October) with total counts of observed calves and adult females used to estimate recruitment (calf:cow ratio; Farnell et al. 1998). The dataset used here consisted of 27 annual estimates during the period 1982 – 2008, and recruitment ranged from 0.09 – 0.62 (Fig. 3.1). The total number of animals classified during the surveys ranged from 393 to 2247. The recruitment estimates used here represent a combined measure of fecundity and calf survival to approximately 4 months of age. Age ratios such as the calf:cow ratio used here are positively correlated with population growth rates (Harris et al. 2008). During the rut, animals are aggregated above treeline in high alpine habitats reducing misclassification errors and increasing detectability of calves. A recent comparison of recruitment estimated aerially with one derived concurrently from individually captured females indicated no meaningful difference in recruitment rate (0.10 vs. 0.095, Hegel unpubl.).

In response to perceived poor recruitment and a declining population, a recovery program was initiated for the herd during 1983 – 1989 (Farnell et al. 1998). During late-winter, wolves were removed from the herd's range to < 20% of pre-removal levels (Farnell and McDonald 1987). Hence, the wolf population was reduced substantially during the years of active removal (Fig. 3.1) with numbers increasing following removal efforts to pre-removal level (Hayes and Harestad 2000). During this time wolf numbers were estimated annually (Farnell and McDonald 1987) as described in Hayes and Harestad (2000). We did not have absolute wolf density estimates for the full range of the Finlayson caribou recruitment time-series; therefore, we generated a relative wolf density index (Wolf) ranging on the unit interval (0, 1). This index represents the proportion of the pre-removal (i.e. not reduced via management actions) wolf population in a year, calculated by $W_t/10.3$, where W_t was the wolf density estimate in year t and 10.3 was the wolf density (wolves/1000 km^2) estimated prior to wolf removal activities (Environment Yukon unpubl.). Years prior to wolf removal and following the wolf population's return to pre-removal levels were valued at 1.0. The relative wolf density index ranged from 0.126 – 1.0 (Fig. 3.1).

3.2.2 Climate and Local Weather Data

We used seasonal PDO values obtained from the Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington (Mantua et al. 1997) (<http://jisao.washington.edu/pdo>). NPI values were obtained from the Climate Analysis Section of the National Center for Atmospheric Research (Trenberth and Hurrell 1994) (<www.cgd.ucar.edu/cas/jhurrell/npindex.html>). Seasons for which index values were obtained are described in Table 3.1 and were selected because they were identified as potentially influencing recruitment in northern mountain caribou in the Yukon. Seasonal PDO values were positively correlated with local weather, such as precipitation and temperature, across the Yukon (Hegel et al. 2010) and this study area (Table 3.2). Relationships between local weather and NPI (Table 3.2) were in the expected opposite direction to those between the PDO and local weather (Mantua et al. 1997, Yang et al. 2005).

Local weather was represented by snow depth data collected at the Hoole River snowcourse station (61°32'N, 131°36'W) located within the Finlayson herd's range (data provided by Water Resources Branch, Environment Yukon). Two snow measurements (cm), collected at the beginning of the month, were used: May-snow represented snow levels immediately prior to calving (May-Snow), and April-snow represented the overwinter (in utero) accumulation of snow. Separate April and May snow depth measurements were used because spring snowmelt often begins in April. Thus, May snow depth is related to both April climatic conditions and overwinter snowfall. Data from multiple seasons were used to allow for a direct comparison of seasons with differing mechanistic effects on recruitment (Table 3.1).

3.2.3 Statistical Analysis

We modeled caribou recruitment by fitting a suite of candidate generalized additive models (GAM; Wood 2006) which allowed us to account for possible non-linearity (Mysterud et al. 2001). If non-linear relationships were not supported, generalized linear models (GLM) were fitted instead. All models were fitted using the binomial family and a logit link function. All models were fitted using the 'mgcv' package (Wood 2006) for the statistical software R 2.9.2 (R Development Core Team 2009). We fitted a suite of candidate models using Wolf and the seasonal NPI, PDO, and local weather variables (Table 3.1), specified as interactions. For GAMs, a tensor-product smooth term represented the interaction. Candidate models were also fitted in which Wolf and the climate/weather variables were specified with separate terms (i.e. no variable interaction). A null model (i.e. no predictors) was also fitted for comparison. We did not include more than one seasonal variable in a model as we regarded this time-series too short to estimate more complex models. All GAM smooth terms were penalized thin-plate regression splines with the degree of smoothing, limited to a maximum of four degrees of freedom (df = 4), selected using generalized cross-validation (Wood 2006).

Candidate models were ranked using the Akaike Information Criterion adjusted for small sample size (AICc; Burnham and Anderson 2002). For each model (i) we calculated ΔAICc_i, which is AICc_i minus the minimum AICc from all models in the candidate set. Models with ΔAICc < 2 and large Akaike weights, indicating the probability that model i is the top model among the candidate set, were interpreted as having the strongest support (Burnham and Anderson 2002).

3.3 Results

The best model of recruitment was represented by the interaction of Wolf and April-PDO (Table 3.3; Fig. 3.2). It explained 80.5% of the deviance relative to the null model and had an Akaike weight of 0.99. Wolf explained 69.3% of the deviance, while April-PDO and the interaction of Wolf and April-PDO explained 11.9% and 5.7% respectively. No other models had ΔAICc < 10. The constant-only (null) model (ΔAICc = 101.5), models with either Wolf (ΔAICc = 572.74) and April-PDO (ΔAICc = 807.66) as single predictors, and the model with Wolf and April-PDO as separate smooth terms (ΔAICc = 67.93) received less support. NPI and local weather were not represented in the top-ranked models, and the ΔAICc values of the best models including these variables were 24.56 and 46.21 respectively (Appendix Table 3.A-1).

The significant interaction between Wolf and April-PDO (Table 3.3) highlighted the important non-additive relationship between these two variables and recruitment. There was a negative effect of increasing wolf density on recruitment across the range of April-PDO values (Fig. 3.2), although this relationship lessened as April-PDO increased suggesting that in "good" springs, climate partly buffered the effect of wolves. The relationship between April-PDO and recruitment was positive at high wolf densities; however with reduced wolf numbers the direction of this relationship changed to one that was slightly negative (Fig. 3.2 and 3.3). For example, predicted recruitment with April-PDO at 2.0 and -1.5 was 0.29 (SE = 0.03) and 0.12 (SE = 0.03), respectively, at high wolf density (Wolf = 1.0). At low wolf density (e.g. Wolf = 0.15) there was a slight negative effect of increasing April-PDO on recruitment (Fig. 3.3). For example, predicted recruitment at April-PDO of 2.0 and -1.5 was 0.45 (SE = 0.04) and 0.55 (SE = 0.10) respectively. The difference in predicted recruitment between these two climatic extremes was not significant given the high amount of overlap of 95% confidence intervals of the predictions. Residuals from the top model were normally distributed (Shapiro-Wilk test: W = 0.97, P = 0.59) and an autocorrelation plot indicated no significant serial autocorrelation.

3.4 Discussion

The presence of only large-scale climate indices in the top ranked models provided support for H1a, that large-scale climate would better explain recruitment patterns than local weather metrics. The lack of the NPI in any of the top ranked models also led us to reject H2, that the NPI would be an equally good predictor of recruitment as the PDO. Finally, our results provide support for H3, that a reduction in predator density would affect the relationship between climate and recruitment.

3.4.1 Regional Climate vs. Local Weather

Our findings, indicating large-scale climate's greater explanatory performance than local conditions, represented by snow depth, are consistent with those previously reported for a variety of ecological systems (Attrill and

Power 2002, Hallett et al. 2004). Given the strong mechanistic link between snow conditions at calving and predation on neonates in northern mountain-dwelling caribou (Bergerud and Page 1987), and the increased effect of local weather on elk population growth following wolf recolonization in the Canadian Rocky Mountains (Hebblewhite 2005), we expected snow conditions to be important for recruitment in the Finlayson caribou herd. Our snow depth measurements were obtained from within the range of the herd. However, this site may not have captured all the spatial variation in snow depth across the herd's range, both in area and elevation, making the PDO a better proxy than snow depth from a single station.

When one localized metric is used to represent weather conditions for a mobile species, it may not represent the full range of conditions experienced by individuals. This is particularly relevant for snow depth which may be more spatially variable than either precipitation or temperature. For species such as northern mountain caribou which disperse away from conspecifics during calving, finding one localized weather measurement to represent the environmental conditions experienced by the population may be difficult. Indeed, northern mountain caribou are most widely dispersed during the calving season.

While snow depth is an important factor influencing predation rates (Huggard 1993), snowmelt patterns may also influence predation rates by creating a more heterogeneous landscape, which may reduce predator searching efficiency and enhance neonate survival (Bergerud and Page 1987, Eastland et al. 1989). If a heterogeneous snowmelt pattern is important for influencing neonate survival, and hence recruitment, an integrated index representing temperature and precipitation prior to calving would thus provide more explanatory power. The complexity of snowmelt patterns may be further enhanced in mountainous and topographically variable terrain. April-PDO may therefore represent the combination of temperature and precipitation during April, immediately prior to calving, which subsequently better describes snow depth and snowmelt heterogeneity, within a broader “spatial window” (Stenseth and Mysterud 2005), than a single local weather metric. The spatio-temporal complexity of how local weather translates to actual environmental conditions may explain why, in some systems, local weather variables that should in theory be strongly related to animal population dynamics, do not necessarily provide the predictive ability expected (e.g. Jonzén et al. 2005). The use of multiple local weather measurements in the Finlayson herd’s range could provide a more spatially complete description of snow depth and a principal components approach to providing a single snow metric (e.g. Mysterud et al. 2007) may prove to be a better explanatory variable than a large-scale index. However, there were not sufficient numbers of weather stations available in the herd’s range to allow for this. This is a typical situation in remote areas where only one station may be available (e.g. Adams 2005).

3.4.2 The Pacific Decadal Oscillation vs. North Pacific Index

There were relatively similar relationships between the NPI and PDO and local weather, however the signal by which the PDO manifested itself into complex local weather patterns was stronger than the NPI for recruitment in the Finlayson caribou herd. In addition to caribou recruitment patterns (Hegel et al. 2010) and collared pika survival (Morrison and Hik 2007) in the Yukon, the PDO is correlated with a variety of broad-scale terrestrial environmental phenomena in North America including forest fires (Skinner et al. 2006) and summer drought (Shabbar and Skinner 2004). The NPI is also related to weather patterns across North America (Trenberth and Hurrell 1994; Yang et al. 2005), and showed comparable, and sometimes stronger, relationships to local weather in this study area to the PDO.

Indeed, the NPI is strongly related to snow conditions in the Canadian Rocky Mountains (Hebblewhite 2005) and may perform better than the PDO in that system. Understanding why this may occur is complicated by the uncertainty of the physical mechanisms driving Pacific decadal variability in North Pacific climate (Miller and Schneider 2000; Mantua and Hare 2002), and the additional complex relationships between the NPI and PDO and other global indices such as the El Niño Southern Oscillation (Tianjun et al. 2002). There remains a need for more investigation, over a broad geographic region, into the performance of different Pacific-based indices in explaining ecological patterns.

3.4.3 Interaction of Wolves and Climate on Recruitment

Our results demonstrate that the effect of April-PDO on recruitment in the Finlayson caribou herd may change direction with substantially reduced wolf numbers. With higher wolf numbers, recruitment increased in years with "better" springs (i.e. higher PDO, less snow on the ground). Predation on neonatal caribou in the Finlayson herd is apparently moderated by spring climate conditions. In good springs, recruitment rates in the absence of active wolf removal approached those when the wolf population was reduced by ~85%. This "environmentally modulated predation" (sensu Newsome et al. 1989) can result from reduced predator efficiency due to an increased ability for prey to disperse in years with lower snow depths at calving thus reducing prey densities and increasing search times (Bergerud and Page 1987), increased vulnerability of prey due to environmental conditions as seen by increased wolf predation success on elk in Yellowstone National Park during severe winters (Mech et al. 2001), and the effect of snow characteristics (e.g. hard vs. soft) on predation success as seen for Canada lynx (Stenseth et al. 2004). Our results are consistent with Melis et al. (2009) who found a significant interaction between winter severity and the presence of large predators affecting the densities of roe deer *Capreolus capreolus* across Europe. They found that winter severity was only a factor shaping population densities when large predators were present. Modulation of predation rates is also observed in aquatic systems where changes in environmental features such as water temperature impose physiological constraints on predator efficiency (Kashi et al. 2005). Climate can also modulate the influence of predators by directly affecting predator abundance and hence subsequent predation impacts on prey (Preisser and Strong 2004).

The reduced and reversed effect of climate on recruitment in the Finlayson herd following wolf reduction differs from similar situations observed elsewhere. Following massive disease-related wolf losses on Isle Royale, the effect of winter NAO on moose population growth increased substantially as bottom-up factors became more influential (Wilmers et al. 2006). Our results indicate that rather than exerting a buffering capacity against climate by keeping population densities sufficiently low enough to limit density dependent effects, the presence of wolves enhanced the effect of spring climate on caribou recruitment dynamics. These contrasting results may be due to differing degrees of bottom-up limitation occurring in each population prior to the reduction of wolves (Vucetich and Peterson 2004) and that the Finlayson caribou herd would not have been as spatially limited as the island moose population of Isle Royale following population increases.

The slightly negative relationship between April-PDO and recruitment following the substantial reduction in wolf numbers suggests an alternative mechanism operating once a substantial portion of predation is removed from the system. April-PDO is positively correlated to earlier snowmelt and temperature (Hegel et al. 2010). In springs with higher PDO, forage green-up may occur earlier and more rapidly. Rapid changes in plant productivity, following high April-PDO, may have a negative effect on calf growth (Pettorelli et al. 2007) and subsequent survival. In mountainous environments, a very warm spring may reduce the heterogeneity of snowmelt, thus reducing the temporal availability of highly nutritious green forage available to lactating females and growing calves. Warmer temperatures may also result in reduced forage quality such as nitrogen content (Lenart et al. 2002), further affecting calf growth. That this relationship was only detected in the absence of a large portion of the primary predation source indicates the dominant effect of predation on recruitment in this population. Population density does not provide an adequate explanation for this observed pattern, as all but one of the observed recruitment rates during years with no wolf removal in Fig. 3.3 (i.e. the gray circles) were obtained after wolf control was implemented and thus densities were higher during these years.

3.5 Conclusion

This study indicates the potential importance of considering climate during management activities such as predator control (Reynolds and Tapper 1996) or reducing the impacts of introduced species (Harding et al. 2001), which could provide insight into their level of success (Keedwell et al. 2002). Our results suggest that wolf removal would be most effective, in terms of increasing calf recruitment, during poor springs. In years with high April-PDO, the effect of wolf removal on recruitment may be reduced. Given the social controversy surrounding predator control (Martínez-Espiñeira 2006), its financial costs (Engeman et al. 2002), and the possible ecosystem effects of top predator reduction (Duffy 2003), understanding how climate may influence a program's success may prove useful for decision making (Knowlton et al. 1999). This could include consideration of upcoming seasonal weather forecasts. For example, the decision to undertake a predator reduction program that must occur in the winter due to logistical and other environmental constraints may use a forecast of upcoming springtime weather as one factor in deciding whether to proceed with the activities. The usefulness of such an approach would largely depend on how well future weather can be forecasted in a particular location and the ability of a management agency to adapt quickly to changing conditions. While spring climate was the most influential season in our study, the effect of seasonal climate on predation should be assessed at a local level and in other systems variables such as winter snowfall may be more influential (Hebblewhite 2005).

Our results may prove useful for understanding the factors affecting the broad-scale decline of woodland (boreal forest and mountain-dwelling) caribou across North America (McLoughlin et al. 2003, Wittmer et al. 2010). Numerous proximate and ultimate factors influence these declines, including human disturbance (Environment Canada 2008), habitat loss (Wittmer et al. 2010), and predation (Wittmer et al. 2005). Incorporating climate variables as non-additive interactions with other influential variables (e.g. % forest cover) could strengthen the predictive power of demographic and population models. Recent work suggests Allee effects may be present in low density mountain caribou populations in British Columbia driven largely by predation and apparent competition with alternate prey (Wittmer et al. 2005). Our results suggest that in poor years (e.g. high snow depth at calving) these Allee effects could be more pronounced. Further, climatic conditions that are generally favorable to alternate prey may indirectly affect caribou through apparent competition. Ultimately, what our research and others' indicates is that the role of predation on the population dynamics of mountain dwelling caribou is complex and its effect may be best understood when considering other ecological factors.

The greater support of the PDO over the NPI in predicting recruitment patterns in the Finlayson caribou herd, and the strong effect of the NPI on ungulate population dynamics elsewhere in western North America (Hebblewhite 2005), coupled with the relatively sparse literature on Pacific-based climatic impacts on terrestrial vertebrate population dynamics, highlights our lack of knowledge on its broad-scale effects, certainly in comparison to the NAO (Stenseth et al. 2003). Assuming one exists; identifying a Pacific-based index that is consistently strong in explaining ecological patterns across western North America would provide researchers a common metric for analysis, which would allow for more direct comparison across study areas and taxa. The stronger support of the PDO over snow depth, and other local weather variables, suggests that while specific processes, such as predation, are assumed to have very strong mechanistic linkages to a single weather variable, these linkages may be more complex than a single metric. The complex spatio-temporal nature of snowmelt (Mysterud et al. 2000), particularly in a dynamic season such as spring, highlights the utility of using large-scale indices to explain ecological patterns, when their relationships to local weather patterns are known (Stenseth et al. 2003), as they inherently capture this variability over space and time (Stenseth and Mysterud 2005).

Finally, the non-additive effect of climate and wolf density found in this study highlights the importance of understanding the mechanistic relationship between climate and the ecological parameter of interest. Interacting ecological variables were important factors shaping roe deer densities across Europe (Melis et al. 2009). The role of large predators on population density was largely context-specific and differed depending on winter severity as well as habitat productivity. The influence of climate on recruitment in the Finlayson caribou herd was most pronounced when wolf density was also accounted for. This indicates the importance of ecological factors extrinsic to the population (e.g. predators) in determining the strength of the climatic effect, similar to the influence of intrinsic factors, such as population density (Mysterud et al. 2001), in affecting the role of climate in influencing population dynamics. Hebblewhite (2005) noted that density-climate interactions for elk in western Canada were weak without the presence of wolves. Indeed, how climate influences populations may be governed by both extrinsic and intrinsic factors, as suggested by the different response to large-scale climate following wolf reduction in the Finlayson caribou herd and the Isle Royale moose population (Wilmers et al. 2006). Generalizing the effect of climate across spatially discrete populations has proven difficult (Martínez-Jauregui et al. 2009). Our research also demonstrates that the effect of climate on a population's dynamics may also vary temporally within that population, further complicating the attempt to find broad-scale climatic influences on ungulate population dynamics.

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Table 3.1. Predicted relationships (a) and mechanisms (b) between seasonal PDO (NPI relationship in parentheses) and local weather variables, and mountain-dwelling caribou recruitment, with unaltered and reduced (following wolf removal) wolf density in the Yukon Territory, Canada (+: positive relationship; -: negative relationship).

a) Seasonal Relationships			
Seasonal Climate/Weather Variable	Predicted relationship with unaltered wolf density	Predicted change in magnitude of the relationship with reduced wolf density	Mechanism
April-PDO (NPI) May-PDO (NPI)	+ (-)	Decrease	1
Winter-PDO (NPI)^{a} Late Winter-PDO (NPI)^{b}	+ (-)	Decrease	2
April-Snow^{c}	-	Decrease	1, 2
May-Snow	-	Decrease	1

b) Mechanism	
1	Conditions resulting in increased snow depth at calving results in greater predation on neonates and hence reduced recruitment. These conditions should become less influential as wolf densities decrease.
2	Increased snowfall during winter results in calves born in poorer condition with reduced survival during their first summer, and higher snow depth at calving which increases predation. With reduced wolf density, more pregnant females may enter winter in poorer condition and thus be more sensitive to winter conditions, suggesting a strengthening relationship with winter climate/weather. However, given the role of winter snowfall on predation of neonates, the effect of winter climate/weather following wolf reduction could also be expected to weaken (i.e. similar to Mechanism 1). Due to the substantial influence of predation on recruitment in these populations, we ultimately expect the weakening of effect size (i.e. Mechanism 1) to outweigh any strengthening of due to increased sensitivity to in utero conditions.

a: Winter (November – April); b: Late Winter (March – May); c: Overwinter snow accumulation measured the beginning of April.

Table 3.2. Correlation between seasonal values of the PDO and NPI and local weather variables in the Finlayson caribou herd range in east-central Yukon Territory, Canada (1982 – 2008). (*P* > 0.05 for all correlations)

Weather Variable	Winter[b]		April		Late Winter[b]	
	PDO	NPI	PDO	NPI	PDO	NPI
Winter Snowfall[a]	-0.30	0.22			-0.18	-0.07
May Snow Depth[a]	-0.08	0.10	-0.17	0.26	-0.19	0.24

a: Data from the Hoole River snowcourse station (61°32'N, 131°36'W); b: Winter: November – April; Late Winter: March – May.

Table 3.3. Parameter estimates of the top generalized linear model of recruitment rate for the Finlayson caribou herd in the Yukon Territory, Canada (1982 – 2008). The model explained 80.5% of the deviance relative to the null model.

Parameter	Coefficient	SE[a]
Intercept	0.312	0.227
Relative Wolf Density Index	-1.823	0.272
April-PDO	-0.191	0.176
April-PDO * Relative Wolf Density Index	0.509	0.229

[a] Bootstrapped standard errors estimated from 1000 simulations.

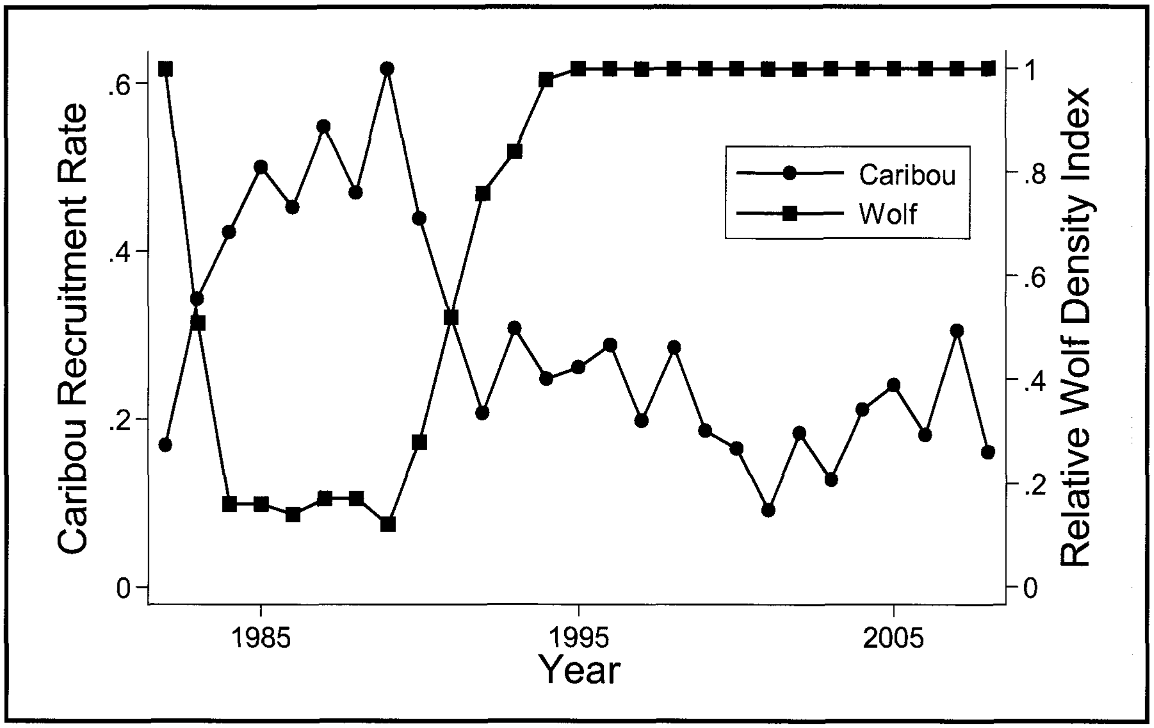

Figure 3.1. Annual caribou recruitment rates (calf:cow ratio) for the Finlayson caribou herd in the Yukon Territory, Canada, and relative wolf density index values in the herd's range (1982 – 2008).

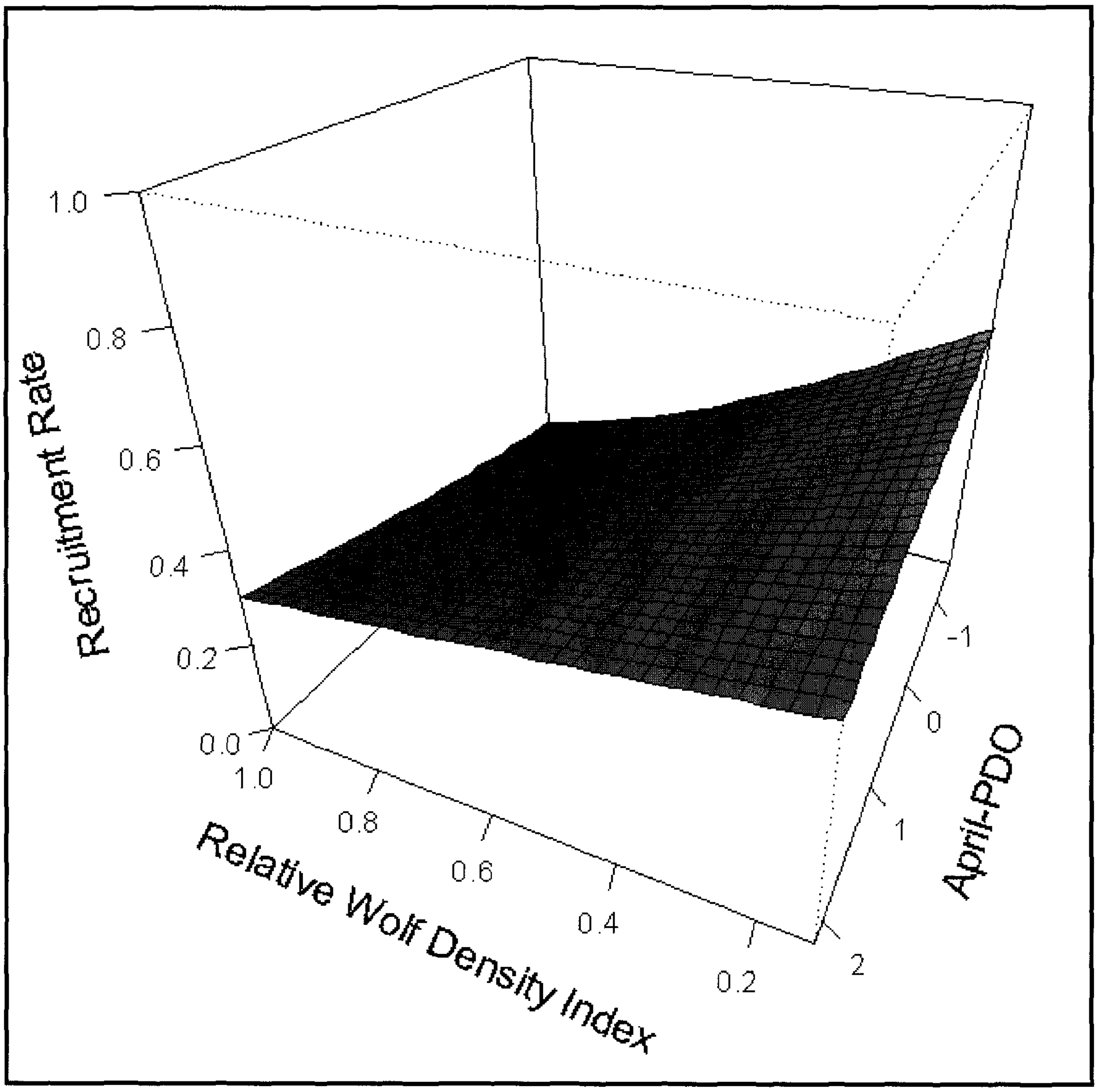

Figure 3.2. Relationship between recruitment (calf:cow ratio) and the relative wolf density index*April-PDO interaction, estimated from a generalized linear model, for the Finlayson caribou herd of the Yukon Territory, Canada.

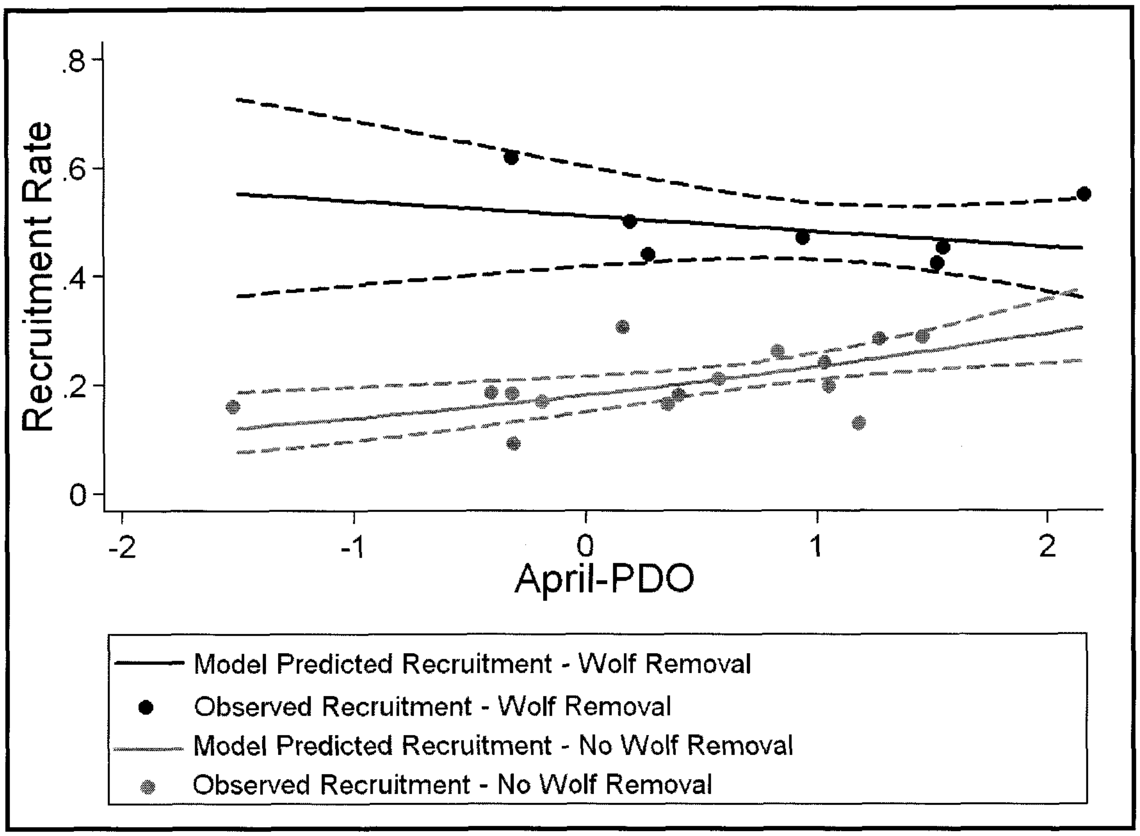

Figure 3.3. Predicted recruitment rates (calf:cow ratio) for the Finlayson caribou herd in the Yukon Territory, Canada, based on a generalized linear model of recruitment including April-PDO and relative wolf density index (Wolf) as covariates (Table 3.3). Solid lines represent predicted recruitment rates during two extremes representing no wolf removal (Wolf = 1.0, gray lines) and active wolf removal (Wolf = 0.15, black lines). Dashed lines indicate 95% confidence intervals of the predictions. Observed recruitment rates during active wolf removal (Wolf ≤ 0.3, black) and no wolf removal (Wolf = 1.0, gray) are indicated by solid circles. Values of April-PDO (-1.5 – 2.15) used for model predictions were restricted to the range of values present in the model training dataset.

Appendix 3A. Chapter 3 Supplementary Table

Table 3.A-1. Models of annual recruitment for the Finlayson northern mountain caribou herd in the Yukon Territory, Canada. The ‘f’ prior to a model term indicates a smoothing function estimated from the data as represented by a generalized additive model. Lack of an ‘f’ prior to model terms indicates a generalized linear model. Seasons are defined in Table 3.1.

Model	K^a	Log-Likelihood	AICc	ΔAICc
Wolf * April-PDO	4	-213.60	437.01	0
Wolf * Late Winter-PDO	4	-224.39	458.60	20.55
f(Wolf) + April-NPI	3.27	-227.42	462.61	24.56
Wolf * April-NPI	4	-228.64	467.10	29.05
f(Wolf * Late Winter-NPI)	4.49	-230.55	472.37	34.32
Wolf * May-PDO	4	-236.95	483.71	45.66
f(Wolf * April-Snow)	4.54	-236.42	484.25	46.21
f(Wolf) + April-Snow	3.59	-238.29	485.22	47.17
Wolf + May-PDO	3	-246.73	500.49	62.45
Wolf + April-PDO	3	-249.47	505.97	67.93
Wolf + Late Winter-PDO	3	-254.67	516.38	78.34
Wolf * Winter-PDO	4	-254.87	519.55	81.50
Wolf + Late Winter-NPI	3	-260.02	527.08	89.04
Wolf * Winter-NPI	4	-267.35	544.52	106.47
Wolf + Winter-PDO	3	-272.07	551.18	113.14
f(Wolf) + May-Snow	3.15	-273.20	553.83	115.79
Wolf * May-NPI	4	-273.13	556.07	118.02
Wolf * May-Snow	4	-275.07	559.96	121.91
Wolf + May-NPI	3	-282.56	572.16	134.12
Wolf	2	-284.12	572.74	134.69
Wolf + Winter-NPI	3	-283.00	573.04	135.00
f(Winter-NPI)	3.44	-578.47	1165.16	727.12
f(Late Winter-PDO)	3.86	-608.45	1226.30	788.26
f(April-PDO)	3.51	-618.64	1245.71	807.66
f(Winter-PDO)	3.52	-634.62	1277.70	839.65
f(May-PDO)	3.44	-639.56	1287.34	849.30
April-Snow	2	-657.61	1319.72	881.67
Late Winter-NPI	2	-708.22	1420.93	982.88
f(May-Snow)	2.16	-714.02	1432.92	994.88
April-NPI	2	-720.30	1445.09	1007.04
Null	1	-723.71	1449.58	1011.53
May-NPI	2	-722.55	1449.59	1011.54

a: Effective number of model parameters.

CHAPTER 4 DEMOGRAPHIC SPATIAL SYNCHRONY IN MOUNTAIN-DWELLING WOODLAND CARIBOU[1]

4.1 Introduction

Spatial population synchrony is the correlated fluctuation, in abundance or other demographic parameter, of spatially distinct populations over time (Ranta et al. 1998). Spatial synchrony is relatively ubiquitous in nature and has been documented in a variety of taxa (Liebhold et al. 2004) from aphids (Hanski and Woiwod 1993) to ungulates (e.g., Grenfell et al. 1998; Grøtan et al. 2005). Investigating the factors influencing the degree of spatial synchrony may aid in identifying mechanisms of population dynamics (Ranta et al. 1995). For management purposes, understanding synchrony is valuable as highly synchronized populations may be at a greater risk of extinction (Heino et al. 1997; Engen et al. 2002). In many instances managers may not be able (e.g., financially, logistically) to monitor all the populations under their responsibility. In these situations, the presence of strong spatial synchrony may aid in inferring the annual dynamics of unmonitored populations from those that are monitored.

Three dominant mechanisms driving spatial synchrony have been identified in the literature: dispersal, shared predation, and environmental covariance (Liebhold et al. 2004; Ranta et al. 2006). First, populations linked via dispersing individuals can be brought into synchrony if they share sufficiently similar density-dependent processes (Ranta et al. 1995; Kendall et al. 2000). Secondly, shared nomadic predators have been demonstrated to synchronize small mammal dynamics through their common effect on two, or more, prey populations (Ims and Andreassen 2000). This mechanism requires individual predators to be able to cover large areas, relative to prey distribution, over short time periods (Ranta et al. 2006). Finally, populations sharing a common density-dependent structure are predicted to be synchronized to a degree equal to their

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[1] Hegel TM, Verbyla D, Huettmann F, Barboza PS (In Review) Demographic spatial synchrony in mountain-dwelling woodland caribou. Population Ecology.

environmental covariance; this is termed the Moran (1953) effect (Benton et al. 2001; Engen and Sæther 2005). These three mechanisms may interact to influence synchrony (Kendall et al. 2000), and habitat characteristics may also influence the degree of synchrony between populations (Paradis et al. 2000; Huitu et al. 2003; Drever 2006) via their effect on one or more of these mechanisms.

Spatial synchrony is often assessed on population abundances (Tedesco et al. 2004) or growth rates (Aanes et al. 2003), and more rarely on demographic rates (Myers et al. 1997; Schaub et al. 2005). However, exploring spatial synchrony of individual demographic parameters provides a more mechanistic (i.e., process-oriented) understanding of the factors affecting synchrony in population dynamics (Bjørnstad et al. 1999). Here we investigate the pattern of demographic spatial synchrony in ten mountain-dwelling woodland caribou herds (populations), hereafter termed mountain caribou, in the Yukon Territory (Yukon), Canada (Fig. 4.1). We examined spatiotemporal relationships in recruitment, as indexed by the fall calf:cow ratio (e.g., Grøtan et al. 2009).

The calf:cow ratio used here to index annual recruitment represents the joint contribution of fecundity and calf survival to 4-5 months of age. Recruitment indexed by age ratios is often strongly related to calf survival (Harris et al. 2008), which is a highly variable demographic parameter in ungulate populations and may explain considerable variation in population growth rate (Gaillard et al. 1998, 2000). Age ratios such as the calf:cow ratio used here are positively correlated with population growth rates (Harris et al. 2008). Mountain caribou in the Yukon are considered to be predator-limited (Seip 1992; Bergerud and Elliot 1998; Hayes et al. 2003) and characterized by relatively high and stable fecundity (Wittmer et al. 2005a) and low calf survival. The majority of calf mortality occurs within the first month of life (Adams et al. 1995a, b; Gustine et al. 2006). Typical of ungulate populations coexisting with large predators, intrinsic density-dependent regulation of population growth is weak (Crête 1999; Wang et al.

2009). Recruitment in these herds shows high annual variability (Hegel et al. 2010). Previous research of mountain caribou recruitment dynamics in the Yukon indicated a strong influence of winter and spring climate affecting environmental conditions at calving (e.g., snow depth), likely influencing predation rates (Hegel et al. 2010). Climatic conditions during seasons predicted to influence fecundity (i.e., pre-conception climate) were poor predictors of recruitment, further supporting calf survival as the vital rate best represented by calf:cow ratios considered here.

Previous research on spatial synchrony in population dynamics has noted the challenge of separating the contributing effects of its three primary mechanisms (Ranta et al. 1995; Kendall et al. 2000). By using recruitment we can specifically focus our investigation on the Moran effect. In ungulates, males are typically the primary dispersers and females exhibit greater fidelity to natal areas (Greenwood 1980; Clutton-Brock et al. 2002). As our recruitment index only considers calves and females, any male dispersal to or from a herd would not affect the magnitude of the ratio. Additionally, adult sex ratios in Yukon mountain caribou are typically greater than 40 bulls:100 cows (e.g., Hayes et al. 2003), and are therefore unlikely to limit the breeding of females (Mysterud et al. 2002). Since these herds exist at low densities and density is a weak regulatory force on their population dynamics, any impact of added immigrant males is likely negligible with respect to a reduction in forage availability. Hence we can rule out dispersal as a likely mechanism influencing synchrony in recruitment in these herds.

Mountain caribou are dispersed during calving (Bergerud et al. 1984; Bergerud and Page 1987) when the majority of mortality occurs, and are distributed over an area substantially larger than either the home range of a wolf pack or grizzly bear. For example, within the Finlayson herd range (~7270 km^2, Table 4.A-1) in the east-central Yukon (Fig. 4.1), over 30 wolf packs were monitored from 1990-96 (Hayes and Harestad 2000). In the southwest Yukon, male and female grizzly bear home ranges averaged 824 km^2 and 305 km^2, respectively (Maraj 2007). Given the large ranges of caribou herds relative to their predators, and the narrow time window during which the majority of predation occurs, we can effectively eliminate shared, or nomadic, predators as a causal mechanism of spatial synchrony in these herds.

Our objectives for this research are threefold. First, we assess the extent of spatial synchrony in snow depth across the Yukon. In doing so, we are able to relate the spatial synchrony in recruitment to spatial covariance in weather across sites. Given patterns of spatial synchrony reported elsewhere (Koenig 2002) we expect relatively strong spatial synchrony in snow depth across the Yukon. Second, we assess the extent of spatial synchrony in recruitment among multiple mountain caribou herds in the Yukon. Varying levels of spatial synchrony in ungulate population dynamics have been reported (e.g., Grøtan et al. 2005, 2008; Post and Forchhammer 2004, 2006), thus we have no *a priori* prediction of the degree of spatial synchrony in caribou recruitment in the Yukon. However, because of a lack of perfect correlation between snow depth and recruitment, we anticipated that the extent of spatial synchrony in caribou recruitment would be less than that of snow depth (Benton et al. 2001). Finally, we assess how habitat characteristics affect the degree of spatial synchrony in these herds. We focus on terrain features since, for example, they influence snow accumulation and ablation patterns in mountainous environments (Elder et al. 1991; Watson et al. 2009; Winstral and Marks 2002), which may subsequently influence ungulate vital rates (Mysterud et al. 2000, 2001; Pettorelli et al. 2005). We predict that herds with more similar terrain features have more synchronous recruitment dynamics.

4.2 Methods

4.2.1 Caribou Recruitment Data

Ten herds (Fig. 4.1) were surveyed from a helicopter to estimate recruitment from 1982 to 2008 as part of caribou monitoring activities in the Yukon (Farnell et al. 1998). Surveys occurred during the fall breeding season from the last week of September through mid-October. Groups of animals were classified and the ratio of total calves to total cows used as an index of annual recruitment at the herd level. Calves were identified by their small size and females were distinguished from immature males by the presence of a black vulva patch (Bergerud 1961). During breeding, animals aggregate on high alpine plateaus, thus making sightability of animals, particularly calves, much greater than in forested habitats. Data on recruitment rates represented 170 herd-years during the period 1982 – 2008. Additional details regarding the study area are provided in Hayes et al. (2003) and Hegel et al. (2010).

A number of management programs aimed at increasing low population sizes have occurred in the Yukon (Farnell et al. 1998). During 1983 – 1989, wolves were annually removed from the Finlayson herd range (Fig. 4.1) to < 20% of pre-removal numbers (Farnell and McDonald 1987; Hayes and Harestad 2000). During 1993 – 1997, a wolf removal and sterilization program occurred in the Aishihik herd range, with some actions overlapping onto the ranges of the adjacent Burwash and Klaza herds (Fig. 4.1; Hayes et al. 2003). The effects of wolf removal on recruitment in the Aishihik and Finlayson herds persisted for five years (Hegel et al. 2010). In the Burwash and Klaza herds, the effect on recruitment was detected two years after active wolf removal began and did not persist once removals ceased (Hegel et al. 2010). Additionally, from 2003 – 2006 a captive-rearing program was undertaken for the Chisana herd (Fig. 4.1) to enhance low recruitment. During late winter, parturient females were captured and transferred to a predator-free facility where they calved and were subsequently released in early June. To avoid potential bias associated with increased survival and recruitment due to the Chisana recovery program, we censored captured females and their surviving captive-born calves from the data (Yukon Fish and Wildlife Branch, unpublished data).

Prior to analysis, the effects of wolf removal and any long-term trend in recruitment were removed (Ranta et al. 2006), by fitting a binomial generalized linear model, with a logit link function, to each herd's time series of recruitment. Models were fitted with 'Year' and variables representing the effect of wolf removal on recruitment as covariates (see Hegel et al. 2010). Subsequent analyses were carried out on residuals (Fig. 4.2).

4.2.2 Snow Depth Data

Snow depth data from 19 stations across the Yukon (Fig. 4.1) were obtained from Environment Yukon (e.g., Water Resources Section 2008). At each station, the snow depth (cm) was measured shortly after April 1. Station elevations ranged from 540 – 1,235 meters above sea level. To maintain temporal consistency with the available caribou recruitment data, only snow depth data from 1982-2008 were used resulting in 487 annual measurements. Occasionally, individual stations were not visited in a specific year (e.g., due to poor weather preventing access to the site) thus resulting in less than the 513 total possible measurements. Data were detrended prior to analysis (Ranta et al. 2006). For each location snow depth was linearly regressed on year and residuals calculated and used for subsequent analysis.

4.2.3 Caribou Herd Ranges and Terrain Data

To assess how terrain relates to the degree of synchrony between herds we summarized a suite of terrain metrics based on their multi-year annual, winter (November – April) and calving (mid- May to first week of June) season distributions. We summarized these features for winter and calving seasons as these were previously identified as key periods influencing recruitment in these herds (Hegel et al. 2010). Annual and winter ranges were estimated using available aerial survey and radio-telemetry data (Table 4.A-1). Parturient mountain caribou are dispersed during calving (Bergerud et al. 1984; Bergerud and Page 1987) and herds do not have ranges *per se*, therefore we summarized terrain features by averaging values of each metric from the set of calving season point locations (Table 4.A-1).

Annual and winter ranges (90% utilization distributions) were estimated from local convex hulls (LoCoH: Getz and Wilmers 2004; Getz et al. 2007), which is a nonparametric approach for estimating utilization distributions. Around each location (root point), a subset of its nearest neighbours is sampled and a convex hull created from this subsample of points. This is carried out for each data point from a herd's full set of points, and the total set of convex hulls are then ordered (smallest to largest) and merged consecutively to create isopleths based on the percentage of points falling within the merged convex hulls. For example, the union of convex hulls that encompasses 50% of all location points is thus the 50% isopleth. The key parameter for this method is the determination of the size of the nearest-neighbour subset around each location point. We used an adaptive approach (*a*-LoCoH in Getz et al. 2007) whereby spheres of varying radii are placed around each root point and all nearest neighbours within that sphere are used for convex hull creation (see Getz et al. 2007 for a detailed description of the methodology). The size of the sphere is determined by the degree of aggregation of the locations such that within a sphere the sum of the distances between all nearest neighbours and the root point are less than or equal to *a*. Hence, small convex hulls are created in high use areas resulting in more defined isopleths. This adaptive radius approach generally produces better home range estimates than either fixed-radius or fixed number of points approaches (Getz et al. 2007). Annual and winter ranges were estimated using the 'adehabitat' package (version 1.8.3; Calenge 2006) for the statistical software R version 2.10.1 (R Development Core Team 2009).

For each herd, we estimated 90% annual and winter range isopleths. Following Getz et al. (2007), we set *a* as the maximum distance between any two points in a herd's dataset. Each herd's annual and winter ranges, and its calving season locations, were imported into ArcGIS 9.3 (ESRI 2009). Terrain metrics (Table 4.1) were summarized within each range and averaged across calving locations. Metrics were derived from a 90-meter digital elevation model (1:50,000 scale).

4.2.4 Data Analysis

For both snow depth and caribou recruitment (i.e., residuals) we assessed the overall regional synchrony $\overline{\rho}$ in the data. It represents the average pairwise cross-correlation ($\rho_{j,k}$) of all combinations of time series (j, k; Bjørnstad et al. 1999). We used a nonparametric covariance function (NCF; Bjørnstad et al. 1999; Bjørnstad and Falck 2001) to estimate the spatial scale of synchrony ($\hat{c}$) which is the distance at which $\overline{\rho}$ is reached. Since data used for spatial synchrony analyses are inherently non-independent, we used a bootstrapping procedure with 500 simulations to estimate confidence intervals on all estimated parameters. Analyses were carried out using the 'ncf' package (version 1.1-3, Bjørnstad and Falck 2001) in the statistical software R version 2.10.1 (R Development Core Team 2009).

To assess the influence of terrain features on spatial synchrony we fitted parametric nonlinear exponential decay models to the $\rho_{j,k}$ of caribou recruitment. Using parametric nonlinear models allowed us to directly compare different seasonal terrain features under a model selection framework. We used a model (Myers et al. 1995, 1997) of the form:

$$\rho(d) = \rho_0 e^{-d/v} \; ; \qquad (4.1)$$

where ρ_0 is the correlation when $d = 0$, d represents the distance (spatial or ecological) between two herds (e.g., the difference in mean elevation between two herds), and v is the decay rate, or *e*-folding scale, which describes the distance at which the correlation is reduced by a factor of e^{-1}, and is also used as a measure of the scale of synchrony (e.g., Myers et al. 1995; Engen et al. 2005).

Following Myers et al. (1997) we fixed $\rho_0 = 1.0$, as we were primarily interested in the shape of the exponential decay. Nonlinear models were fitted using ordinary least-squares in Stata/SE 10.1 (StataCorp 2009). Prior to analysis, $\rho_{j,k}$ were transformed using a Fisher's z-transformation (Zar 1998), which removed the potential for model predictions to range beyond -1 to +1. Fitted values were subsequently back-transformed to the original (-1, +1) scale for reporting. As noted above, due to lack of independence in the data, reported parameter estimates and standard errors were generated via bootstrapping with 500 simulations.

Candidate models (i) were ranked using Akaike's Information Criterion (AIC, Burnham and Anderson 2002) adjusted for sample size (AIC*c*). Delta-AIC*c* (ΔAIC*c*) values were calculated by subtracting the AIC*c* of model i from the model with the smallest AIC*c* value in the candidate set. Models having ΔAIC*c* less than 2 were inferred as having strong support, models with ΔAIC*c* ranging from 2-10 having weak support, and those with ΔAIC*c* > 10 having virtually no support (Burnham and Anderson 2002). Akaike weights (w_i) were also calculated providing a measure of the probability of model i being the "top" model in the candidate set (Burnham and Anderson 2002).

4.3 Results

The average regional synchrony ($\overline{\rho}$) in snow depth (residuals) was 0.46 (95% CI: 0.37 – 0.55) and pairwise correlation coefficients between snow stations (n = 171) ranged from -0.17 to 0.85 with the majority being positive, and roughly followed a normal distribution (Fig. 4.3a). The distance at which $\overline{\rho}$ was reached ($\hat{c}$) was 330.2 km (95% CI: 236.3 – 370.0). The *e*-folding scale (v in Eq. 4.1) was 393.7 km (95% CI: 314.0 – 518.3). The maximum distance between any two stations was 660 km and synchrony decreased linearly as the distance between stations increased (Fig. 4.4).

The average regional synchrony ($\overline{\rho}$) in caribou recruitment (residuals) was 0.07 (95% CI: -0.13 – 0.29) and pairwise correlation coefficients between herds (n = 45) ranged from -0.86 to 0.89 (Table 4.2). The distribution of correlation coefficients for caribou recruitment was also roughly normally distributed (Fig. 4.3). The distance at which $\overline{\rho}$ was reached was 170.0 km (95% CI: 69.5 – 282.8); roughly half that for April snow depth. The *e*-folding scale (*v* in Eq. 4.1) was 124.8 km (95% CI: 69.5 – 278.0). The maximum distance between herds was 560 km and the pattern of synchrony exhibited an inverse quadratic relationship with spatial distance whereby nearer herds had more synchronous recruitment, with the degree of synchrony decreasing to a distance of approximately 250 km. After this, the degree of synchrony rose again, with more distant herds also exhibiting higher levels of synchrony (Fig. 4.5a). There was no difference in either $\hat{c}$ or the shape of the distance-synchrony relationship when using annual or winter range centers or the median coordinates of calving locations to represent the spatial location of herds. We therefore used annual range centers for all further analyses.

Herd-specific values of terrain metrics are provided in Table 4.A-1. Only two models relating caribou recruitment synchrony to terrain and distance were supported based on ΔAIC*c* and Akaike weights (Table 4.A-2). Spatial distance between herds was the most supported model among the candidate set (ΔAIC*c* = 0, *w* = 0.73). Due to the declining then subsequent increasing relationship between distance and synchrony, we fitted this model with a quadratic function. To maintain consistency with the exponential decay models, the constant term in the distance model was fixed to 1.0. For comparison, we also fitted spatial distance within the exponential decay model (Eq. 4.1) which had weak support (ΔAIC*c* = 12.01). The only terrain variable model with any substantial support represented difference in elevation variability of calving season distribution (Elev-

SD in Table 4.1; ΔAIC*c* = 2.16, *w* = 0.25), indicating herds having more similar variability in elevation of calving areas had more synchronous recruitment. The models including spatial distance and C-Elev-SD explained 32% and 25% of the variation in the data, respectively (Table 4.3). Spatial distance and difference in C-Elev-SD were weakly correlated (*r* = -0.11, *P* = 0.47).

Synchrony between herds decreased to roughly zero as spatial distance increased to approximately 250 km, and after approximately 300 km it subsequently rose to a maximum level (Fig. 4.5a). With respect to terrain, synchrony decreased to zero as the difference in C-Elev-SD between herds reached approximately 25 m (Fig. 4.5b). To ensure that the two observations having the greatest spatial distance between herds (Fig. 4.5a) were not overly influential on the overall fit of the model, we refitted the spatial distance model withholding those two data points. Model results were nearly identical to those reported in Table 4.3 providing confidence that our results were not overly influenced by outliers.

4.4 Discussion

Synchrony in recruitment among mountain caribou herds in the Yukon is influenced in part by both spatial environmental covariance, represented by spatial distance between herds, and differences in terrain features of calving areas. Our finding of an inverse quadratic relationship between synchrony and distance was unexpected given both the linear decay of April snow depth synchrony with increasing distance across the Yukon, and other reported patterns of spatial synchrony of environmental variability (Koenig 2002) and ungulate population dynamics (e.g., Grøtan et al. 2005).

The initial decay of recruitment synchrony with increasing distance between herds and the overall spatial scaling of synchrony are consistent with the pattern of spatial synchrony in April snow depth. The lower spatial scaling of recruitment synchrony compared to local weather was expected (Benton et al.

2001) as a variety of processes likely influence recruitment beyond snow depth before calving. The spatial scale of recruitment synchrony reported here ($\hat{c}$ = ~165 km) is similar to those reported for ungulate population dynamics elsewhere, such as 191 km for Norwegian roe deer (Grøtan et al. 2005), although substantially larger than the ~15 km scaling distance for Swiss ibex (*Capra ibex*; Grøtan et al. 2008). At a circumpolar scale Post and Forchhammer (2006) reported synchronous dynamics among caribou and reindeer populations in Greenland and Russia, respectively, separated by over 6500 km. The variability in synchrony of Yukon caribou recruitment (Fig. 4.3b) could be due to observed spatial variability in population-specific responses (i.e., forcing) to large-scale climate (Hegel et al. 2010). Grøtan et al. (2008) suggested that large spatial variability in ibex population responses to climatic variables may be the reason for the generally low spatial synchrony in that system. This may be due to the highly mountainous and heterogeneous terrain in both the Yukon and Switzerland resulting in more variable climate forcing. The relationship between spatial population synchrony and similarity in response to the North Atlantic Oscillation among caribou and reindeer populations of Greenland and Russia was positive and linear (Post and Forchhammer 2006).

The presence of an increasing relationship between spatial distance and synchrony after approximately 300 km suggests that some additional factor(s), positively correlated with distance, are influencing mountain caribou recruitment synchrony in the Yukon. Kausrud et al. (2007) found a similar quadratic relationship between distance and synchrony in gerbil (*Rhombomys opimus*) populations; however, they also reported a similar pattern between environmental variability (i.e., forage productivity) and distance, thus providing a mechanism for the observed pattern of spatial synchrony. No such pattern was identified in our study.

A number of factors may have influenced the quadratic relationship between recruitment synchrony and distance. Recruitment in these herds is largely influenced by predation (Hayes et al. 2003), which interacts with climate in a non-additive manner (Hegel et al. In Press). Similar interspecific interactions between herds, independent of distance, could result in more synchronous recruitment dynamics at large distances. Spatial synchrony can propagate through food webs (Haynes et al. 2009) and the synchronous fluctuation of other species' populations could confound the relationship between recruitment synchrony and distance via "biological filtering" (Ripa and Ranta 2007). In our system, herds may be synchronized when predator densities are also independently synchronized between herd ranges. Synchronous densities of alternative prey such as moose may subsequently synchronize predator densities and thus caribou recruitment (Wittmer et al. 2005b; McLellan et al. 2010), possibly via asymmetric apparent competition (DeCesare et al. In Press). This mechanism differs from the shared nomadic predator mechanism (Ims and Andreassen 2000) in that it does not require the same individual predator(s) as the synchronizing force. Rather, two (or more) herds may be synchronized by the same predator species, but independently.

If such a mechanism is occurring where moose density subsequently influences mountain caribou recruitment, a lagged effect would be anticipated such as observed in the southwest Yukon where Dall's sheep and snowshoe hare (*Lepus americanus*) cycles are inversely synchronized likely through the effect of shared predators between the species (Wilmshurst et al. 2006). In that system high snowshoe hare density was correlated with reduced Dall's sheep lamb productivity in the following one and two years. Although we controlled for reduced wolf densities following management activities, moose and the primary predators of caribou are all harvested species in the Yukon. Thus, predator and alternate prey density across space may be influenced by ecological mechanisms as well as anthropogenic effects. Further, differing levels of disturbance on the landscape (e.g., access, industrial development, fire) could have habitat-related effects on predator and alternate prey densities, which may subsequently be filtered to caribou (Wittmer et al. 2007). We did not have comprehensive data on these other species covering the same spatio-temporal frame as the caribou recruitment data presented here and were therefore unable to test this hypothesis.

We focussed our assessment of terrain factors influencing synchrony to variables which we believed could influence environmental covariation between herds through similar climatological downscaling (Pettorelli et al. 2005). However, other habitat factors may also influence mountain caribou recruitment. For example, woodland caribou survival and population viability in more heavily managed landscapes in southern British Columbia, Canada, is influenced by forest age structure which may affect predation rates on caribou due to the relationship with moose density (Wittmer et al. 2007, 2010). Fire may also influence recruitment through loss of forage (i.e., lichen, Klein 1982; Joly et al. 2009) and changes in forest structure (Edwards 1954). Furthermore, human activities may also reduce the effectiveness of important habitats (e.g., Seip et al. 2007) and calving animals may be particularly at risk from disturbance (Wolfe et al. 2000; Vistnes and Nellemann 2001).

We specifically chose April snow depth as our representation of environmental variability as this factor has strong mechanistic linkages to predation rates on mountain caribou calves (Bergerud et al. 1984; Bergerud and Page 1987), which is generally the largest source of mortality (Bergerud and Elliot 1986; Adams et al. 1995a; Gustine et al. 2006). Hence, we chose terrain factors which we believed had a mechanistic relevance for their influence on environmental variation (i.e., snow depth) and thus recruitment. The strong performance of elevation variability in calving sites, relative to other terrain metrics, provides further evidence as to the importance of snow at parturition for these populations. With access to greater variability in elevation, parturient female mountain caribou may be better able to “track” snowmelt ablation patterns to remove themselves from predators and other calving females

(Bergerud and Page 1987). Greater variability in snowmelt patterns may increase the ability of calving caribou to hide from predators as increased snowpatch heterogeneity on the landscape may reduce predator's searching efficiency (Eastland et al. 1989). Oosenbrug and Theberge (1980) noted that individuals in the Burwash herd (Fig. 4.1) demonstrated attraction to emerging snowfree sites in May. Mysterud et al. (2001) reported a similar pattern for red deer in Norway in which the availability of increased diversity (i.e., variability) in elevation and aspect to individual animals was positively related to body weight. This was due to an animal's ability to track plant phenology across this diversity, with more variable terrain prolonging the access to high quality forage in the spring. Similarly, Wang et al. (2009) used the standard deviation of elevation within population ranges as a proxy for resource heterogeneity. In the Yukon, herds with similar elevation variability in their calving areas may have similar snow ablation patterns and thus more synchronous recruitment rates resulting from either correlated predation rates and/or nutritional effects on juveniles, and subsequent survival, due to similar springtime plant phenology (Pettorelli et al. 2007).

The weak average regional synchrony in mountain caribou recruitment across the Yukon was unexpected as we anticipated that it would be largely influenced by April snow depth (i.e., environmental noise), which was more strongly synchronized across space. A number of factors may have influenced this finding. Lande et al. (1999) noted that estimation errors in population abundance should bias synchrony low. Errors in our estimates of recruitment would also therefore be anticipated to bias synchrony low.

Our index of recruitment represents a combination of two processes: fecundity and calf survival. Identifying a signal of synchrony could be confounded by our inability to separate synchrony in each of these rates. However, pregnancy rates in mountain-dwelling caribou are generally high and consistent across years (Wittmer et al. 2005a), and with the exception of extremely severe winters, adult female reproductive success is consistently high, possibly due to the high losses of neonatal calves, precluding females from providing resources to their offspring (Adams and Dale 1998). Thus, given the amount of interannual variation (Fig. 4.2), our index of recruitment (calf:cow ratio) likely tracks calf survival more strongly than fecundity (e.g., Harris et al. 2008). Additionally, previous analyses using portions of these data (Hegel et al. 2010, In Press) found strong mechanistic relationships with environmental predictors influencing calf survival and not female fecundity. While some error is inevitable in the estimation of population parameters, had error in recruitment estimates been substantial it is doubtful that such mechanistic models would have been supported. Rather, random error (i.e., noise) in recruitment estimates would have cancelled out the ecological signal. Use of residuals to explore spatial synchrony, while necessary (Ranta et al. 2006), may also have added a source of error into the data as they themselves are estimates (Chatfield 2003).

Two other factors provide more plausible explanations for the weak average regional synchrony. First, synchronous dynamics may not be constant over time (Ranta et al. 1997b). Post and Forchhammer (2004) reported non-constant spatial synchrony in caribou population dynamics in Greenland, with synchrony increasing with an increasing large-scale climatic trend. The time series used by Ranta et al. (1997b) and Post and Forchhammer (2004) were substantially longer than ours (i.e., multiple decades) and whether non-constant synchrony was present in our relatively shorter time series of recruitment data is uncertain. As most of our herd's time series were not complete over the entire time span of the full dataset, a moving window analysis (Ranta et al. 1997b) to assess changing synchrony was not possible. Second, the weak regional average synchrony may be due to weaker cycling in these caribou herds. Low synchrony in noncyclic populations may be due to weaker lagged density dependence (Ranta et al. 1997a). Paradis et al. (2000) suggested this as a factor in the low synchrony in a number of British bird species. The weak regulatory force of density in these herds may be a factor in the low regional average synchrony observed in the Yukon.

Is then the Moran effect acting on recruitment synchrony in mountain caribou in the Yukon? Given the differing pattern of spatial synchrony in recruitment compared to April snow depth, evidence of such an effect is equivocal. Typically, evidence of declining synchrony with increasing distance is treated as evidence that a Moran effect is occurring, assuming a similar pattern occurs with environmental spatial covariance. However, focussing solely on distance may not necessarily confirm the presence of a Moran effect (Abbott 2007). Environmental variability is often represented by weather as it can be strongly related to population dynamics. However, biologically meaningful environmental variability may be represented by other variables (e.g., predator and/or alternative prey densities). For populations affected by multiple interacting factors, possibly across trophic levels, measuring and identifying this environmental variability may be more challenging than focussing solely on weather. This may result in an aspatial Moran effect if these variables are not spatially correlated. To incorporate meaningful factors affecting population synchrony, a broadened view of spatio-temporal environmental variability may be necessary to enhance our understanding of a population's dynamics.

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Table 4.1. Metrics used to assess the relationship between recruitment synchrony and terrain in mountain caribou in the Yukon Territory, Canada.

Metric	Units	Description
Distance	km	Spatial distance between herd centers
Elev-Mean	meters	Average elevation
Elev-Max	meters	Maximum elevation
Elev-Min	meters	Minimum elevation
Elev-Range	meters	Difference between maximum and minimum elevations
Elev-SD	meters	Standard deviation of elevation representing elevation variability
Northness	N/A	Calculated as the cosine of aspect (°) ranging from -1 to 1, where 1 represents north and -1 represents south
Northness-SD	N/A	Standard deviation of northness representing aspect variability along a north-south gradient
Eastness	N/A	Calculated as the sine of aspect (°) ranging from -1 to 1, where 1 represents east and -1 represents west
Eastness-SD	N/A	Standard deviation of eastness representing aspect variability along an east-west gradient

Table 4.2. Inter-herd synchrony (Pearson correlation coefficients) of annual recruitment residuals and inter-herd spatial distance (km) for 10 mountain caribou herds in the Yukon Territory, Canada (1982 – 2008). Correlation coefficients (bold values indicated $P < 0.10$) are found in the upper diagonal of the table and spatial distance between herds provided in the lower diagonal.

	Aishihik	Burwash	Carcross	Chisana	Ethel Lake	Finlayson	Ibex	Klaza	Tatchun	Wolf Lake
Aishihik		**0.43**	0.27	**0.84**[a]	0.24	**0.49***	**-0.44**	**0.55**	**-0.50**	0.18
Burwash	69		0.13	**0.45**	0.08	**0.48***	0.13	0.38	-0.13	-0.17
Carcross	233	293		-0.03	0.30	0.19	0.42	-0.30	-0.25	-0.56
Chisana	175	108	399		-0.38	**0.72***	**-0.69***	0.18	**-0.60***	**0.89***
Ethel Lake	219	261	325	328		-0.45	**0.60**	0.42	0.32	0.08
Finlayson	374	443	237	546	304		-0.09	-0.35	-0.29	**-0.86***
Ibex	179	233	69	337	314	292		-0.02	0.23	-0.10
Klaza	79	108	280	185	153	371	238		0.10	**0.78**
Tatchun	160	222	224	313	101	246	215	129		-0.50
Wolf Lake	358	426	161	533	356	111	228	378	272	

a: $P < 0.05$.

Table 4.3. Parameter estimates for the two most supported models relating: a) spatial distance between herds and b) difference in calving season elevation variability (C-Elev-SD) between herds, to mountain caribou recruitment synchrony in the Yukon Territory, Canada. Model parameters were estimated using Fisher z-transformed correlation coefficients.

	Parameter Estimate	SE^{a}
a) Distance + Distance^2		
Distance	-0.0076	$9.3*10^{-4}$
Distance^2	$1.5*10^{-5}$	$2.5*10^{-6}$
σ^2	0.50	
R^2	0.32	
b) $e^{\frac{-(C-Elev-SD)}{v}}$		
v	16.59	9.91
σ^2	0.52	
R^2	0.25	

a: Standard errors generated from 500 bootstrap simulations.

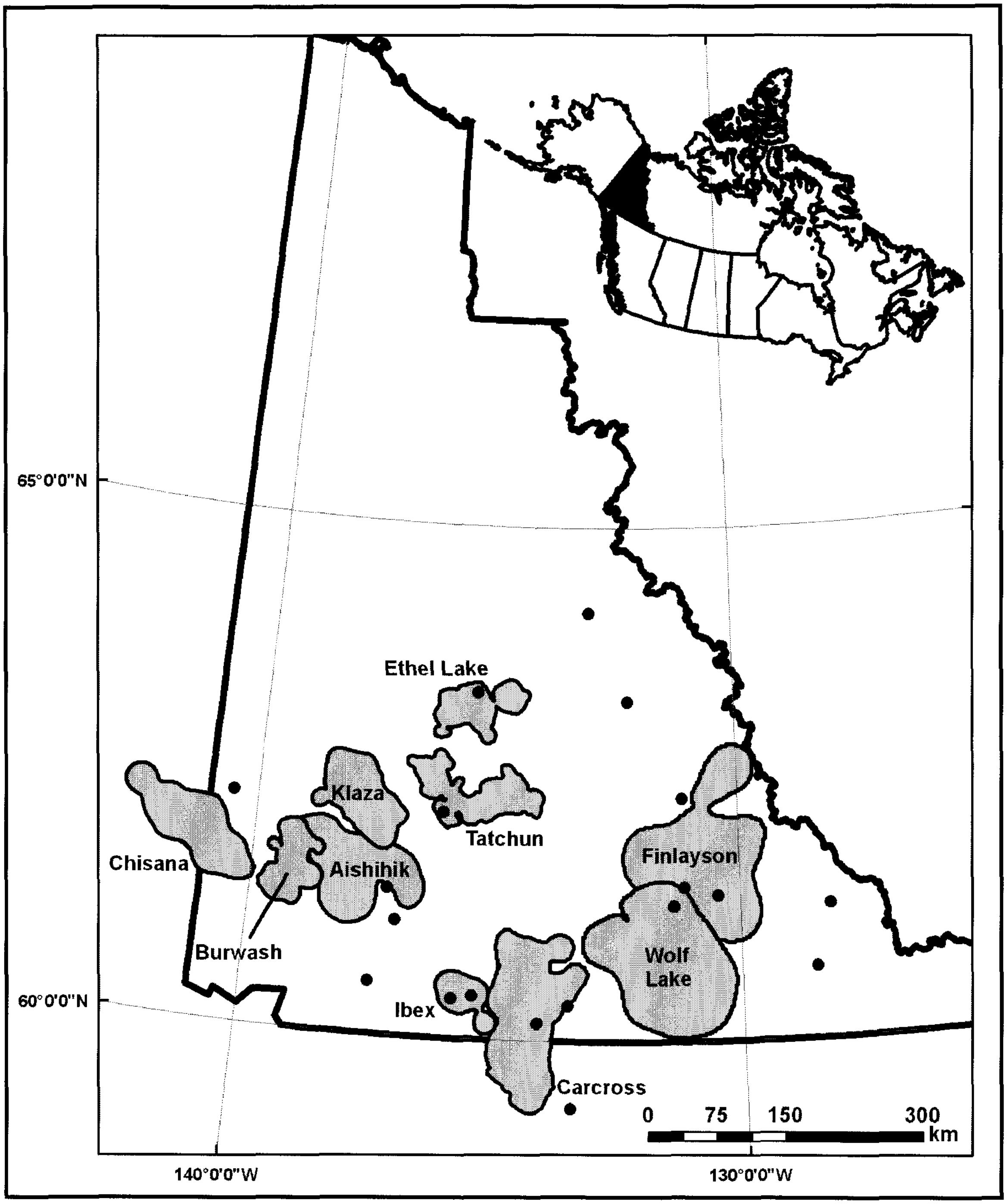

Fig. 4.1. Locations of the 10 mountain caribou herds (shaded polygons) and 19 snowcourse stations (•) in the Yukon Territory, Canada, for which synchrony in annual recruitment and April snow depth was assessed, respectively.

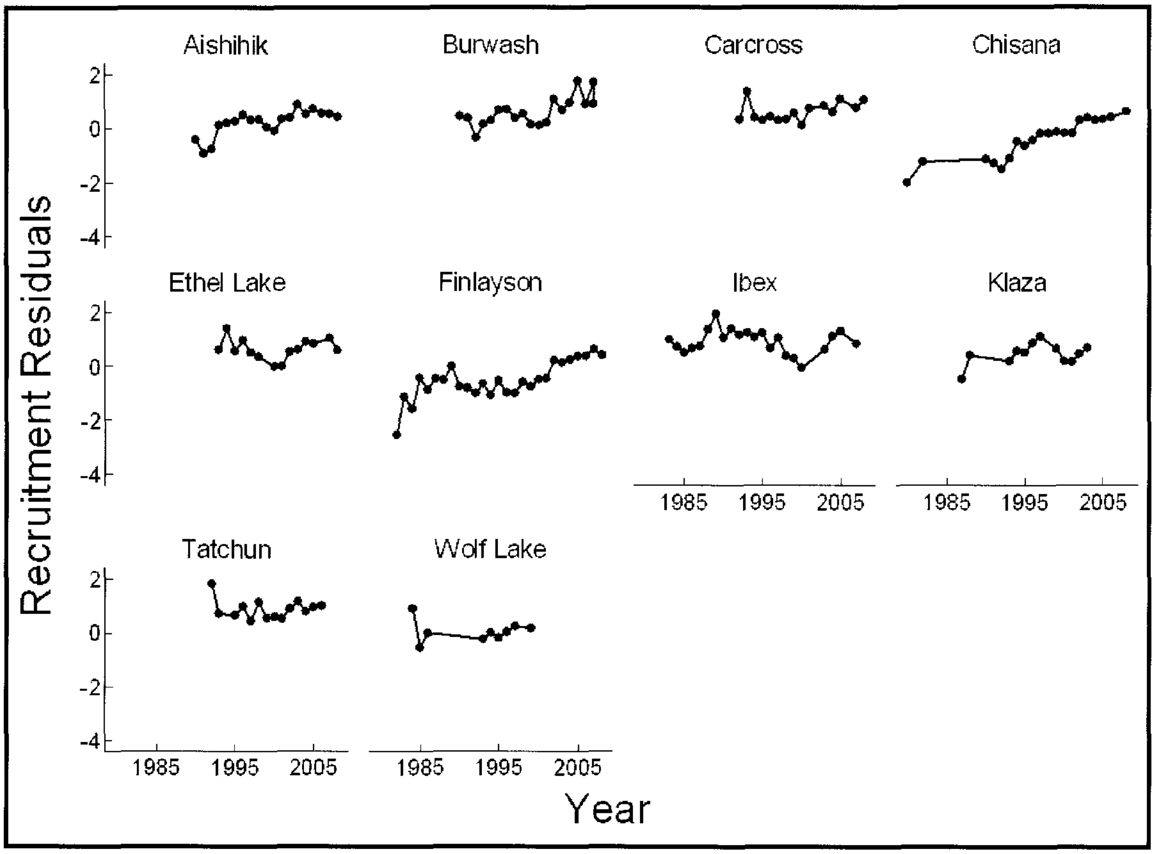

Fig. 4.2. Residuals used to assess synchrony in recruitment in ten mountain caribou herds in the Yukon Territory, Canada (Fig. 4.1). Residuals were calculated from raw recruitment (calf:cow ratio) rates after detrending and removing the effect of wolf removal.

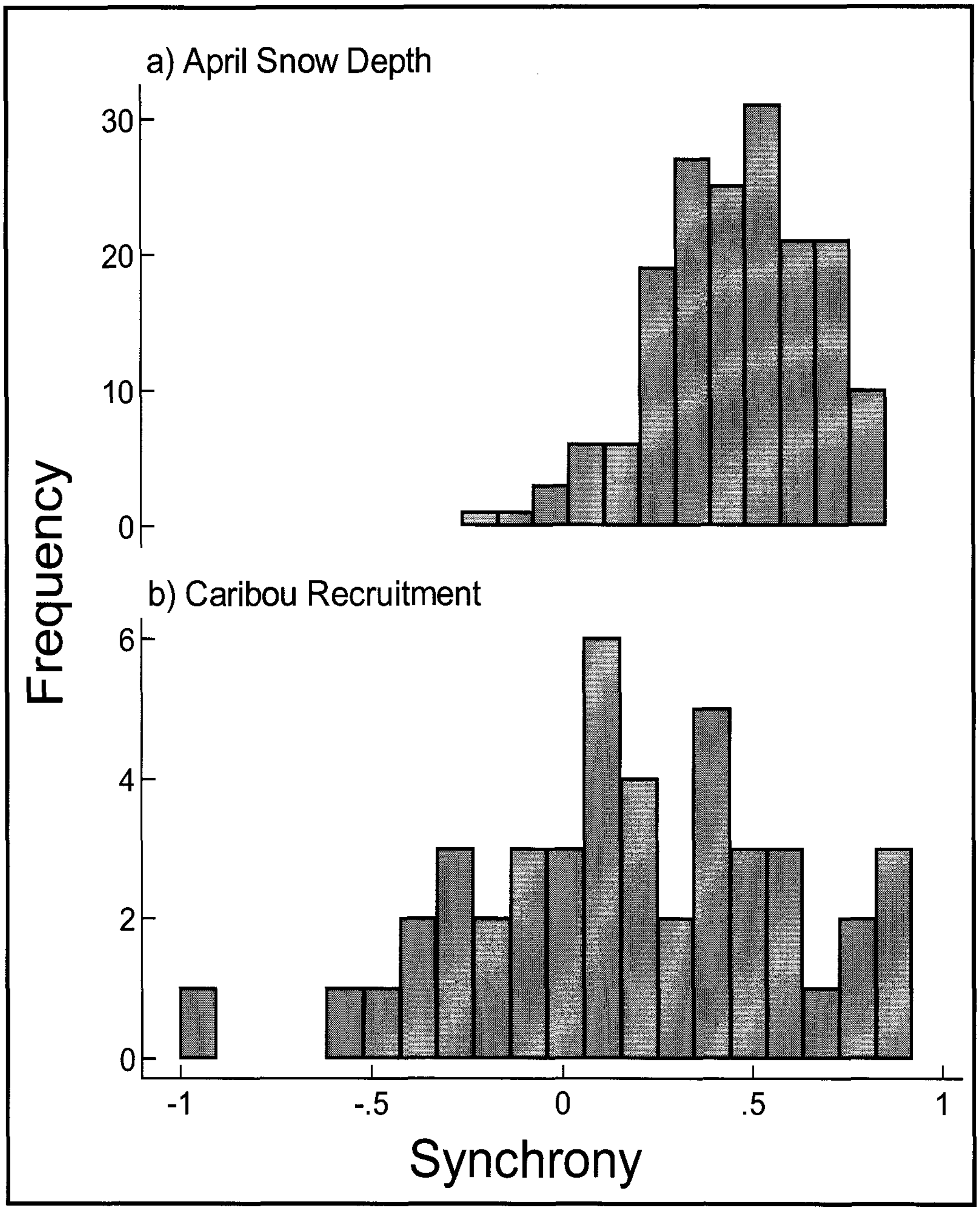

Fig. 4.3. Frequency histograms of spatial synchrony (pairwise Pearson correlation coefficients) in a) April snow depth residuals (*n* = 171), and b) mountain caribou recruitment residuals (*n* = 45) in the Yukon Territory, Canada (1982 – 2008).

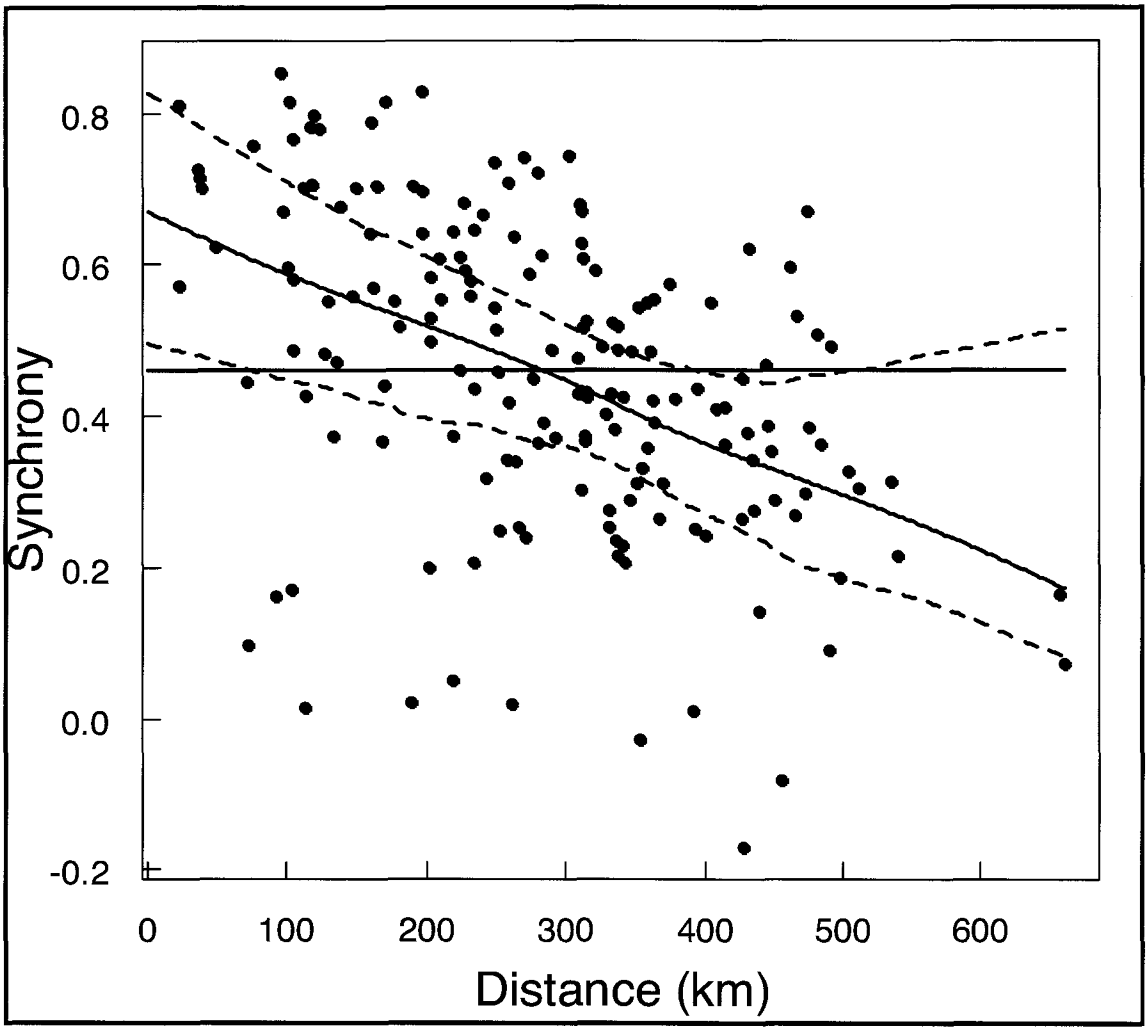

Fig. 4.4. Spatial synchrony of April snow depth residuals in the Yukon Territory, Canada (1982 – 2008) in relation to the distance (km) between snowcourse stations. Observed synchrony measures (pairwise Pearson correlation coefficients) are represented by filled circles (*n* = 171). The mean spatial nonparametric covariance function is represented by the solid line,with the dashed lines representing bootstrapped (B = 500) 95% confidence intervals. The solid horizontal line ($\bar{\rho}$ = 0.46) is the regional average spatial synchrony.

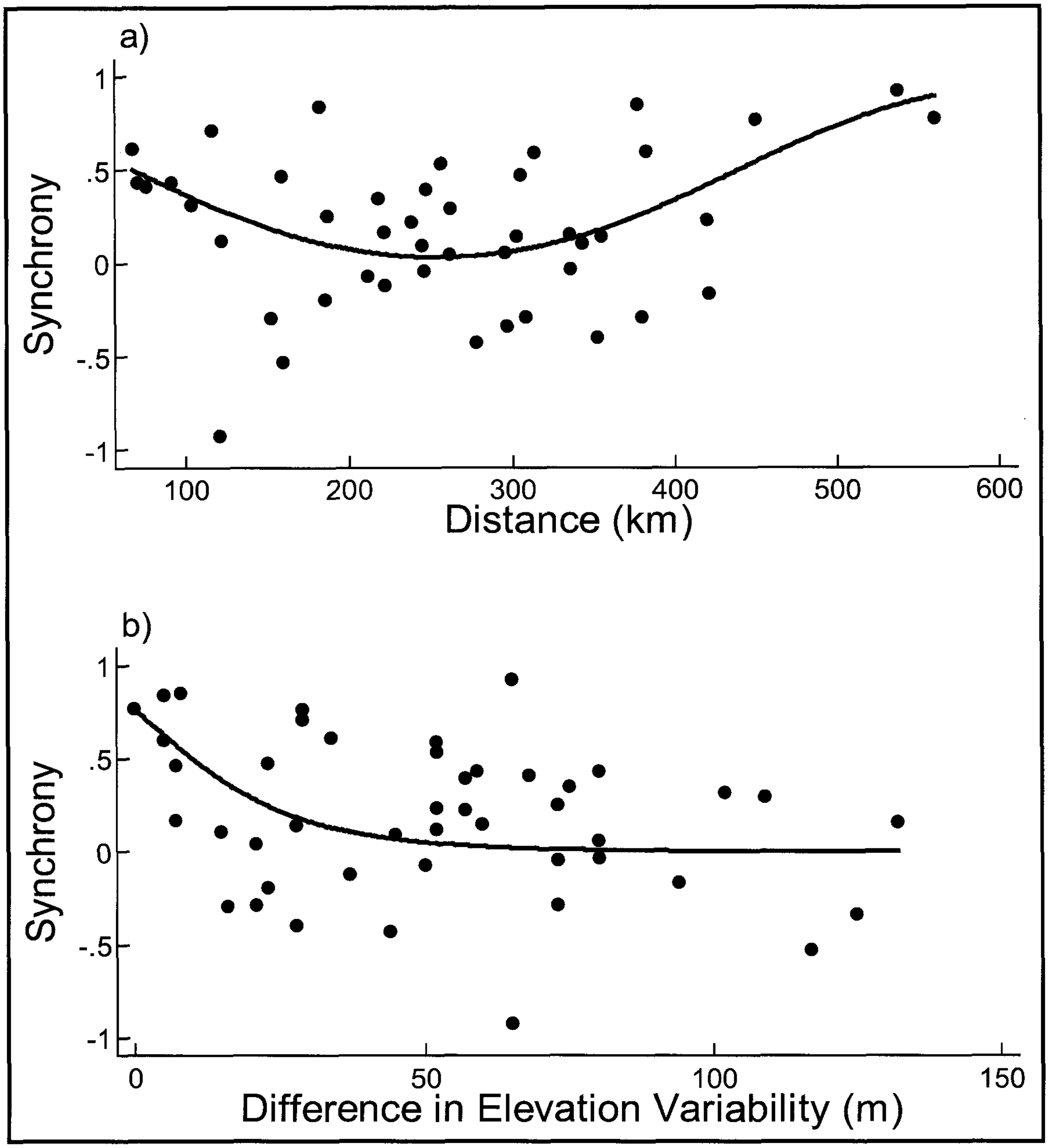

Fig. 4.5. Observed and fitted values of synchrony in mountain caribou recruitment residuals in the Yukon Territory, Canada. Filled circles indicate observed synchrony measures (pairwise Pearson correlation coefficients) and solid lines represent fitted predictions from models (Table 4.2) relating a) spatial distance between herds, and b) the difference in variability (standard deviation) of calving distribution elevation (Elev-SD in Table 4.1). Model predictions were initially generated as Fisher z-transformed values, and subsequently back-transformed for reporting.

Appendix 4A. Chapter 4 Supplementary Tables

Table 4.A-1. Terrain metrics and details regarding data availability and range areas for a) annual, and seasonal [b) winter; c) calving] distribution of 10 mountain caribou herds in the Yukon Territory, Canada, used to assess synchrony in recruitment.

Variable[a]	Aishihik	Burwash	Carcross	Chisana	Ethel Lake	Finlayson	Ibex	Klaza	Tatchun	Wolf Lake
a) Annual Distribution										
Elev-Mean (m)	1379.21	1326.43	1061.75	1392.93	1168.35	1235.16	1417.19	1250.45	1111.73	1254.57
Elev-Max (m)	2320	2314	2184	2765	2177	2317	2129	1995	2108	2178
Elev-Min (m)	784	685	612	590	597	753	950	632	546	709
Elev-Range (m)	1536	1629	1572	2175	1580	1564	1179	1363	1562	1469
Elev-SD (m)	266.73	301.08	301.81	316.88	284.21	279.00	232.23	196.25	310.21	237.25
Northness	-0.0062	-0.0049	-0.0088	-0.0097	-0.0031	-0.0090	-0.0032	-0.0037	-0.0070	-0.0083
Northness-SD	0.7082	0.7076	0.7065	0.7070	0.7074	0.7067	0.7070	0.7075	0.7066	0.7070
Eastness	0.0040	0.0039	0.0063	0.0071	0.0025	0.0055	0.0051	0.0024	0.0018	0.0037
Eastness-SD	0.7060	0.7065	0.7076	0.7071	0.7068	0.7074	0.7072	0.7067	0.7076	0.7072
# observations	2338	895	1444	6510	346	4568	673	1032	429	1710
a[b] (km)	178	105	234	203	105	214	79	123	150	208
90% Isopleth Area (km²)	5060	1438	6216	4362	1459	7270	838	2701	3219	7687
b) Winter Distribution										
Elev-Mean (m)	1044.92	847.82	1150.65	1304.70	1071.02	943.20	1322.27	928.48	1173.90	1285.59
Elev-Max (m)	1738	1685	1857	2099	2092	1736	2471	1991	2085	2223
Elev-Min (m)	709	475	526	883	754	566	586	612	658	784
Elev-Range (m)	1029	1210	1331	1216	1338	1170	1885	1379	1427	1439
Elev-SD (m)	138.73	190.65	172.92	219.42	252.63	219.49	306.93	222.49	290.95	263.85
Northness	-0.0130	-0.0088	-0.0053	-0.0041	-0.0128	-0.0071	-0.0110	-0.0120	-0.0114	-0.0072
Northness-SD	0.7063	0.7069	0.7073	0.7073	0.7057	0.7064	0.7070	0.7052	0.7064	0.7077
Eastness	0.0062	0.0038	0.0011	0.0020	0.0091	0.0064	0.0066	0.0082	0.0050	0.0051
Eastness-SD	0.7077	0.7073	0.7069	0.7069	0.7084	0.7078	0.7071	0.7088	0.7077	0.7065
# observations	849	292	671	1961	103	1974	236	426	109	699
a (km)	152	100	212	203	105	166	57	113	109	158
90% Isopleth Area (km²)	4148	1247	2537	4302	800	2843	467	2075	2089	2522
c) Calving Distribution										
Elev-Mean (m)	1492	1384	1257	1346	1233	1267	1596	1352	1357	1330
Elev-Max (m)	2095	2039	1894	2307	1693	1804	2009	1928	1821	1746
Elev-Min (m)	771	742	656	608	801	759	1089	763	690	816
Elev-Range (m)	1324	1297	1238	1699	892	1045	920	1165	1131	930
Elev-SD (m)	275	309	332	280	200	280	252	207	259	215
Northness	0.009	0.001	0.0422	-0.0003	-0.0034	-0.057	0.0653	-0.0394	-0.141	-0.125
Northness-SD	0.704	0.687	0.718	0.718	0.639	0.755	0.739	0.7212	0.695	0.6756
Eastness	0.0166	-0.196	-0.0003	-0.0022	-0.0417	0.0433	0.259	0.0214	-0.029	-0.0594
Eastness-SD	0.707	0.693	0.68	0.696	0.768	0.646	0.618	0.681	0.704	0.72
# observations	257	96	116	1143	29	130	24	137	51	173

a:Terrain variables defined in Table 4.1; b: Parameter determining the radius placed around each location for estimation of local convex hull ranges using LoCoh.

Table 4.A-2. Results of nonlinear exponential decay models (Eq. 4.1) relating synchrony (n = 45) in mountain caribou recruitment in the Yukon Territory, Canada, to differences in terrain features, and spatial distance (Distance), between herds. Only estimable models are reported as not all models with variables listed in Table 1 converged during estimation. The model including the distance variable is represented by a quadratic function. All models were fitted such that ρ_0, the synchrony when the model variable equals 0.0 (i.e., no difference between herds), was fixed to 1.0.

Variable[a]	*K*[b]	Log-likelihood	AIC*c*	ΔAICc	*w*[c]
Distance + Distance^2	3	-32.00	70.58	0	0.73
C-Elev-SD	2	-34.23	72.74	2.16	0.25
C-Northness	2	-38.19	80.66	10.08	< 0.01
W-Elev-Range	2	-38.38	81.05	10.47	< 0.01
W-Elev-SD	2	-38.70	81.69	11.11	< 0.01
W-Elev-Max	2	-38.80	81.89	11.31	< 0.01
A-Elev-Mean	2	-38.94	82.17	11.59	< 0.01
C-Elev-Mean	2	-39.35	82.99	12.41	< 0.01
A-Elev-Max	2	-39.55	83.38	12.80	< 0.01
A-Northness	2	-39.58	83.45	12.87	< 0.01
C-Elev-Min	2	-39.67	83.62	13.04	< 0.01
C-Eastness	2	-39.87	84.02	13.44	< 0.01
W-Elev-Min	2	-39.94	84.16	13.58	< 0.01
C-Elev-Range	2	-40.37	85.02	14.44	< 0.01
W-Elev-Mean	2	-40.37	85.03	14.45	< 0.01
A-Elev-Range	2	-40.54	85.37	14.79	< 0.01
C-Elev-Max	2	-40.54	85.37	14.79	< 0.01
A-Elev-SD	2	-40.96	86.20	15.62	< 0.01
W-Eastness-SD	2	-41.11	86.50	15.92	< 0.01
C-Eastness-SD	2	-41.34	86.97	16.39	< 0.01
A-Northness-SD	2	-41.49	87.27	16.69	< 0.01
W-Northness-SD	2	-40.79	88.17	17.59	< 0.01

a: Variables defined in Table 1. The 'A', 'C', and 'W' before each variable indicates whether the variable represents Annual, Calving, or Winter features, respectively; b: Number of model parameters including σ^2;
c: Akaike weight.

CHAPTER 5 GENERAL CONCLUSION

5.1 Dissertation Summary

Recruitment in mountain-dwelling woodland caribou in the Yukon demonstrates substantial annual variability both temporally and spatially (Fig. 2.2). Understanding mechanisms contributing to this variability can be used for managing and conserving these herds. Pacific-based climate provides one source of this annual variability. Recruitment in these herds is influenced by climatic conditions during winter preceding birth and at or immediately before calving (Objective 1). The weak influence of climate preceding conception (late September to early October), which would influence female body condition and subsequently fecundity (Cameron *et al.* 1993; Langvatn *et al.* 2004), indicates that on average, pregnancy rates are not a limiting factor for recruitment. Mountain-dwelling caribou in the Yukon (Farnell & Gardner 2002) and British Columbia (Wittmer, Sinclar & McLellan 2005; Gustine *et al.* 2006) demonstrate generally high and stable pregnancy rates. Given this low annual variability in pregnancy rate, a weak pre-conception climate effect is understandable. This further suggests that forage-limitation is not a contributing factor for recruitment dynamics.

Results from Chapter 2 indicate two possible mechanisms explaining recruitment patterns in these herds. First, the presence of a climatic effect during gestation (i.e. winter) may result in females losing their calves in years with severe winters. Parturition rates are generally more variable than pregnancy rates (Farnell & Gardner 2002; Gustine *et al.* 2006). During severe winters (e.g. high snowfall), females may be unable to devote sufficient resources to fetal development. Second, environmental conditions at calving caused by overwinter snowfall, for example, or weather patterns at or immediately before calving (Chapter 3), may result in parturient females unable to disperse away from predators and/or other parturient females (Bergerud & Page 1987) or possibly direct losses of neonates due to harsh weather conditions although Miller & Gunn

(1986) suggest this source of neonate mortality is unlikely. This may result in higher predation rates on neonates during these years or reduced calf survival during summer if the nutritional quality of forage resources is inadequate (Pettorelli *et al.* 2007). The majority of research on climatic effects on ungulate population dynamics focuses on winter effects. Our results demonstrate that investigating climate effects during different seasons is warranted depending on the various mechanisms by which climate acts on vital rates.

Given the value of using large-scale climate indices for investigating ecological processes (e.g. Stenseth *et al.* 2003), identifying an appropriate climate index is critical (Objective 2). In the Yukon, the Pacific Decadal Oscillation (PDO) proved a useful index in this study (Chapter 3) and elsewhere (Hik & Carey 2000; Morrison & Hik 2007; Joly *et al.* In Press). While the North Pacific Index proved a good predictor in the Canadian Rocky Mountains (Hebblewhite 2005), the PDO was a better predictor in the Yukon. Our research (Chapter 3) also demonstrated that large-scale climate indices were better predictors than local weather measurements (Objective 3) in modeling recruitment patterns. This may reflect the complexity of how weather interacts to result in "on the ground" environmental conditions actually experienced by caribou. Particularly with respect to snowfall patterns, these can be influenced by temperature, precipitation and wind patterns that may be difficult to capture in one local metric. Additionally, given the wide-ranging spatial distribution of these herds (Fig. 1.2), a single local weather measurement may not be able to capture the broader spatial variability. Large-scale indices may better capture this spatial variability as well as incorporating a broader window of variability (i.e. seasonally) making these climate indices good predictors (Stenseth & Mysterud 2005). This finding may not be applicable in other systems and would largely depend on the strength of the relationship between a chosen climate index and local weather. Further, in systems where one single weather variable is the primary ecological driver, an integrated climate index may in fact be too complex and thus a single weather variable would be more useful (e.g. Ogutu & Owen-Smith 2003).

The varied factors affecting caribou do not act in isolation and assessing how they interact may provide a more complete ecological understanding of the processes influencing recruitment (Objective 4). Our research has shown that both climate and wolf predation interact to influence recruitment and that their individual effects are non-additive, that is their effects vary depending on levels of the other (Chapter 3). The effect of wolf predation (measured through wolf density) was stronger during poorer springs (low April-PDO) whereas the effect of April-PDO was virtually eliminated during peak wolf removal in the Finlayson herd. This effect was striking in that it indicates that springtime climate only has a strong effect in the presence of an additional variable (i.e. wolves). This is likely due to how spring climate influences environmental conditions at calving and subsequently how those environmental conditions affect predation rates. These findings clarify the importance of knowing the ecological processes affecting a variable of interest, such as recruitment, in order to accurately interpret how different variables influence it. Without this mechanistic knowledge the likelihood of faulty inference and management will increase.

Spatial synchrony in population dynamics is a relatively ubiquitous pattern across taxa (Liebhold, Koenig & Bjørnstad 2004). We assessed the degree of spatial synchrony in recruitment of mountain-dwelling caribou herds across the Yukon (Chapter 4, Objective 5). Average spatial synchrony in recruitment was low; however, the degree of synchrony between herds ranged widely. Spatial distance between herds was the best predictor of the level of synchrony between herds. However, the inverse quadratic pattern of this synchrony-distance effect was unexpected suggesting additional factors are influencing recruitment patterns. The lack of such an inverse quadratic pattern in snow depth across the Yukon generally rules out covariation in weather patterns at larger distances. The best terrain predictor of synchrony between herds was the similarity of calving site elevation variability, suggesting that these herds may have more similar climatological downscaling within their ranges. A possible explanation for the weak average spatial synchrony in recruitment reported here is the high level of landscape heterogeneity found across the Yukon; thus reducing the similarity in environmental conditions experienced by different herds.

5.2 Management Implications

1. The strong effect of the PDO on recruitment reported here, added to the PDO's effect on Dall's sheep horn growth (Hik & Carey 2000) and collared pika survival (Morrison & Hik 2007), indicates the PDO is a meaningful large-scale climate index for studying environmental phenomena in the Yukon. Given the remoteness of many areas of the Yukon and the lack of weather stations, using the PDO to investigate how annual environmental variability affects ecological dynamics is a viable tool for wildlife managers. Additionally, that the PDO proved a better predictor of recruitment than local weather measurements indicates the potential importance of using an integrated index of annual environmental variability than one single weather metric. Given the complexities of how different weather variables interact to influence ecological patterns, focusing solely on a single weather metric may not provide the complexity necessary to accurately identify factors affecting those patterns. If management decisions are to be informed by an understanding of how annual environmental variability shapes ecological patterns, missing or incomplete information can have significant effects on the decision-making process resulting in inaccurate decisions being made.
2. Results from Chapter 2 suggest that on average, female body condition is not a likely factor affecting the variability in recruitment patterns observed in the Yukon. Thus, management actions directed towards recruitment should focus either on factors affecting parturition rates, such as late winter habitat, or early calf survival. However, the recruitment index used here cannot discern between

parturition and early calf survival, and both demonstrate substantial annual variability. Therefore this research cannot reliably determine which vital rate management actions should be directed toward without additional research. Nevertheless, late winter, calving, and post-calving habitat are important considerations when assessing environmental impacts of anthropogenic effects in caribou range. Impacts on these ranges may be dynamic dependent upon the annual climatic conditions. Thus, impacts of anthropogenic activities could be assessed under a range of annual conditions to more accurately reflect their influence on caribou.

3. Understanding how climatic variability influences recruitment dynamics, and hence herd sizes, could be considered in developing dynamic harvest systems. If managers have an understanding of the number of recruits into a herd, this information can be used to ensure harvest is conducted in a sustainable manner. This may be particularly important following a number of years with poor climatic conditions (i.e. low PDO) in which recruitment may be low. Maintaining a high harvest rate during these years could result in overharvesting, thus exacerbating reduced recruitment. Information on the effect of climatic variability on recruitment could also be provided to the hunting public to inform them of changes in animals available for harvest such that they can adapt their own expectations to changing conditions.

4. The strong interaction effect between wolf density and spring climate demonstrates the importance of understanding the mechanistic processes which effect recruitment. Management actions directed at predation (e.g. wolf control) should consider how external annual environmental variability may influence their results. In years having good springs (i.e. high PDO), recruitment with and without wolf removals in effect near one another (Fig. 3.3). Thus, the success, or failure, of a management intervention may largely be influenced by non-manageable factors such as climate. Prior to undertaking expensive and

controversial actions such as predator control, a thorough understanding of relevant ecological relationships should be known.

5.3 Future Research Recommendations

1. A more detailed understanding of how the PDO is related to local weather variables across the Yukon would assist managers in understanding the mechanisms by which it influences ecological processes. This would include examining the PDO-weather relationship using more sites and across a range of terrain gradients, as these terrain features influence the climatological downscaling process. Additionally, because of the Arctic Ocean's influence from the north, an assessment of the PDO's influence geographically would be useful as it would indicate where the PDO's influence is weakened or lost.
2. The recruitment index used in this research (i.e. fall calf:cow ratio) incorporates both parturition rates and early calf survival rates. These vital rates have differing factors operating on them mechanistically and for management actions directed at recruitment to be delivered most effectively, research that allows the calf:cow index to be decomposed into its constituent rates is necessary.
3. This research focused on temporally varying factors influencing recruitment; however, more static factors possibly interacting with climate, for instance, may affect recruitment. These may include landscape features, habitat characteristics, and fire history. Since environmental assessments of impacts caused by anthropogenic activities within caribou ranges are often associated with their effects on habitat, incorporating these features into models of recruitment could assist managers in predicting their effects on caribou populations.
4. Coefficients from these climate-based models of recruitment should be incorporated into broader caribou population models. A number of herds in the Yukon have had multiple population estimates completed. Assessing how well these recruitment models predict known population sizes would be valuable

information to understand how sensitive population growth rate is to the PDO, and hence how much variation in population growth rate is explained by climatic processes.

5. Additional research examining what factors influence the degree of recruitment synchrony between herds will greatly assist managers in identifying important ecological mechanisms affecting caribou population dynamics. These could include other habitat factors such as fire history or human disturbance, or inter-specific interactions including predator and alternate prey densities.

5.4 References

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