How are changing environmental conditions affecting barren ground caribou movement and habitat use in Canada's north?

by

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Abstract

The Arctic is currently experiencing some of the most dramatic warming effects globally due to climate change. Barren ground caribou (*Rangifer tarandus groenlandicus*) herds in Canada's north are particularly susceptible to climate change as they occupy Arctic and sub-Arctic environments and as grazers respond directly to changing vegetation conditions.

Examining the associations between barren ground caribou and their environment across their entire range presents specific and substantial challenges. Large herd ranges make in-situ habitat monitoring studies difficult and expensive. Additionally, the environments barren ground caribou inhabit are extremely remote and not spatially consistent between years. As such, new techniques are required that address the large scale, remote, and temporally variable nature of these animals. Within this PhD Dissertation, I integrate newly developed remotely sensed environmental data sets with multiple caribou data sets to explore how changing environmental conditions are affecting barren-ground caribou movement and habitat use in Canada's north.

Barren ground caribou's effects on summer range productivity were assessed to explore top down controls on vegetation productivity. Based on my results, I argue that while there is some association between barren ground caribou density and future summer range vegetation productivity, it is unlikely that range degradation is a major cause of herd declines in the herds examined here.

Habitat conditions (vegetation productivity, lichen mat condition, and fire disturbance) were documented across herd ranges to assess how barren ground caribou habitat is changing through time. These habitat conditions were then linked to movement metrics derived from barren ground caribou telemetry data to assess how changing habitat conditions are affecting caribou movement patterns. I found widespread, rapid changes in barren ground caribou habitat in line with predicted and documented climate change effects in the Arctic, and I detected significant alterations in movement metrics associated with these changes in habitat.

In all cases, remotely sensed environmental indicators were useful for describing aspects of barren ground caribou habitat. I was able to link habitat conditions to barren ground caribou at both the individual and herd levels and described novel linkages between barren ground caribou and their environment.

Lay summary

Changing climates in Canada's North are resulting in rapidly changing terrestrial environments. Plant communities are shifting away from tundra species and being replaced by shrub and forest species. Additionally, forest fires patterns are changing which further influences species composition. These changes in plant species in turn affect the animals which graze on them, in particular barren ground caribou. As herbivores, any changes in vegetation directly affect barren ground caribou's ability to access nutrition and use their habitats. This dissertation aimed to investigate how barren ground caribou habitat has changed since the mid-1980s and how these changes are influencing barren ground caribou habitat use.

I detected widespread changes in vegetation, lichen, and fire across the ranges of five herds located primarily in the Northwest Territories and Nunavut, Canada. Generally speaking, herd ranges are becoming more productive and have less lichen. Forest fires tended to eliminate foraging in areas they affected.

Preface

My supervisory committee, manuscript co-authors, and I developed the research questions, hypotheses, and research objectives through a series of meetings and discussions throughout my degree. The majority of the research presented here has been published in peer-reviewed journals, with each publication listed below. In each manuscript I was responsible for developing the overall approach, analysis, data processing, and the writing. Co-authors were involved as advisors, providing important feedback on manuscript development and in certain circumstances provided environmental data inputs – specifically the NTEMS data set used in Chapters 4 through 6.

Chapter 3: **Rickbeil, G.J.M.**, Coops, N.C., Adamczewski, J. (2015) The grazing impacts of four barren ground caribou herds (*Rangifer tarandus groenlandicus*) on their summer ranges: an application of archived remotely sensed vegetation productivity data. Remote Sensing of Environment, 164: 314-323.

Chapter 4: **Rickbeil, G.J.M.**, T. Hermosilla, N.C. Coops, J.C. White, M.A. Wulder, T.C. Lantz (2017) Changing northern vegetation conditions are influencing barren ground caribou (*Rangifer tarandus groenlandicus*) post-calving movement rates. In Review.

Chapter 5: **Rickbeil, G.J.M.**, Hermosilla, T., Coops, N.C., White, J.C., Wulder, M.A. (2017) Estimating changes in lichen mat volume through time and related effects on barren ground caribou (*Rangifer tarandus groenlandicus*) movement. PloS one, 12(3), p.e0172669.

Chapter 6: **Rickbeil, G.J.M.**, T. Hermosilla, N.C. Coops, J.C. White, Wulder, M.A. (2016) Barren ground caribou (*Rangifer tarandus groenlandicus*) behaviour after recent fire events; integrating caribou telemetry data with Landsat fire detection techniques. Global Change Biology, Published On-Line, DOI: 10.1111/gcb.13456.

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AVHRR – Advanced Very High Resolution Radiometer

dNBR – Differenced Normalized Burn Ratio

EVI – Enhanced Vegetation Index

GAMM – Generalized Additive Mixed Model

GLS – Generalized Least Squares Regression

GPS – Global Positioning System

LVE – Lichen Volume Estimate

MODIS – Moderate Resolution Imaging Spectroradiometer

NBR – Normalized Burn Ratio

NDVI – Normalized Difference Vegetation Index

NWT – Northwest Territories

NTEMS – National Terrestrial Ecosystem Monitoring System

TS – Theil-Sen’s Non-Parametric Regression

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I am hugely indebted to my MSc and PhD supervisor Dr. Nicholas Coops. Dr. Coops is a force and this Dissertation would have never happened had he not forgotten my name in his office almost 6 years ago. This was not a career path I expected to find myself on but Nicholas saw something in me and I am better for it. I feel privileged that I have called him my supervisor and will continue to call him my friend.

My supervisory committee played a major role in the development of this Dissertation and my development as a scientist. Dr. Jan Adamczewski has continuously provided strong feedback regarding caribou ecology and their importance in the north. I am especially grateful to him for inviting me into his home on multiple occasions to get some firsthand experience regarding caribou management at the government level. Dr. Trevor Lantz provided critical feedback, especially during the development of the vegetation productivity work, and Dr. Sarah Gergel was equally important for suggestions and feedback on all topics.

This Dissertation would have been far poorer has it not been for the input of my co-authors on the various manuscripts which have been published from this work. Dr. Mike Wulder and Joanne White are two of the best collaborators I have ever worked with. They are timely, professional, and most importantly, talented researchers and I thank them both for their help. Dr. Txomin Hermosilla was the driving force behind the NTEMS project which was a data set I relied upon heavily. Your work and your friendship are both fantastic.

A few other scientists deserve recognition in getting me to this point. Dr. Nancy Mahony and Dr. Mark Drever from Environment Canada have both provided input, co-authorship, and work throughout the years. Dr. Trisalyn Nelson and Mathieu Bourbonnais from what was the SPAR

lab at the University of Victoria both helped with advice on telemetry data among other things. Dr. Suzie Lavallee, Greg Greene, and Cora Skaien were fantastic field buddies for years. I am also grateful for the financial support the National Science and Engineering Council of Canada and the UBC Faculty of Forestry has provided to me for both my MSc and PhD.

I have been far too lucky with friends over the years and many directly supported this research with advice – Dr. Doug Bolton, Dr. Piotr Tompalski, Dr. Wiebe Nijland, Dr. Andres Varhola, Igancio San-Miguel and everyone else in the IRSS lab. You made years of staring at a computer not only bearable but fun.

Greg Day has gotten me into some of the most fun and most ridiculous situations of my life – thank you? David and Thomas Bernardino have been surrogate brothers over the years, and Carlos and Yvonne Bernardino and Angela and Doug Henning surrogate parents. Julia and Marcus, you two make up the two other legs of my tripod and I don't know where I'd be if you weren't in my life always. My aunts and uncles on both sides have always been fantastic to me and I am grateful to them all. In particular, aunt Fran and uncle Ken, your support and generosity is unparalleled and I am lucky to have you. My brother Scott and my sister Erin - I love you both very much and I am thankful I got so lucky with my family. And my parents – Jim and Doreen – as always you're the best thing I've got going and I love you. Keep enjoying that retirement!

For Elliot

Someday this might be you writing about birds

And for Wren

Who knows what you’ll do – I do know it will be amazing

And for Ron Swanson Rickbeil

Thanks for the help

Chapter 1: Introduction

1.1 Barren ground caribou

Barren ground caribou (*Rangifer tarandus groenlandicus*) are the most numerous large herbivore that fulfils a portion of their life history north of the treeline in Canada's Arctic and represent North America's longest-range large mammal migrant (Berger, 2004; Festa-Bianchet et al., 2011). They are typically grouped into migratory herds which have distinct calving and summer ranges (Gunn and Miller, 1986; Schaefer et al., 2000); winter ranges are usually larger and may overlap between neighbouring herds (Schaefer et al., 2000). Barren ground caribou affect Arctic and sub-Arctic habitats, playing an important role in modifying these environments through grazing and trampling (Manseau et al., 1996; Zamin and Grogan, 2013).

Migratory barren ground caribou herds undergo large rapid decadal fluctuations in abundance (Gunn, 2003). These fluctuations are often loosely synchronized across herds (Vors and Boyce, 2009); however, this is not always the case (Joly et al., 2011). Since the 1980s all herds monitored by the Northwest Territories (NWT) Government have declined in abundance, in some cases by more than an order of magnitude (see Table 2.1 in Section 2.2.1.3.).

As grazers, caribou diets vary by season depending on forage availability and nutritional needs (Jandt et al., 2008); however, terricholous lichen mats (primarily *Cladonia* type lichens) form a portion of caribou diets at all times (Bergerud, 2000) and are the majority of caribou forage in winter months (Joly et al., 2010). Terricholous lichens are high in digestible energy, making them valuable (and highly available) winter forage when energy demands are high (Jandt et al., 2008; Joly et al., 2010). Terricholous lichens are consumed rapidly by fire owing to their low moisture content and location (Jandt et al., 2008). However, when individuals, especially cows during spring and summer, are focused on gaining fat stores, lichens are less of a focal forage owing to their low protein and fat content (Cebrian et al., 2008; Joly et al., 2010).

1.1.1 Barren ground caribou herds examined in this Dissertation

The five herds forming the basis of my thesis are located in the Northwest Territories and Nunavut, Canada. These five herds are all monitored by the Government of the Northwest Territories who provided data access for this Dissertation. Their winter range extends south into the northern Boreal forest, while their summer ranges and calving grounds occur on the continental tundra north of the treeline. Collectively, the area these five herds utilize is approximately 700 000 km^2. From west to east, these herds are known as: the Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Ahiak/Beverly.

1.1.2 Barren ground caribou movement

Migration is an adaptive behavior that allows animals to increase their access to nutritional resources (Baker, 1978; Fryxell et al., 1988; Holdo et al., 2009), reduce their exposure to predation (Fryxell et al., 1988; Seip, 1991, Heard et al., 1996), and lessen parasite loads/avoid parasitism (Folstad et al., 1991; Hughes et al., 2009). The development of migratory behavior in populations is commonly found in locations where environmental resources vary seasonally, resulting in spatially and temporally variable population growth rates (Fryxell et al., 1988; Millner-Gulland et al., 2011).

Barren ground caribou take advantage of this aspect of migration, moving north from their wintering ground tracking the green up of tundra vegetation (Heard et al., 1996; Bergerud, 2000). In the fall, barren ground caribou migrate south towards the Boreal forest treeline where they typically over winter as it provides access to nutrition in the form of ground lichens with softer snow cover than on the tundra (Festa-Bianchet et al., 2011). Migration, in particular the movement away from the Boreal forest in the spring by pregnant females, lessens the predation risk of barren ground caribou from wolves which occupy the Boreal forest at much higher densities than the tundra (Heard et al., 1996).

1.1.3 Top-down influences of barren ground caribou versus bottom-up influences of habitat conditions

The concept of top-down versus bottom-up controls in trophic systems refers to which trophic levels exert the most influence on the other trophic levels in the system (Hunter and Price, 1992; Power, 1992). In low productivity terrestrial Arctic ecosystems a top-down hypothesis referred to as the exploitation ecosystem hypothesis (Fretwell, 1977; Oksanen et al., 1981) argues that in absence of significant predation pressure top-down herbivory can regulate vegetation. Barren ground caribou grazing on vegetation has been shown to regulate vegetation productivity in both semi-domesticated reindeer herds in Scandinavia (Skogland, 1985; Tveraa et al., 2013) and wild caribou herds in Greenland (Post and Pedersen, 2008) and Quebec, Canada (Manseau et al., 1996). The concept of top-down grazing effects of barren ground caribou on their summer range will be assessed in Chapter 3 (Figure 1.1).

Conversely, bottom-up habitat conditions can affect caribou in numerous and complex ways. Bottom-up influences on caribou can include: forage productivity (Heard et al., 1996; Bergerud, 2000), vegetation community composition, vegetation structure (affecting wind speed which affects insect harassment (Hagemoen and Reimers, 2002; Weladji et al., 2003)), disturbance history (Joly et al., 2010), and snow among others. Environmental influences, including forage conditions and fire disturbances, on barren ground caribou will be assessed in Chapters 4, 5, and 6 of this Dissertation (Figure 1.1).

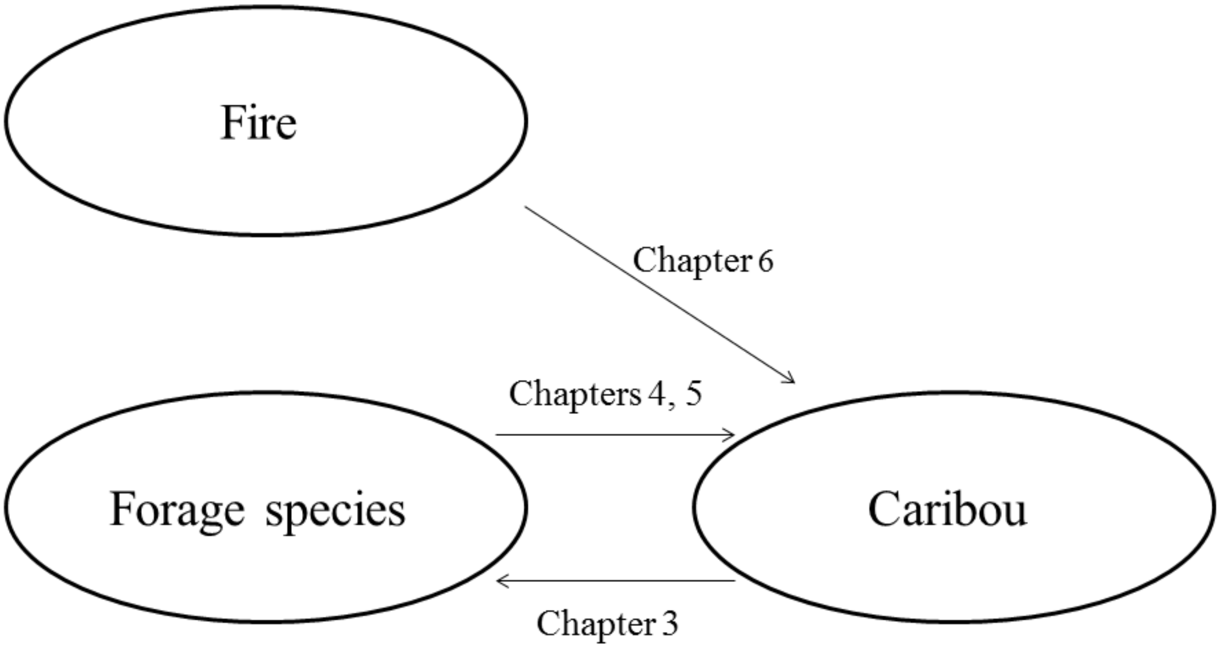

Figure 1.1 Conceptual structure of the research presented in this Dissertation. Arrow direction indicates whether a Chapter is examining top-down (Chapter 3) or bottom-up (Chapters 4, 5, and 6) effects.

1.2 The Arctic and Boreal environments

Barren ground caribou spend much or all of the year north of the latitudinal treeline in tundra ecosystems (Figure 1.2) (Bergerud 2000), although some populations, particularly in the northeast, spend the entire year or much of it on the tundra. Tundra ecosystems vary with regard to their dominant vegetation or organism type (i.e. lichens), with graminoid communities, moss/lichen dominated communities, shrub communities, and landscapes which are predominantly barren. All these different ecosystems do share some common traits. They are relatively low productivity areas in terms of biomass, with short growing seasons and long winter dormancy periods (McGuire et al. 2006). Rapid temperature increases in the spring result in rapid green-up, allowing plants to take advantage of short growing seasons (Chapin et al. 2000). In tundra ecosystems, disturbance rates are not well documented (Jones et al. 2013); however, tundra fires do occur and can result in vegetation community shifts given certain conditions are met (Bret-Harte et al. 2013).

Shrub expansion (or shrubification) has rapidly transformed many areas of the low Arctic (Lantz et al., 2010, Myers-Smith et al., 2011). In the Tuktoyaktuk Coastlands the influx of green alder (*Alnus viridis*) and dwarf birch (*Betula nana exilis*) has significantly reduced the amount of lichen and graminoid dominated tundra within several decades (Fraser et al., 2014). Myers-Smith et al. (2011) detected significant shrub proliferation at the northern extent of each population's range, indicating that warming temperatures may be driving the expansion. Based upon multiple data sets, including remotely sensed data, large portions of tundra are becoming greener across the Arctic (Chapin et al., 2000; Euskirchen et al., 2006; Kimball et al., 2006; Myers-Smith et al., 2015; Xu et al., 2013).

The Boreal forest (Figure 1.2), used during late fall, winter, and early spring by migratory barren ground caribou, is a continuous biome in North America stretching from Alaska to Labrador/Newfoundland, as well as across Europe and Russia. It is a low productivity forest, forming the northern extent of continuous tree growth in the northern hemisphere. Historically, the Boreal forest in Canada has been dominated by spruce (black and white) and pine (lodgepole and jack) stands (Chapin et al. 2000); however, evidence suggests that in some regions deciduous and mixed wood stands are becoming more frequent due to changing permafrost conditions and fire regimes (Johnstone et al. 2010a, 2010b). Boreal forests can have discontinuous permafrost layers at varying depths (Chapin et al. 2000) and have well developed organic layers, especially in black spruce dominated areas (Hart and Chen 2006). Fire is the most prevalent disturbance type in the Boreal forest, with large, stand replacing fires occurring frequently (Kasischke and Turetsky, 2006). The area burned in the Boreal forest has been shown to have increased substantially over the past century (Kasischke and Turetsky, 2006; Kelly et al., 2013), with larger fires and longer burning seasons being the likely causes. Severe fires which remove organic layers, melt permafrost (Chapin et al., 2010), and destroy aerial black spruce seed banks (Johnstone et al., 2009) are the most likely to shift the previous black spruce dominated ecosystem towards a deciduous dominated ecosystem (Johnstone et al., 2010a; 2010b).

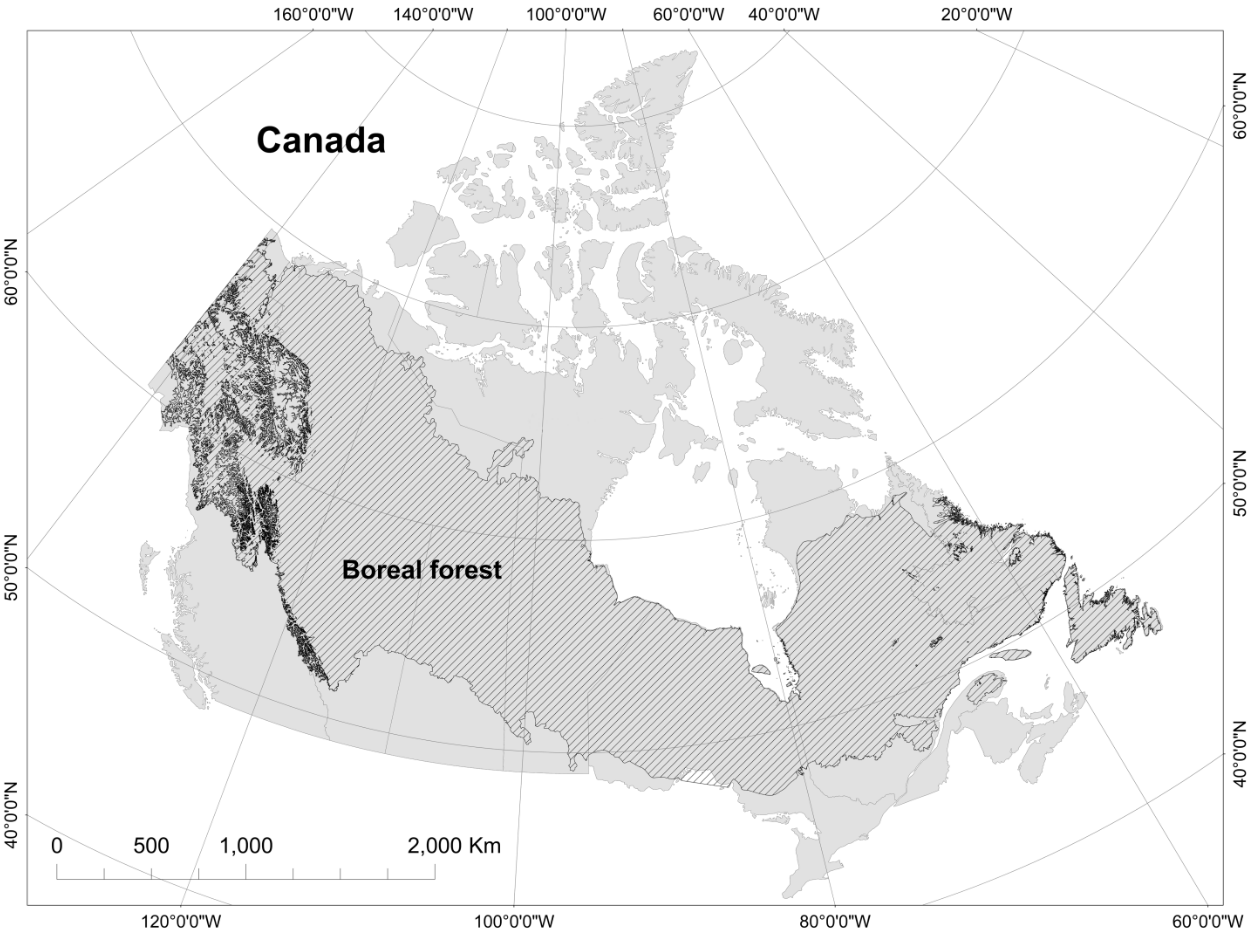

Figure 1.2 The generalized extent of the Boreal forest (Brandt 2009) in Canada.

1.3 Remote sensing for spatially and temporally assessing barren ground caribou habitat

Assessing how migratory tundra caribou interact with their environment presents substantial challenges. They are highly mobile species, traveling thousands of kilometers in any one year (Bergerud 2000; Berger 2004); categorizing their environment thus requires data which are equally expansive. Additionally, caribou utilize habitat in the northern portion of Canada where in-situ data collection is both difficult and expensive. Fortunately, satellite remote sensing programs are available to address some of these challenges by monitoring vegetation at a global scale in a repeatable manner through time (Woodcock et al. 2008, Wulder et al. 2012). The selection of which remotely sensed data product should be used needs to be considered in context of the question being asked. If inter-annual information is required (i.e. tracking green-up or detailed productivity changes through a year) the coarse spatial resolution sensors (250m – 1 km pixels) with high temporal repeat (near daily acquisition) such as the Moderate Resolution Imaging Spectroradiometer (MODIS) or the Advanced Very High Resolution Radiometer (AVHRR) could be used. Conversely, if fine spatial resolution data is required to describe fine scale landscape level changes or link to highly accurate GPS telemetry data then Landsat may be more appropriate (30m resolution with a 16 day acquisition period). As such, the two primary remotely sensed data sets used in this Dissertation were MODIS and Landsat. MODIS was used where information on inter-annual vegetation dynamics at broad scales was needed while Landsat was used to link barren ground caribou movement patterns to their environment.

1.4 Research objectives

1.4.1 Research question

The overall research question addressed in this Dissertation is– how are changing environmental conditions affecting barren-ground caribou movement and habitat use in Canada's north?

1.4.2 Sub-research questions

This research question has been further divided into four sub-questions:

Chapter 3. Is caribou density related to summer range vegetation productivity at the landscape scale?

Chapter 4. How do changing Arctic and Boreal vegetation productivity conditions affect caribou movement rates post-calving?

Chapter 5. How do changes in lichen mat volume affect barren ground caribou movement rates across different seasons?

Chapter 6. How do fire disturbances affect barren ground caribou movement?

1.5 Dissertation overview

The proceeding Chapters of this Dissertation will focus on answering these four sub-questions and the overall research question presented above. Chapter 2 will detail the study area and data used in this Dissertation. Chapters 3 through 6 will address each sub question in order, and Chapter 7 will summarize findings, highlight areas of novel research, and suggest directions for future research.

Chapter 2: Study area and data sources

2.1 Study area

This Dissertation examines five herds occurring in the Northwest Territories and Nunavut, Canada. Collectively, the ranges of the five herds encompass over 700 000 km^2 of Boreal and tundra habitats. The winter ranges of each herd are primarily located in Boreal forest habitat, with spring and fall ranges occurring near the tree line (Bergerud, 2000). Summer ranges are generally north of the tree line on the tundra while the calving grounds are located near the Arctic Ocean at the northern extent of each herd's range. From west to east, these herds are known as: the Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Ahiak/Beverly (Figure 2.1).

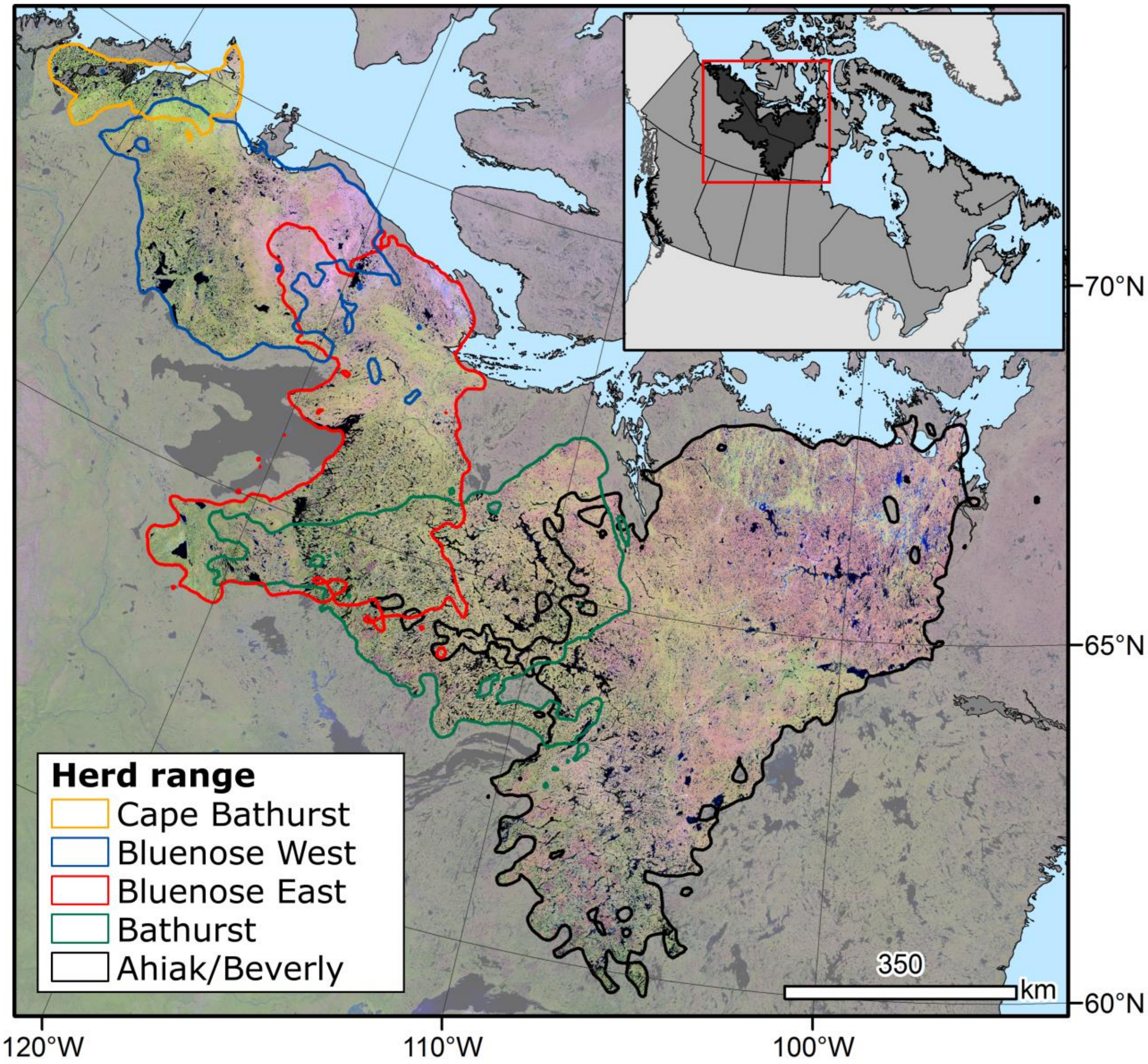

Figure 2.1 A composite, cloud free, false color Landsat image (Bands: 5, 4, 3) centered on August 1st 2011 with the herd range outlines of the five herds studied here.

2.2 Caribou data

2.2.1 Caribou telemetry data

2.2.1.1 Argos telemetry data

Satellite (Argos Doppler class 2 and 3) collar telemetry data was used in Chapter 3 to delineate summer ranges using caribou telemetry data from 1996 to 2013. Argos class 2 and 3 satellite collar data have a location error of less than 500 m and 250 m respectively 68% of the time (www.argos-system.org), representing less than half a pixel in maximum error when using remotely sensed data at 1-km spatial resolution. However, other studies, primarily focusing on marine mammals, have noted greater errors in accuracy, with Le Bouef et al. (2000) detecting errors up to 2-km for location classes 2 and 3. The numbers of collars varied among years and herds and were fixed on both bulls and cows. The Cape Bathurst data set, representing the minimum, included 26 collared animals, while the Bluenose West data set, representing the maximum, included 92 collared animals.

2.2.1.2 GPS telemetry data

GPS telemetry data was used in Chapters 4, 5, and 6 to calculate individual animal movement metrics. Depending on the herd, GPS collar data collection was initiated between 2006 and 2008 and is ongoing. GPS telemetry data provides animal locations (latitude/longitude coordinates) as well as a time stamp for each data point. GPS error in Canada’s north is typically less than 20 m (less than one 30 x 30 m Landsat pixel). Track data corresponding to an individual were used if they had at least one complete year of tracking and a minimum of three GPS points per day, resulting in a maximum time step of eight hours (some individuals were tracked at five hour time steps). In total, 258 animals (223 cows and 35 bulls) were tracked across all five herds (resulting in 325 388 GPS data points), with a maximum of 66 individuals for the Bluenose West herd and a minimum of 30 individuals for the Ahiak/Beverly herd.

2.2.1.3 Telemetry data, movement metrics, and animal behavior

Animal behaviour has been described using proxy measures derived from animal tracking data (Zollner and Lima, 1999; Dodge et al., 2008; Calenge et al., 2009; Cuiti et al., 2012). When foraging animals such as barren-ground caribou are searching for food they tend to move in a slow fashion and turn at large angles between subsequent GPS relocations (Zollner and Lima, 1999). When they are focused on movement, they tend to move in more rapid fashion and in more linear segments (Morales et al., 2004). It is important to note that there are numerous other factors affecting movement patterns for caribou (see Hebblewhite and Haydon, 2010 for a general summary of GPS collar limitations), including but not limited to: predator and insect avoidance, rutting, and landscape features such as impassable terrain and water. Consequently, movement does not directly imply behavior. The metrics used in this Dissertation represent movement (velocity and/or turning angle); while some effort has been made to relate findings to potential effects of habitat conditions on caribou behavior my focus has been to maintain the direct link between habitat and movement metrics and only offer possible ecological explanations regarding habitat and behavior.

2.2.2 Caribou herd data

2.2.2.1 Herd size estimates

Herd size estimates were used in Chapter 3 to assess the number of barren ground caribou on summer ranges for a given year. The Government of the Northwest Territories' mean herd size estimates were used as true estimates of herd size by year. Between 1986 and 2013, each herd's population size has been estimated in differing years and at varying intervals (Table 2.1) (See Boulanger et al. (2014) for details of methods). Estimates for the Bathurst herd are based on calving ground photo surveys. Calving ground photo surveys involve estimating the number breeding females on the calving ground. Survey blocks are defined based on the density caribou from an initial systematic survey. Thereafter, higher density blocks are flown and photographed at 30-40% coverage, with lower density blocks flown visually at full coverage. A composition survey is used to determine the proportion of breeding females in each block. As about half the herd are males, yearlings, and non-pregnant cows not on the calving grounds, an estimate of herd-wide pregnancy rate and an estimate of sex ratio are used to account for the remainder of the herd. Estimates for the Cape Bathurst and Bluenose-West herds are based on post-calving photo surveys conducted in July when caribou may form dense groups of hundreds or thousands in response to insect harassment. Post-calving surveys involve identifying where these groups of caribou are located using radio-collars and photographing them from small fixed-wing aircrafts for counting. Herd size is then estimated using a Lincoln-Petersen Index, modified for radio-telemetry data, to account for caribou not seen or photographed (see Nagy and Johnson (2006) for details of methods). Estimates for the Bluenose-East herd are based on post-calving surveys from 2000 - 2010 and on a calving photo survey in 2013; both calving and calving photo surveys were carried out for this herd in 2010 (Adamczewski et al. 2014).

Table 2.1 Abundance estimates and 95% confidence intervals from 1986 to 2013 for the five herds analyzed here (Government of the Northwest Territories data). Abundances lacking confidence intervals indicates that a full photographic census of the herds calving grounds was conducted, therefore the number of animals counted was recorded as the herd abundance.

Year	Cape Bathurst	Bluenose-West	Bluenose-East	Bathurst	Beverly/Ahiak
1986	13 476	88 369±6889		472 000±11 101	
1987	12 516±3504	106 887±4655			
1988					189 561±70 961
1990				351 683±16 039	
1992	19 278±5397	112 360±25 556			
1993					86 728±17 943
1994					276 000±106 600
1996				349 046±17 519	
2000	11 089±1756	76 376±14 347	119 584±25 419		
2003				186 005±8626	
2005	2434±257	20 800±2040	70 081±8120		
2006	1821±149	18 050±527	66 754±5182	128 047±5944	
2009	1934±349	17 897±1310		31 895±10 932	
2010			98 646±7125		
2011					124 189±13 996
2012	2427	20 465±3490		34 690±9756	
2013			68 295±18 040		

2.2.2.2 The Ahiak and Beverly herds

There is considerable debate regarding the current status of the Beverly herd, estimated at 276,000 individuals (95% CI = 106 600) in 1994. By 2009, however, the Beverly herd had almost completely abandoned its traditional inland calving grounds south of Garry Lakes (Adamczewski et al., 2015). The current gap in knowledge regarding the fate of the Beverly herd relates to whether the abandonment of its calving grounds was due to a large-scale shift to the traditional calving grounds of the Ahiak (or Queen Maude Gulf) herd beginning in the 1990s (Nagy et al., 2011; Campbell et al., 2012) or a large numerical reduction in Beverly herd size after which the remnant herd shifted to the Ahiak calving grounds to maintain the advantage of gregarious calving in 2006-2009 (Adamczewski et al., 2015). Here, I use the term Ahiak/Beverly to refer to these herds in the Dissertation but make no assessment of whether they currently represent one or two herds. The telemetry data used to assess individual movements of the Ahiak/Beverly herd occurs post 2006 and therefore is taken to represent both herds as one.

2.3 Environmental data

2.3.1 MODIS/AVHRR fPAR data

Remotely sensed estimates of productivity were acquired from both MODIS and AVHRR and used in Chapter 3 to estimate yearly vegetation productivity on herd summer ranges. One data source was the fPAR product available from the MODIS sensors which employs a physically based algorithm that describes the propagation of light throughout vegetation canopies (Tian et al. 2000). The fPAR algorithm uses up to 7 spectral bands to correct for sun angle, ground reflectance, and viewing angle differences. Snow, cloud, barren ground, and water masks were applied to ensure only pixels of the highest quality, and which employed only the primary fPAR algorithm (with or without saturation), were used in the productivity analyses.

In the case of AVHRR, fPAR was computed following models developed by Fontana et al. (2012) and Coops et al. (2014) (for detailed methods as well as validation of the AVHRR data used here, see Fontana et al. (2012)). As part of the development of the AVHRR fPAR archive, AVHRR NDVI was related to MODIS fPAR data during the two sensor's overlapping time periods and a linear, land cover-dependant transformation was applied (Los et al. 2000) to allow the MODIS and AVHRR fPAR data to be combined into a single fPAR archive (Fontana et al. 2012; Coops et al. 2014). Both the MODIS fPAR and AVHRR fPAR products have a spatial resolution of 1 km and provide fPAR estimates ranging from 0 to 100, with 100 indicating 100 % of light available for photosynthesis was absorbed within a given pixel. The MODIS fPAR product has an eight day temporal resolution while the AVHRR fPAR product has a ten day temporal resolution.

Currently, fPAR is employed less than vegetation metrics such as the normalized difference vegetation index (NDVI; a simple band ratio) to represent vegetation productivity; however, when calculating gross primary productivity of above ground vegetation biomass, it is fPAR rather than NDVI that is required as a model input (Monteith 1972). Changes in annual fPAR can be summarized using indices such as the Dynamic Habitat Index (DHI), which has been used successfully to describe vegetation productivity in multiple studies across Canada (Coops et al. 2008; Coops et al. 2009) and Australia (Berry et al. 2007). The DHI estimates three components of landscape productivity – the yearly sum or overall productivity, the seasonality (the change between the maximum and minimum productivity throughout the year), and minimum annual productivity (not considered here as all Arctic vegetation goes to 0 in terms of fPAR values owing to the short growing season).

2.3.2 Landsat spectral data

Landsat spectral data developed by White et al. (2014) and Hermosilla et al. (2015a; 2015b) was used in Chapters 4, 5, and 6 to estimate barren ground caribou habitat conditions. White et al. (2014) describe a pixel-based image compositing method that identifies best-available-pixels (BAP) using a series of pixel scoring functions appropriate to conditions present in Canada. These functions score each pixel observation based upon (i) Landsat sensor, (ii) acquisition day of year, (iii) distance to clouds and cloud shadows, and (iv) atmospheric opacity (related to presence of haze, smoke). For instance, measures from Landsat-5 are prioritized over Landsat-7; acquisition day of year is prioritized to target August 1 (within a plus / minus 30 day possible acquisition window); with scoring to avoid pixels near clouds or haze. Pixels with the highest scores are selected to produce the BAP image composites for a particular year. Pixels where no observations meet the BAP criteria are labelled as data gaps. BAP composites generated using this approach are further refined using pixel-level temporal screening to identify noise and remove remaining sources of possible atmospheric contamination (e.g., haze or unscreened clouds). Using the temporal series for each pixel (1984–2012), proxy infill values are generated for data gaps and noisy pixels, following the methods presented in Hermosilla et al. (2015), to create gap-free surface reflectance image composites (Figure 2a).

This results in Canada-wide, annual, Landsat surface reflectance composites with no spatial or temporal data gaps from 1984 to 2012 (Hermosilla et al., 2016) which has been called the National Terrestrial Ecosystem Monitoring System (NTEMS). Random Forests (Liaw and Wiener, 2002) were then used to classify change events based on spectral, temporal, geometrical data into an agent of change: fire, harvest, road, and non-stand replacing changes (e.g., vegetation stress) (Hermosilla et al., 2015b). This product is built using an augmentation of Canadian Landsat archive data (White and Wulder, 2014) with that of the United States Geological Survey where analysis ready image products are available on a free and open basis (Wulder et al., 2012).

2.3.3 MODIS land cover data

Broad scale land cover data was derived from the Canada Center for Remote Sensing's annual MODIS land cover product, which describes 19 land cover classes across Canada at 250 m spatial resolution from 2001 to 2011 (Pouliot et al., 2014). The 2011 year was used to represent current conditions.

Chapter 3: The grazing impacts of four barren ground caribou herds on their summer ranges; an application of archived remotely sensed productivity data

3.1 Introduction

Barren ground caribou are the most numerous large herbivore that fulfils a portion of their life history north of the treeline in Canada's Arctic and represent North America's longest-range large mammal migrant (Berger, 2004). They are typically grouped into herds which have distinct calving and summer ranges (Gunn and Miller, 1986; Schaefer et al. 2000); winter ranges are usually larger and may overlap between neighbouring herds (Schaefer et al., 2000). Barren ground caribou affect their Arctic and sub-Arctic habitats, playing an important role in modifying these environments through grazing and trampling (Manseau et al., 1996; Zamin and Grogan, 2013).

Barren ground caribou herds undergo rapid (within a few decades) large fluctuations in herd abundance (Gunn, 2003). These fluctuations are commonly loosely synchronized across herds (Vors and Boyce, 2009); however, this is not always the case (Joly et al., 2011). Since the 1980s all monitored herds occurring within the Northwest Territories (NWT) have declined in abundance, in some cases by more than an order of magnitude (See Table 1 in Methods – Caribou herd size estimates).

Overgrazing and trampling (hereby referred to as overgrazing) on herd summer ranges resulting in forage degradation has been proposed as a possible factor contributing to caribou and reindeer (*Rangifer tarandus*) herd fluctuations (Skogland, 1985; Manseau et al., 1996; Tveraa et al., 2013). Overgrazing on herd summer ranges resulting in range degradation, in particular, was suggested as contributing significantly to the decline in the George River herd in Quebec/Labrador, Canada, when the herd size exceeded 600, 000 individuals (Manseau et al., 1996). Additionally, overgrazing effects have been clearly demonstrated in heavily managed reindeer herds in Scandinavia (Skogland, 1985; Tveraa et al., 2013). This hypothesis indicates that as herd densities increase, a reduction in forage quantity and/or quality occurs. Overgrazing effects were demonstrated at the plot level using exclosure experiments on caribou and reindeer summer ranges (Manseau et al., 1996; Olofsson et al., 2010) where a near doubling of certain preferred forage species' biomass was observed in one exclusion study (Zamin and Grogan, 2013). The overgrazing hypothesis has not, however, been extended from the plot to the landscape level for barren ground caribou, which is a critical step if it is to be supported or rejected as a possible cause of herd fluctuations in abundance. The recent declines of multiple herds of caribou in continental North America provides a unique opportunity for a natural experiment examining the effects of changes in herd density on productivity at the landscape scale (Zamin and Grogan, 2013) without relying on artificial exclosures.

Assessing how caribou interact with their environment presents substantial challenges. They are highly mobile species, traveling thousands of kilometers in any one year (Berger, 2004). Categorizing their environment thus requires data which are equally expansive. Additionally, caribou utilize habitat in the northern portion of Canada and in-situ data collection in Canada's tundra is both difficult and expensive. Fortunately, satellite remote sensing programs are available to address these challenges by monitoring vegetation at a global scale in a repeatable manner through time, in some cases starting in the 1970s or 1980s. In particular, the Moderate Resolution Imaging Spectroradiometer (MODIS) allows for near daily coverage of Canada's tundra ecosystems and has a suite of vegetation indices for assessing how these ecosystems are changing through time. Unfortunately, these indices are only available since satellite launch, limiting their historical archive to 2002, which does not provide a long enough sequence to detect changes occurring over longer time frames than the archive. Recent work has extended certain MODIS products back in time by correlating them with imagery acquired by older sensors with longer archives. Specifically, Fontana et al. (2012) developed relationships between reflectances observed by MODIS and the Advanced Very High Resolution Radiometer (AVHRR) to extend satellite observations from the present back to 1987. As a result, it is now possible to use remote sensing archive data to assess caribou – vegetation productivity relationships over a 27 year period dating from 1987 to 2013 using these two datasets.

An important vegetation metric calculated from the MODIS and AVHRR reflectance information is the fraction of photosynthetically active radiation (fPAR) absorbed by vegetation in a given pixel. The fPAR metric describes vegetation productivity, ranging from 0 or no light interception due to vegetation (barren ground) to 100, or complete light interception owing to vegetation (Knyazikhin et al., 1998). In terms of vegetation, fPAR values measured throughout the growing season can describe the amount of green leaf cover within a pixel (Coops et al., 2008). Currently, fPAR is employed less than vegetation metrics such as the normalized difference vegetation index (NDVI); however, when calculating gross primary productivity of above ground vegetation biomass, it is fPAR rather than NDVI that is required as a model input (Monteith, 1972).

Changes in annual fPAR can be summarized using indices such as the Dynamic Habitat Index (DHI) which has been used successfully to describe vegetation productivity in multiple studies across in Canada (Coops et al., 2008; Coops et al., 2009a) and Australia (Berry et al., 2007). While originally applied as an index to describe plant communities (Coops et al., 2009a; Fitterer et al., 2012) and animal diversity (Coops et al., 2009b; Andrew et al., 2012; Fitterer et al., 2013; Rickbeil et al., 2014b), DHI is also a useful predictor of individual coastal bird species distributions (Rickbeil et al., 2014a) and for describing forage conditions for moose (*Alces alces*) in Ontario, Canada (Michaud et al., 2014). The DHI estimates three components of landscape productivity – the yearly sum or overall productivity, the seasonality (the change between the maximum and minimum productivity throughout the year), and minimum annual productivity (not considered here as all Arctic vegetation goes to 0 in terms of fPAR values owing to the short growing season). The yearly overall productivity metric relates to the amount of photosynthetically active plant biomass in a given pixel (Coops et al., 2008; Coops et al., 2014). The seasonality metric offers a means to evaluate changes in variability in vegetation productivity, which is especially important in Arctic environments where plant green up and senescence occurs quite rapidly.

The decline of multiple caribou herds within the NWT as well as the development of long term productivity data presents an opportunity to examine how caribou herd densities and vegetation productivity interact. Specifically, I asked the following question – is caribou density related to summer range vegetation productivity at the landscape scale? I hypothesize that: (1) caribou density will be negatively related to overall vegetation productivity, and (2) caribou density will be negatively related to vegetation seasonality; both effects being attributed to a reduction in annual vegetation productivity due to grazing pressure. Lastly, (3) I expect that more intensely grazed areas on each herd's summer range will have a greater increase through time in overall productivity and seasonality owing to the larger release of grazing pressure on these areas due to the recent declines in herd densities.

3.2 Methods

3.2.1 Study area

The four herds examined in this study are the Cape Bathurst, Bluenose-West, Bluenose-East and Bathurst herds. For detailed location maps and herd range maps see Figure 2.1. Figure 3.3 shows an estimated spatial distribution of each of these herds on their summer range. The Ahiak/Beverly herd was excluded owing to the lack of Argos telemetry data in the late 1990s and early 2000s.

3.2.2 Environmental data

3.2.2.1 *Productivity data*

For details of MODIS and AVHRR fPAR data see Section 2.2.2.1. Two of the three DHI metrics were calculated for this study: overall productivity, and seasonality (Figure 3.1). In all cases, a temporal curve was developed for each pixel to represent the entire growing season by plotting fPAR values by day of year (in steps of eight days for MODIS and ten days for AVHRR) from March 1st to November 31st. Dates that were missing owing to masking were interpolated linearly from neighbouring dates. Once each curve was built, values were extracted at eight day increments to ensure that each pixel used an identical amount of values to calculate each metric.

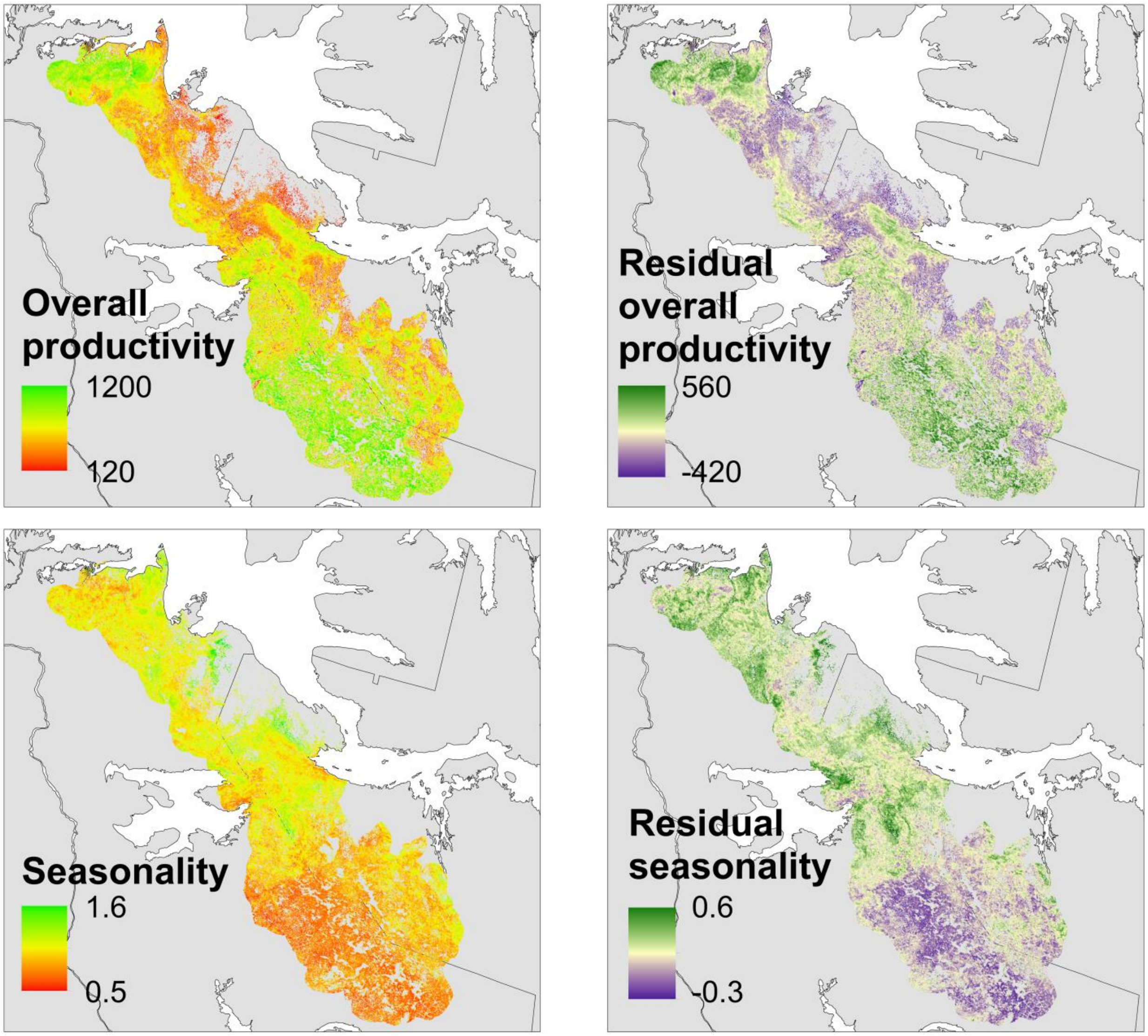

Figure 3.1 Maps of overall productivity (sum of 8 day interval fPAR values) and seasonality of productivity (coefficient of variation of 8 day interval fPAR values) for 2003 across the combined summer ranges of all four herds studied here. Additionally, the residual maps of productivity and seasonality related to growing season length are shown for the same year (for details on the productivity – growing season length models, see the Vegetation productivity and growing season length section in Results). Water and barren ground pixels have been masked in all cases.

Overall productivity was calculated as the sum of all values throughout the growing season (defined as when fPAR values exceeded 10% of the maximum value of the curve to when fPAR values returned below 10%) by pixel, while seasonality was calculated as the coefficient of variation of all values by pixel (Figure 3.2; for more detailed descriptions of DHI metrics see Coops et al. (2008)).

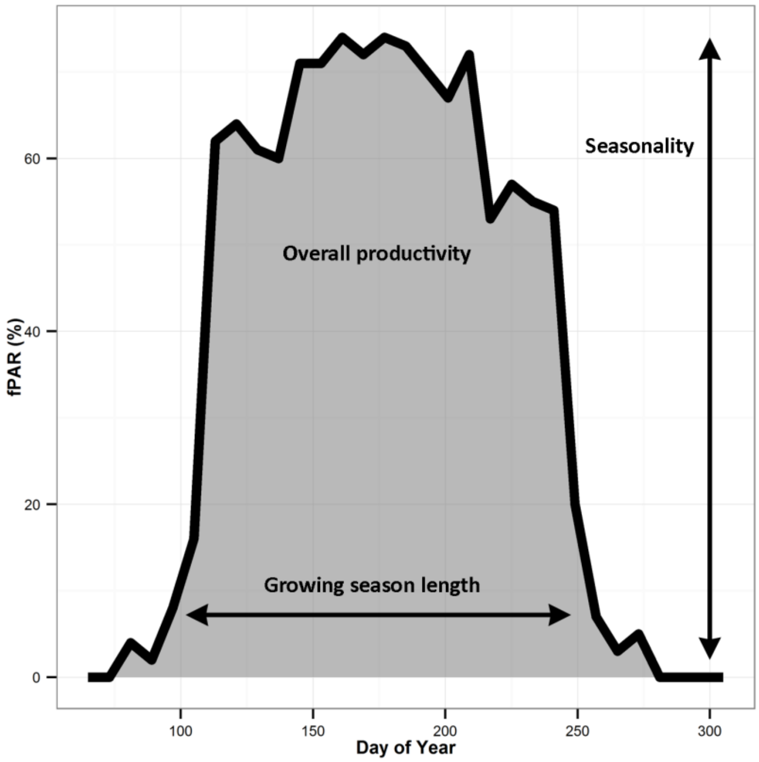

Figure 3.2 An example fPAR curve showing fPAR values (% as a value out of 100) plotted throughout the growing season. Overall productivity (shaded in grey) estimates the accumulation of vegetation biomass throughout the year, while seasonality examines the change in productivity from peak to trough. Growing season length was estimated as the amount of time where fPAR values exceeded 10% of the maximum of the curve.

In addition to overall productivity and seasonality, growing season length (Figure 3.2), which significantly affects vegetation productivity in Arctic environments (Euskirchen et al., 2006; Kimball et al., 2006), was estimated using the temporal curves of fPAR data, calculated as the number of days when fPAR values exceeded 10% of the maximum value of the curve to when fPAR values returned below 10%.

3.2.3 Caribou data

3.2.3.1 Caribou telemetry data

For details of Argos telemetry data see Section 2.2.1.1. Satellite relocations were used to build summer ranges by animal and year by filtering relocations by date (relocations collected in July and August were used to represent summer range; Russell et al., 1993; Nagy, 2011). Brownian bridges (Horne et al., 2007), developed using the adehabitatHR package (Calenge, 2006) in R (R Core Team, 2015), were used to build utilization distributions for each individual. Brownian bridges incorporate both spatial and temporal information from animal trajectories assuming a bivariate normal error distribution, and allow for explicit modeling of relocation error. The 0.95 isopleth was used to define an animal's home range (see Powell (2000) for an argument for and against using 0.95 for defining an animal's home range). Sigma 1, which refers to the average location error, was set at 250 m which is half the maximum error associated with class 2 locations and the maximum error associated with class 3 locations, while Sigma 2, which relates to the movement rate of the animal, was estimated using maximum likelihood (Horne et al., 2007). This resulted in a stack of summer ranges for each herd. Individual ranges were then summed to produce one summer range raster by herd, similar to the herd migration corridors produced by Sawyer et al. (2009), with each 1 km cell indicating how many summer ranges included that location, varying from a maximum of 54 for the Bathurst herd to 93 for the Bluenose West herd (Figure 3.3). To further eliminate erroneous relocations, as well as limit random forays from one particular animal, all pixels with a value of 1 were eliminated from each herd's summed summer range.

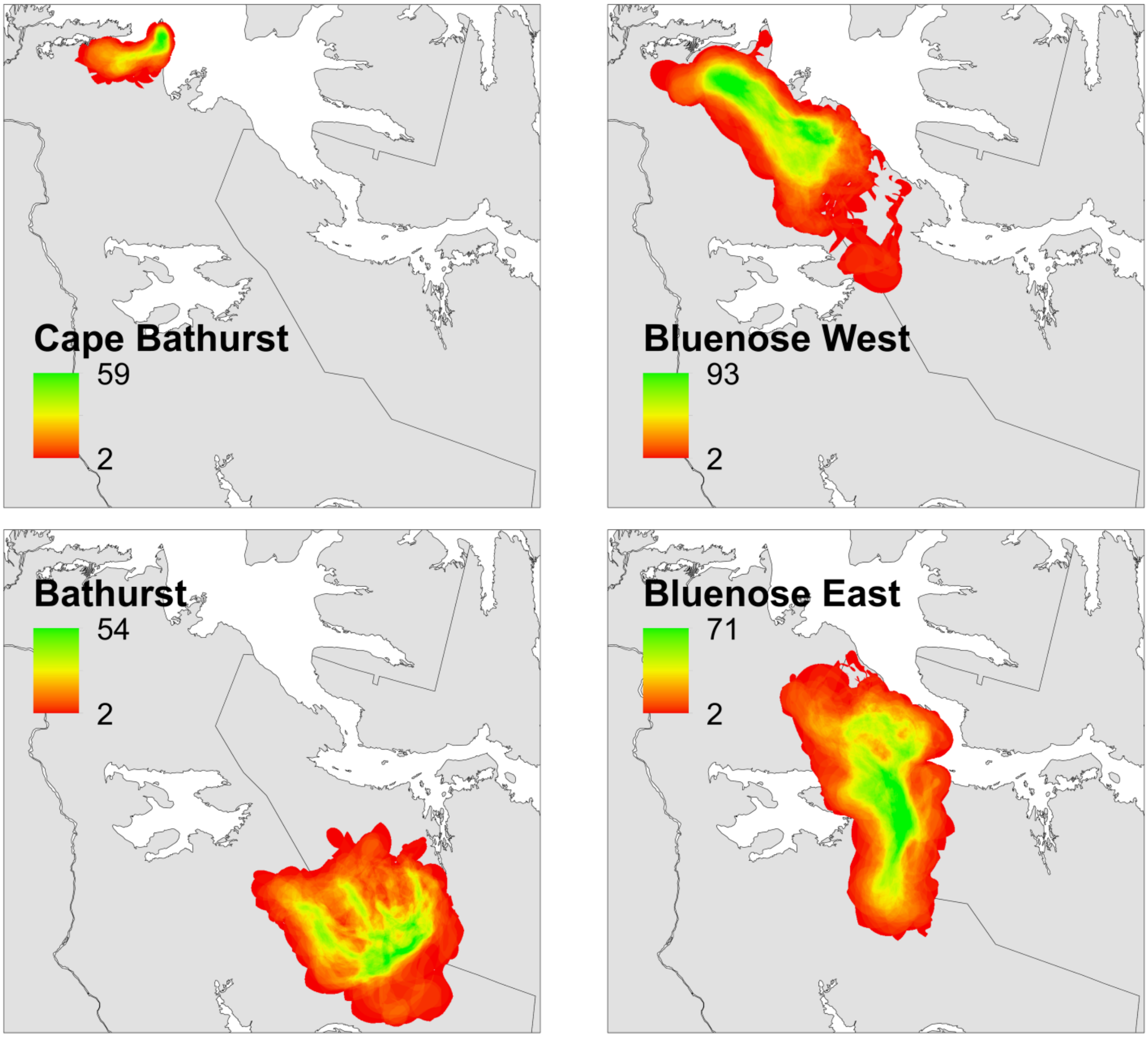

Figure 3.3 Herd summer range maps, with values representing the number of individual caribou summer ranges which included each pixel, for all caribou herds considered.

3.2.4 Caribou herd size estimates

For details of herd size estimates see Section 2.2.1.3. Herd abundance estimates were converted to densities by dividing abundance by the total size of the herd summer range extent.

3.2.5 Statistical analyses

3.2.5.1 Vegetation productivity and growing season length

Commonly, when evaluating grazing and vegetation productivity in cattle grazed systems, reference sites exterior to the grazed areas are selected to control for climatic effects on productivity (Bastin et al., 2012). This can be challenging for caribou across the tundra due to limited data on ungrazed areas. Alternatively, Archer et al. (2004) suggest that assessments of grazing impacts on productivity take climate into account directly within the analyses, and this was the approach taken here. The first analyses conducted examined how climate, more specifically growing season length, affected productivity across the study area. In the case that vegetation productivity was significantly related to growing season length, the residuals of this relationship would be used in analyses of grazing effects on productivity to account for the variation in the productivity variable owing to climatic variation (Archer et al., 2004).

Overall productivity and seasonality were related individually to growing season length on a by pixel basis. For the analyses, 50 pixels were selected at random by year for 1987 to 2013 (resulting in 1350 data points) and productivity and growing season length data were extracted. Linear generalized least squares (GLS) models with a maximum-likelihood iterator, built using the package “nlme” (Pinheiro et al., 2013) in R (R Core Team, 2015), were employed to relate growing season length to overall productivity and seasonality.

Autocorrelation of model residuals was a concern in all models employed. For models with repeated measures in time, an auto-regressive temporal correlation structure of order 1 (which estimates temporal correlation between years as exponentially decreasing as the time between data points increases) was included in the GLS models and tested to see if model performance improved due it’s inclusion (Joly et al. 2011). For analyses that used data from randomly selected pixels, spatial autocorrelation structures were similarly incorporated and tested for their ability to improve model performance. The corrected Akaike information criterion (AICc), calculated using the package “AICcmodavg” (Mazerolle, 2013), was used to select the most parsimonious model when comparing models that did and did not incorporate any kind of correlation structure (Burnham and Anderson, 2002).

Here, pixels were randomly selected through time; therefore, models were built with and without spatio-temporal autocorrelation structures (exponential models) to account for potential autocorrelation issues (Zuur et al., 2009).

3.2.5.2 Vegetation productivity and caribou density

Caribou density and herd were used to predict the following year’s overall productivity and seasonality using GLS with a maximum-likelihood iterator with an interaction term. The following year’s productivity conditions were used as the dependent variable, as the productivity curves showed accumulation of biomass prior to caribou arriving on their summer range. The interaction terms between the caribou density and herd were removed if there was no improvement in model performance owing to their inclusion, tested using likelihood ratio tests (Zuur et al., 2009). Because these analyses incorporated measures that were repeated in time, each model was built with and without an auto-regressive temporal correlation structure (order 1) (Zuur et al., 2009).

3.2.5.3 Changes in vegetation productivity through time and grazing pressure

The change through time of vegetation productivity in high vs low grazed areas was assessed by building a grazing pressure surface, similar in concept to that of Paudel and Andersen (2010), but different in computation. The summer range estimates (Figure 3.4), which are stacked individual caribou summer ranges resulting in an overall sum for each pixel of how many summer ranges incorporated a particular pixel, were rescaled to a 0 – 1 index and then multiplied by each herd's change in density from 1986 to 2013. This allowed for an overall index of the magnitude of grazing pressure release to be calculated for each pixel. In some cases the herd summer ranges overlapped, therefore, each herd's individual indexes were summed to produce one grazing pressure surface for the study area. Because population estimates began in 2000 for the Bluenose East herd, they were not included in this analysis. High versus low grazing pressure areas were then defined as falling above or below the overall mean of the grazing pressure surface (Figure 3.4).

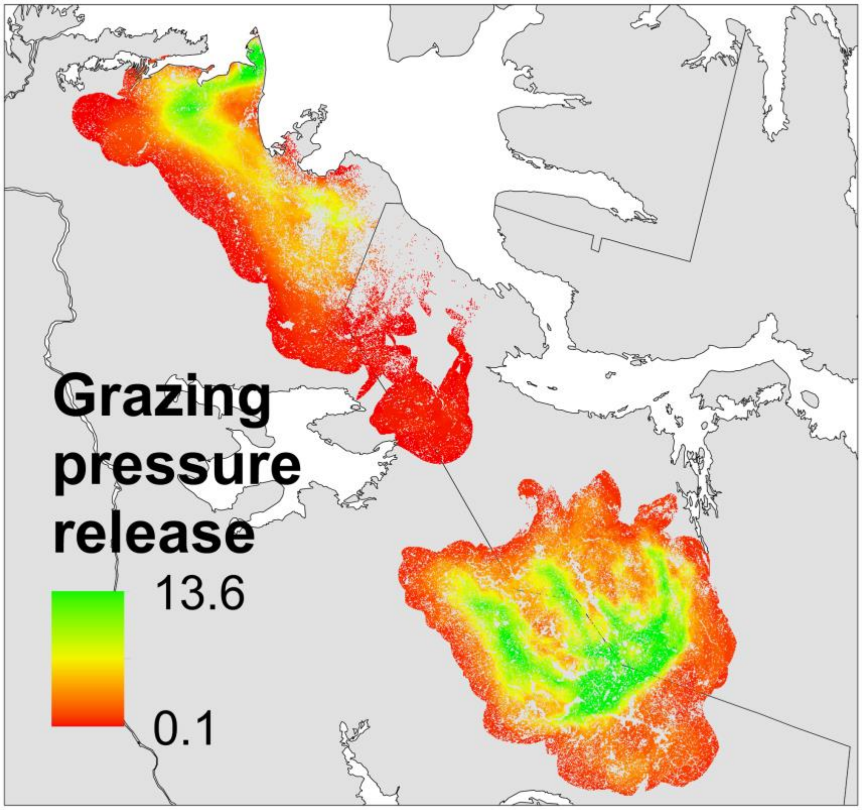

Figure 3.4 The grazing pressure release surface, calculated by multiplying each herd's summer range values (rescaled to a 0 – 1 index, see Figure 4 for raw values) by their respective change in density from 1986 to present and then summed

across herds (excluding the Bluenose-East herd due to a lack of herd estimates beyond 2000), with water and barren ground pixels masked.

The response variables for analyzing changes in productivity owing to release from grazing pressure were changes in the residuals (derived from the linear growing season length – overall productivity/seasonality models) of vegetation productivity and seasonality through time. This was calculated using the Theil-Sen's (TS) approach (Sen, 1968; Michaud et al., 2012; Fraser et al., 2014). Images were stacked by year to form a 3 dimensional array, with latitude and longitude forming the x and y axes, and residual overall productivity or residual seasonality (1987 to 2013) as the z axis. The slopes of all pairwise combination of years (points along the z axis) were calculated for each pixel, with the median value being returned as representing the overall trend of that pixel. The expectation of our 3rd hypothesis is that these median slopes will be greater, on average, in areas where there has been a greater release from grazing pressure, defined using our grazing pressure surface. Five hundred pixels were randomly selected from both the residual overall productivity and residual seasonality TS rasters from both the high and low grazing pressure areas (resulting in 1000 samples for each analysis) and compared using GLS with a maximum-likelihood iterator. Because assessing changes in productivity owing to grazing pressure release involved randomly selecting pixels, models were built with and without spatial autocorrelation structures (exponential).

3.3 Results

3.3.1 Vegetation productivity and growing season length

A positive relationship was found between growing season length and overall productivity (d.f. = 1, F = 550.8, P < 0.0001) while a negative relationship was detected between seasonality and growing season length (d.f. = 1, F = 2032.3, P < 0.0001). Both models incorporated a spatio-temporal autocorrelation structure using an exponential model (overall productivity nugget = 0.31, range = 400 km; seasonality nugget = 0.31, range = 960 km). Because of this climatic effect on productivity, when examining both productivity – grazing relationships, the residuals of the growing season length – productivity metric relationships were used (Archer et al., 2004; see Figure 3.1).

3.3.2 Vegetation productivity and caribou density

The best model for the residual overall productivity – caribou density relationships incorporated caribou density and herd with an interaction between the two (Figure 3.5). Including the interaction between caribou density and herd significantly improved the model’s log likelihood (d.f. = 3, L = 25.4, P <0.001) and was significantly related to residual overall productivity (d.f. = 3, F = 7.26, P = 0.002). An Ar1 temporal correlation structure was incorporated in the final model. Residual overall productivity was negatively related to caribou density across all four herds, with overall productivity responding similarly to the 3 herds which occurred exclusively at lower densities (Bluenose East, Bluenose West, and Cape Bathurst, with slopes between -152.3 and -193.1). The response of overall productivity to the Bathurst herd, however, was less than the other three herds examined (slope = -20.4).

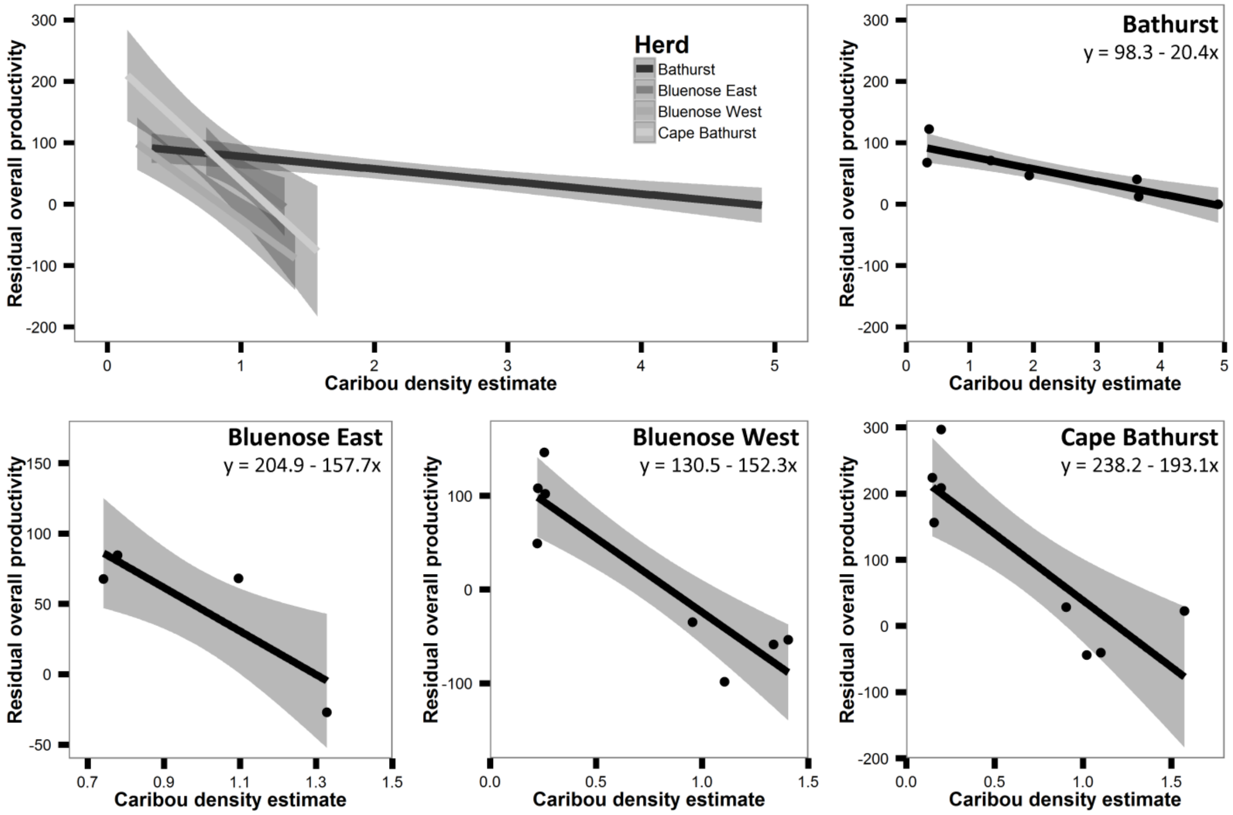

Figure 3.5 Residual overall productivity (derived from the overall productivity versus growing season length model) related to caribou density on herd summer ranges (caribou/km^2) and herd. Confidence bands indicate 95% confidence intervals. n = 7 for Bathurst, n = 4 for Bluenose East, n = 8 for Bluenose West, and n = 8 for Cape Bathurst.

The best model for the residual seasonality of productivity – caribou density relationships was a model incorporating caribou density and herd with an interaction between the two (Figure 3.6). Including the interaction between caribou density and herd significantly improved the model's log likelihood (d.f. = 3, L = 15.4, P = 0.002) and was significantly related to residual overall productivity (d.f. = 3, F = 4.14, P = 0.02), hence its retention in the final model. An AR1 temporal correlation structure was incorporated in the final model. Residual seasonality was positively related to caribou density in across all four herds, with slopes varying from 0.02 for the Bathurst herd to 0.05 for the Bluenose East herd.

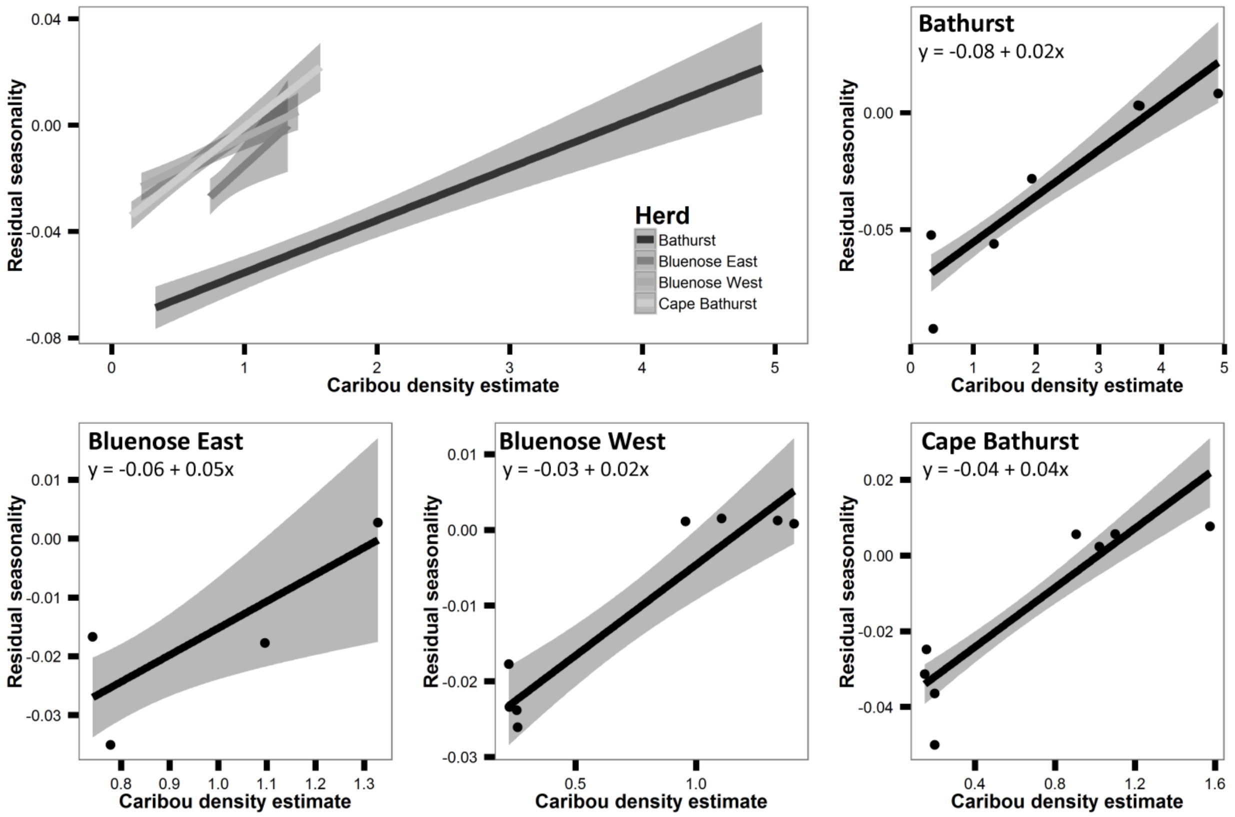

Figure 3.6 Residual seasonality (derived from the seasonality versus growing season length model) related to caribou density on herd summer ranges (caribou/km^2) and herd. Confidence bands indicate 95% confidence intervals. n = 7 for Bathurst, n = 4 for Bluenose East, n = 8 for Bluenose West, and n = 8 for Cape Bathurst.

3.3.3 Changes in vegetation productivity through time and grazing pressure

Caribou density was negatively related to residual overall productivity and positively related to residual seasonality. Therefore, the residual overall productivity TS slope should be positively associated with grazing pressure release and the residual seasonality TS slope should be negatively associated with grazing pressure release. The best model for assessing residual overall productivity TS slopes incorporated an exponential spatial correlation structure (range = 44.5 km, nugget = 0.52). High versus low grazing pressure release areas had a (moderate) significant difference in mean residual overall TS slopes (d.f. =1, F = 4.05, P = 0.04), with high having a mean TS slope of 7.13 (SE = 0.64), compared to the low mean TS slope of 6.29 (SE = 0.42). The best model for relating the difference in TS slopes to residual seasonality also incorporated an exponential spatial correlation structure (range = 183.2 km, nugget = 0.16). High versus low grazing pressure release areas had a (moderately) significant difference in mean residual seasonality TS slopes (d.f. = 1, F = 3.81, P = 0.05), with high having a mean TS slope of -0.0040 (SE = 9.5 x 10-4) compared with low's mean NT slope being -0.0037 (SE = 1.4 x 10-4).

3.4 Discussion

The results of our analyses supported our first hypothesis that an increase in caribou density will reduce overall vegetation productivity. Our second hypothesis, which was that an increase in caribou density will reduce vegetation seasonality, was rejected. Lastly, our third hypothesis, which predicted that areas with a greater release from grazing pressure will see a greater response in terms of the change through time of residual overall productivity and seasonality, was weakly supported for both productivity metrics. In all analyses, archived remotely sensed productivity data proved a useful tool for evaluating landscape level grazing impacts of barren ground caribou.

Our findings on the effects of caribou density on overall vegetation productivity support the numerous studies that employed exclosure experiments to assess caribou grazing effects on vegetation productivity. Manseau et al. (1996) found a more than doubling effect on grazed plant productivity when comparing ungrazed reference sites to grazed areas on the summer range of the George River herd at very high numbers; changes included depletion of lichens and damage to shrub vegetation. Zamin and Grogan (2013) detected a 1.7 to 2 fold increase in browse shrub leaf biomass, as well as a significant increase in conifer leaf biomass when using an exclosure approach on the summer range of the Bathurst herd at relatively low numbers. Olofsson et al. (2010) detected an increase in both vegetation productivity and net nitrogen mineralization inside exclosures when examining intensively grazed reindeer range in Sweden. Some studies have demonstrated that grazing can have a positive effect on vegetation productivity. For example, Olofsson et al. (2001) found that heavily grazed sites had the highest primary productivity on reindeer ranges in in Norway.

The effect of caribou density on vegetation productivity found here was, however, less in magnitude than is typically found in exclosure experiments, and may highlight a key limitation of exclosure experiments. Exclosure experiments simulate a condition which rarely occurs in nature – a complete removal of grazing pressure altogether. This would explain the large signal detected in most caribou exclosure experiments, where grazing is entirely removed from the system (Manseau et al., 1996; Olofsson et al., 2010; Zamin and Grogan, 2013). In the summer ranges of the herd examined here, a complete removal of grazing pressure for any length of time is unlikely and may in part be responsible for the discrepancy between our findings and exclosure experiments.

Surprisingly, vegetation seasonality increased positively with caribou density. Our hypothesis was that increased herd densities would reduce the fPAR growth curve uniformly throughout the year, and therefore reduce seasonality. However, as the herds are highly migratory, it seems unlikely that the bulk of each herd would be present at one location throughout the entire growing season (Berger, 2004). An area which was grazed intensively for a few weeks to a month would likely see a reduction in leafy foliage and potentially observed fPAR values. This reduction in the temporal fPAR curve would increase variation in fPAR throughout the growing season which would manifest in an increased estimate of seasonality. The assessment of seasonality and growing season length clearly displayed a negative relationship between the two variables and supports this hypothesis. In this way, broad-ranging migratory caribou may rarely maintain the prolonged pressure on vegetation that occurs on intensively managed reindeer ranges.

The results of the high versus low intensity grazing pressure on changes in productivity through time were less conclusive than the vegetation productivity versus density analyses. One possible explanation for lack of a strong grazing pressure signal is that our herd range maps adequately estimated the extent of the summer range of each herd (or under estimated it but still captured enough pixels for trend detection) but failed to describe the spatial distribution of each herd within their summer range. I feel this is the most likely scenario given the number of animals within each herd versus the number of individual caribou summer home ranges used to delineate and describe each herd's summer range. Vegetation type was not considered here, and I would not expect grazing pressure to affect forests, grasslands, shrub, and moss/lichen ecosystems equally (however, moss/lichen and grasslands comprised 85% of the land cover in the study are according to the Canadian Center for Remote Sensing Circa 2000 Canadian land cover map; Pouliot et al., 2014). Tundra vegetation can be highly heterogeneous at a number of scales. Commonly, caribou select for shrub/grassland/lichen habitats during summer foraging and avoid more productive forested areas, which could confound this analysis. Or, it is possible that by accounting for changes in growing season length, the associations between grazing pressure release and changes in productivity were removed. I recognize that caribou and reindeer are selective feeders and by careful choice of plants and plant parts (e.g. selection of *Eriophorum* spp. inflorences at high nutrient content; Cebrian et al., 2008) are able to increase nutrient intake of high-quality forage that result in “multiplier” effects of increased growth and productivity (White, 1983, Cebrian et al., 2008).

Given these results, it seems likely that while there is a relationship between the number of caribou on each herd’s summer range and the productivity of the vegetation on the summer range, it was likely not a factor limiting herd size in the herds examined here and had a limited contribution to the declines observed in these herds observed from 1987 to 2013. The results for the Bathurst herd in particular, which experienced substantially higher densities than the other herds and had a less negative association with overall productivity, indicate that an overgrazing effect was likely not the main driver of the reduction in herd abundances that have been documented since the 1980s. This would agree with the body of work indicating that density independent factors (i.e. climate) likely are the main cause of the observed large-scale fluctuations in herd numbers over time (Gunn, 2003; Vors and Boyce, 2009; Joly et al., 2011). Additionally, the large declines in herd densities observed in the early 2000s in the NWT occurred when herd numbers were well below observed historic maximums (e.g. the Bathurst herd; Boulanger et al., 2011), indicating a density independent negative effect on herd sizes. At lower herd size, hunter harvest has in some herds become a significant factor in declines (Boulanger et al., 2011) and predator-prey relationships may change in herds reaching low numbers (Bergerud et al. 2008).

Caution is needed in generalizing about the results of grazing and browsing on vegetation on caribou and reindeer ranges; effects will vary depending on animal density and the type of vegetation studied (winter versus summer range, lichens versus shrubs and graminoids). Density-dependent effects of high numbers in intensively managed reindeer in Scandinavia (see Skogland, 1985; Tveraa et al., 2013) have been clearly demonstrated but these densities may not often be maintained for extended periods in broad-ranging barren ground caribou herds. Plants respond differently to grazing or browsing (Bryant et al., 1983, McNaughton, 1983). Lichens are easily depleted (Manseau et al., 1996) while graminoid vegetation may respond to moderate grazing with increased productivity (McNaughton, 1983).

Lastly, the approach outlined here attempted to account for climatic variation in this system before assessing the effects of overgrazing, however, it is likely that some effects of climate were overlooked. Climate is warming in the Arctic (Gaversen et al., 2008), and this is manifesting in changes in vegetation productivity (Euskirchen et al., 2006; Kimball et al., 2006). It is possible that the effects of climate were not fully accounted for here, and the results of this study should be interpreted with this in mind.

Chapter 4: Changing northern vegetation conditions are influencing barren ground caribou post-calving movement rates

4.1 Introduction

Ecological changes being documented in Arctic, sub-Arctic, and Boreal terrestrial environments are among the most rapid on Earth (Chapin et al., 2000; Serreze et al., 2000; Kelly et al., 2013; Price et al. 2013). Fire regimes in the western Boreal forest have shifted considerably even in the past 50 years (Kelly et al., 2013; Joly et al., 2010; de Groot et al., 2013) with some locations showing a doubling of annual area burned over the past 4 decades (Kasischke and Turetsky, 2006). Tall shrub proliferation has rapidly transformed many areas of the low Arctic (Lantz et al., 2010, Myers-Smith et al., 2011). In the Tuktoyaktuk Coastlands the growth and proliferation of green alder (*Alnus viridis*) and dwarf birch (*Betula nana exilis*) has significantly reduced the extent of lichen and graminoid dominated tundra within several decades (Fraser et al., 2014). Myers-Smith et al. (2011) documented increased shrub expansion at the northern limits of many shrub communities, indicating that warming climates may be driving shrub proliferation. However, there was extensive spatial variation for the climate-shrub expansion association leading the authors to conclude that soil moisture may limit shrub expansion in certain locations. Based upon measurements from multiple data sources including remotely sensed data, large portions of Arctic tundra are becoming more productive, likely as a result of longer growing seasons that have resulted in increased productive vegetation (Chapin et al., 2000; Euskirchen et al., 2006; Kimball et al., 2006; Myers-Smith et al., 2015; Xu et al., 2013).

Changes in vegetation of this magnitude are likely to profoundly impact northern wildlife. Barren ground caribou are the most numerous large mammal in the Canadian north (Bergerud, 2000) and are circumpolar in their global distribution (Vors and Boyce, 2009). They are long-distance migrants (Berger, 2004; Vors and Boyce, 2009; Festa-Bianchet et al., 2011), calving on shores of the Arctic Ocean and commonly overwintering several hundred kilometers to the south in the northern Boreal forest (Bergerud, 2000; Joly et al., 2012; Gustine et al., 2014). Barren ground caribou are grouped into herds based on their fidelity to calving grounds (Gunn and Miller, 1986; Schaefer et al., 2000) with certain herds numbering in the hundreds of thousands (Bergerud, 2000). Each of the five herds considered here (described in more detail in Methods) has experienced a significant reduction in herd size since over the past 3 decades (Nagy and Johnson, 2006; Adamczewski et al., 2014), in some cases by more than an order of magnitude (i.e. the Bathurst herd, Boulanger et al., 2014).

Barren ground caribou's annual migration allows them to access young, highly nutritious vegetation during spring (Heard et al., 1996; Bergerud, 2000), to avoid predators during calving (Heard et al., 1996), and to lessen parasite loads/avoid parasitism (Folstad et al., 1991; Hughes et al., 2009). As large mammalian herbivores, barren ground caribou respond directly to vegetation conditions across their range (Bergerud, 2000), making documentation of range conditions paramount to conservation efforts. Overgrazing on summer ranges has been proposed as a cause of herd decline for wild barren ground caribou (George River herd; Manseau et al., 1996). Semi-domesticated reindeer in Fennoscandinavia have been shown to influence tundra and forest vegetation conditions (Olofsson et al. 2001; Kitti et al. 2009; Tveraa et al., 2013); however, the concept of overgrazing is an elusive and debated concept for these managed herds (Mysterud, 2006).

Since vegetation dynamics directly affect barren ground caribou, changes in the composition, biomass, or forage quality of vegetation communities are expected to lead to changes in caribou behavior. For instance, increasing biomass due to shrub proliferation may result in landscapes that are more difficult for caribou to travel through. Terricholous lichens forms the major portion of caribou diets during winter in the Boreal forest (Joly et al., 2010); and recent studies suggest that increased shrub cover is reducing lichen cover and biomass (Fraser et al. 2014). Tussock cottongrass (*Eriophorum vaginatum*) forms a major portion of the spring diet in caribou (Cerbrian et al., 2008; Jandt et al., 2008), and shrub expansion in some regions is reducing the cover of this species (Fraser et al. 2014). Additionally, the two species of tall deciduous shrubs (dwarf birch (*Betula nana*) and green alder (*Alnus viridis*)) which were found to be expanding in terms of range in the Tuktoyaktuk Coastlands (Fraser et al. 2014) are not preferred forage species of caribou being well defended chemically from herbivory (Christie et al., 2015). However, caribou will selectively forage on certain shrub species (e.g. species of willow (*Salix* spp.); Heard et al., 1996, Christie et al., 2015); encroachment of shrub species which offer some nutritional benefit may not result in the same magnitude of lost forage opportunities.

Due to factors including remoteness, growing season length, and cost, gathering in situ data on vegetation dynamics across the range of barren ground caribou herds present substantial difficulties. Herd ranges encompass thousands of square kilometers of habitat in remote areas that are expensive to assess (Bergerud, 2000; Berger, 2004). Additionally, if habitat changes are to be documented, repeat measures of habitat conditions over time are required. These challenges are encouraging the development of novel methods for tracking habitat conditions in the north that involve using ex-situ data such as space-borne remote sensing (Falldorf et al., 2014; Rickbeil et al., 2015; Rickbeil et al., 2016). There are multiple remote sensing platforms and sensors that can be employed for habitat change analysis. The Moderate Resolution Imaging Spectroradiometer (MODIS) onboard NASA satellites Terra and Aqua is an attractive option that offers a wide range of environmental spectral indices and has a rapid revisit time allowing for both within-year and between-year changes to be quantitatively documented. However, MODIS data is spatially coarse (250 - 1000 m pixel sizes), and due to its 1999 launch, only has data products available from 2000 onwards. The data can be combined with longer term NOAA-AVHRR imagery to extend the archive, however there are issues with sensor compatibility, including the match between spectral channels, spatial resolution, and radiometric bit depth, among other issues (Fontana et al., 2012).

A less-explored option, particularly in northern environments, is data from the Landsat series of satellites. Landsat offers a finer spatial resolution (30 m), with greater spatial detail at a cost of a narrower swath width and longer revisit times between acquisition opportunities (Wulder et al., 2015). This can result in challenges due to the combined effects of actual acquisitions (e.g., number of images collected for a given location), and collection date (phenology represented) combined with atmospheric-effects (i.e., cloud, shadow, haze contamination). Since the advent of the Landsat program in 1972, Canada has been an active International Cooperator, receiving and archiving images for the Canadian landmass, with well over 600,000 images available representing all Landsat sensors (White and Wulder, 2014). Internationally, Canada is among the nations with the most spatially and temporally dense representation of Landsat imagery (Wulder et al., 2015). The 2008 opening of the Landsat archive (Woodcock et al., 2008) has fostered the development of highly sophisticated and consistent image-processing routines that maximize the information content of the archive (Hansen and Loveland, 2012; Wulder and Coops, 2014). As an example, new pixel-based compositing approaches have emerged to produce spatiallycontiguous, cloud-free, radiometrically-consistent surface reflectance image composites, combining multiple Landsat scenes (Griffiths et al., 2013, White et al., 2014, Hermosilla et al., 2015). Gap-free image composites and annual change data are now available across Canada, removing one of the major barriers to assessing caribou habitat in the north using Landsat data.

The objective of this study is to document changes in barren ground caribou habitat, specifically vegetation productivity, and assess how changes in vegetation productivity affect caribou movement rates using a productivity index generated from comprehensive, annual, Landsat-derived 30 m data. Since the measure of productivity used here was collected in summer (July and August) it is most directly applicable to the post-calving portion of the year, which occurs at the same time (Nagy, 2011). Additionally, post-calving is a period where access to forage and forage quality are critical for adding fat and providing milk to calves making a post-calving assessment of vegetation productivity's association with movement rates not only appropriate given the data but also ecologically important. Based on previous research, we anticipate that vegetation productivity will have increased across all herd ranges (Kimball et al., 2006; Myers-Smith et al., 2015). However, our hypothesis is that rates of increase in vegetation productivity will be larger in locations that have or are currently transitioning from tundra to shrub dominated habitat (for habitat definitions see Methods – Land cover data). Shrub proliferation is occurring in many locations across the low Arctic (Lantz et al., 2010; Fraser et al., 2014; Myers-Smith et al., 2015) and these transition zones offer the largest potential increase in vegetative cover and greenness and are sensitive to warming climates (Epstein et al., 2004). We hypothesize that increasing vegetation productivity in tundra and grassland habitats will result in reduced movement rates owing to increased forage biomass availability while increasing productivity in shrub habitats will lead to elevated movement rates due to reduced forage opportunities and increased insect harassment.

4.2 Methods

4.2.1 Study area

For details of the study area see Section 2.1. The five herds examined in this Chapter are: the Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Ahiak/Beverly.

4.2.2 Barren ground caribou telemetry data

For details of GPS telemetry data see Section 2.2.1.2. By relating velocity (used here due to the use of two different time steps; Dodge et al., 2008; Calenge et al., 2009) to vegetation productivity estimates barren ground caribou movement rates were linked to productivity estimates for the post-calving period in different vegetation community types allowing for inferences to be made regarding possible effects of vegetation on behavior for this time period.

4.2.3 Landsat spectral data

For details of the NTEMS data product see Section 2.3.2. The enhanced vegetation index (EVI) was calculated yearly from the visible and near-infrared bands in the composite images in order to represent vegetation productivity conditions across caribou ranges. EVI (Huete et al., 2002) has been shown across a range of studies to be highly correlated to primary production throughout the growing season at hardwood and conifer-dominated sites globally (Sims et al., 2008). Similar to the normalized difference vegetation index (NDVI), EVI employs the red and near-infrared bands to estimate primary productivity. However, EVI also employs the blue band and three coefficients to correct for atmospheric and vegetation canopy influences on pixel reflectance values. Xiao et al. (2005) further demonstrated that EVI is more sensitive than NDVI in identifying subtle changes in the seasonal dynamics of leaf phenology.

4.2.4 Land cover data

For details of land cover data see Section 2.2.2.2. All forest classes (temperate or sub-polar needleleaf; sub-polar taiga needleleaf forest; temperate or sub-polar broadleaf deciduous; mixed forest) shrub classes (temperate and sub-polar; polar shrubland), grassland (temperate and sub-polar; polar grasslandland), and tundra classes (sub-polar or polar barren-lichen-moss) were simplified to produce a forest, shrub, grass, and tundra land cover map at 250 m spatial resolution (see Table 4.1 for land cover class distributions between herd ranges), which was then resampled to a 30 m spatial resolution to match that of Landsat. For the post-calving movement analyses only tundra, grassland, and shrub habitats were assessed owing to the lack of telemetry data occurring in forested areas during this time.

Table 4.1 Percentage of each vegetated land cover class by herd range for the year 2011.

Land Cover	Ahiak	Bathurst	Bluenose East	Bluenose West	Cape Bathurst
tundra	16%	2%	7%	12%	3%
Grassland	70%	52%	63%	51%	62%
Shrub	5%	9%	8%	4%	27%
Forest	9%	37%	23%	33%	3%

4.2.5 Statistical analyses

4.2.5.1 EVI across herd ranges

Changes in annual EVI were assessed using Theil-Sens (TS) non-parametric regression (Sen, 1968; Michaud et al., 2012; Fraser et al., 2014) (Figure 4.1A). The TS approach calculates all pairwise slopes for a given variable through time by pixel throughout the image stack (1984-

2012) and then returns the median slope as a change metric. TS slopes are less sensitive to outliers than traditional linear regression and, as a result, are becoming more commonly used in time series analyses at the pixel level (Michaud et al., 2012; Rickbeil et al., 2015). Slope significance was determined using non-parametric Mann-Kendall tests (Kendall, 1975; Fraser et al., 2014) (Figure 4.1B).

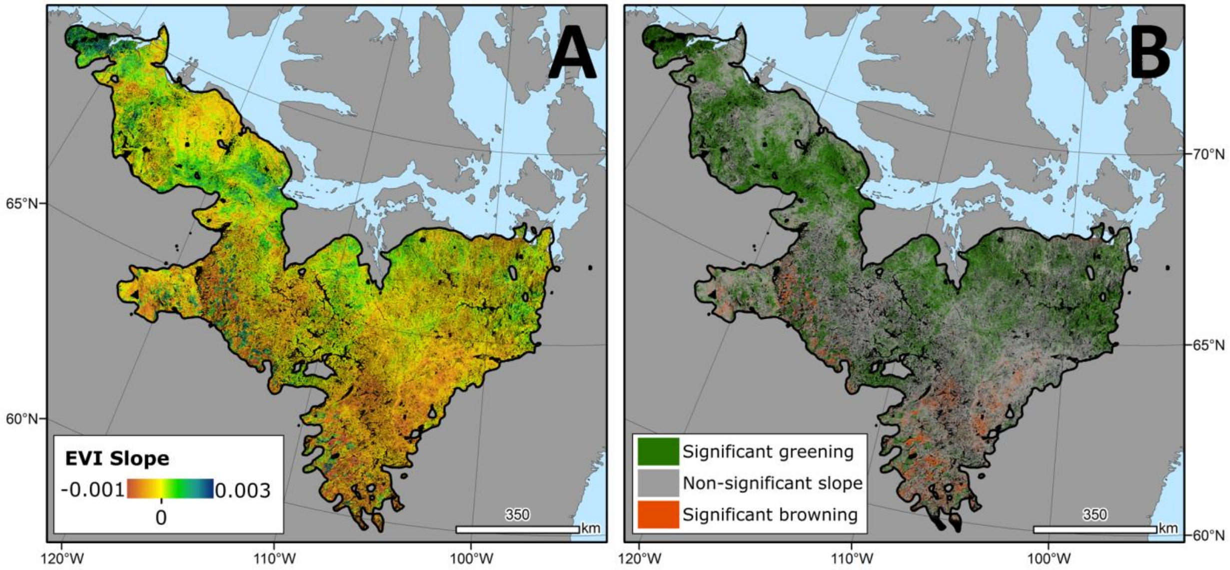

Figure 4.1(A) EVI Theil-Sen's slopes and (B) Mann-Kendall significance tests for across all five herd ranges. Greening indicates a significant positive slope while browning indicates a significant negative slope.

To examine variation in EVI TS slopes for each herd, two hundred random samples were then taken from each land cover class from each herd's range. Pixels containing water were eliminated and land cover and EVI slope values were extracted. These values were then analyzed in a generalized least squares regression (GLS) with a maximum-likelihood iterator, built using the package "nlme" (Pinheiro et al., 2013) in R (R Core Team, 2013). A GLS model was used as it allows for the inclusion of spatial autocorrelation functions to account for issues with spatially structured model residuals (Zurr et al., 2009). Variable selection began with full models incorporating all variables (land cover type and herd) with an interaction term. The Interaction term was then removed and both models were compared using a likelihood ratio test to select the most parsimonious model (Zuur et al., 2009). Both models were assessed for spatially structured residuals using semi-variograms. Since both models displayed spatially structured residuals, Gaussian spatial correlation structures were added and the models were subsequently re-examined.

4.2.5.2 Caribou movement

Individual barren ground caribou movement velocities (m/hour) were associated with EVI values at GPS fix locations during the post-calving phase of the year- July and August (Russell, Martell, and Nixon, 1993; Nagy, 2011) - for tundra, grassland, and shrub habitats. Generalized additive mixed models (GAMM) with a negative binomial link were used to account for over-dispersion in the data. GAMMs allow for non-linear responses to be appropriately estimated while assigning unique animal identifiers nested within herd as random effects, thereby accounting for repeated measures per animal (Cuiti et al., 2012) and variation in movement velocities between herds. 1000 samples were taken from each herd for each habitat class, when possible. In some cases less than 1000 points were available for a particular herd in a particular habitat class; if there were over 500 data points available all points were retained for the particular habitat model. Less than 500 points resulted in a herd being excluded from that habitat's model. When a herd was included in a particular model with less than 500 data points a lack of model convergence tended to occur. When sample sizes were reduced to maintain equal sampling across all herds singular models tended to occur owing to the complex nature of the nested random effects and small sample sizes. As a result, the tundra movement analysis lacked data from the Bathurst herd (272 data points) and the grasslands analysis lacked data from the Ahiak/Beverly herd (92 data points). Model residuals were tested for spatial autocorrelation using semi-variograms (Zuur et al., 2009). All models had significant levels of spatial autocorrelation in their residuals, and Gaussian spatial correlation structures were therefore added to the GAMM models (Zuur et al., 2009).

4.3 Results

4.3.1 EVI across herd ranges

In all cases the number of significant positive EVI TS slopes was greater than the number of significant negative EVI TS slopes (Table 4.2). The Cape Bathurst herd had the highest percentage significant positive slopes (53.4%) while the Bluenose West herd had the lowest percent negative slopes (0.7%). The Ahiak/Beverly herd had both the lowest percent positive slopes (24.5%) and the highest percent negative slopes (5.7%).

Table 4.2 The percentage of significant positive, negative, and non-significant Theil-Sen's slopes across each herd's range.

Herd	% Positive	% Negative	%Non-significant
Cape Bathurst	53.4	1.0	45.6
Bluenose West	45.0	0.7	54.3
Bluenose East	38.2	3.7	58.1
Bathurst	29.5	4.1	66.4
Ahiak/Beverly	24.5	5.7	69.8

EVI TS slopes were found to vary significantly across herd ranges and land cover types (F = 6.57, P < 0.001), with a significant interaction detected between the herd range and land cover type (Log Likelihood Ratio = 69.14, P < 0.001) compared with the model lacking an interaction term) (Figure 4.2). The final model also included a Gaussian spatial autocorrelation structure. The Cape Bathurst and Bluenose West herds had the largest overall TS slopes, with the shrub class in the Cape Bathurst herd having the largest median EVI slope. The median TS slope

(0.0015) for the Cape Bathurst shrub class would result in a 13 % increase in mean shrub EVI values (mean shrub EVI = 0.33) across a 28 year period. Across all herd ranges either grass or shrub land cover classes had the largest median EVI slopes. Generally, EVI slopes became increasingly negative following a west to east gradient across herd ranges.

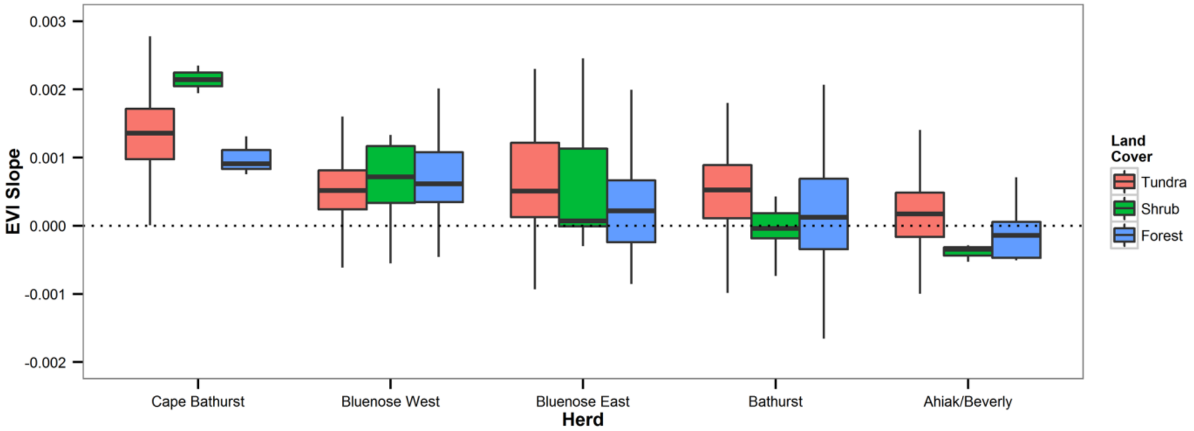

Figure 4.2 Boxplots (.5, .25, .5, .75. 95 delineations) of Theil-Sen's EVI slopes for forest, grass, shrub, and lichen/moss land cover classes across the five herds examined here.

4.3.2 Caribou movement

Caribou tended to move most slowly, on average, through shrub habitats (mean velocity = 201 m/hour, sd = 295 m/hour) when compared with tundra (mean velocity = 460 m/hour, sd = 474 m/hour) and grassland habitats (mean velocity = 349 m/hour, sd = 437 m/hour). In tundra habitats, caribou movement rates decreased (F = 3.60, p = 0.04, RMSE = 493 m/hour) with increasing EVI values until an EVI value of approximately 0.3 after which movement rates did not change with increasing EVI values (Figure 4.3). Caribou movement rates declined in nearly linear fashion in grassland habitats with increasing EVI values (F = 5.77, p = 0.02, RMSE = 524 m/hour). Movement rates in shrub habitats peaked at intermediate EVI values, approximately EVI = 0.33 (F = 2.39, p = 0.05, RNSE = 431 m/hour).

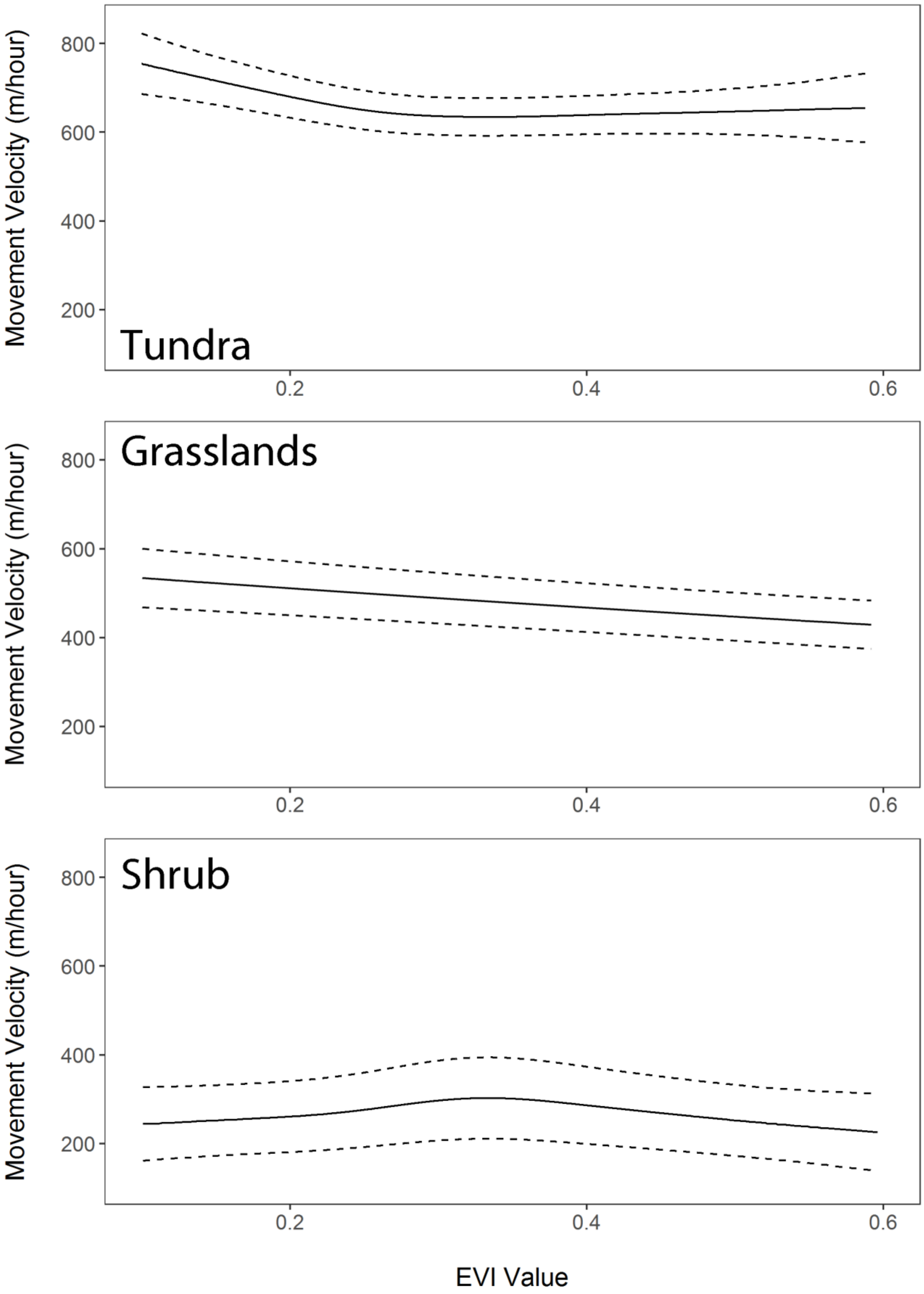

Figure 4.3 Predicted GAMM relationships between caribou movement velocity and EVI values in tundra, grassland, and shrub land cover classes. Dotted lines represent one standard error from the mean prediction.

4.4 Discussion

Consistent with our hypothesis, our results indicate that forest, shrub, grassland, and lichen/moss vegetation communities across all five herd ranges became more productive from 1984 to 2012. The percentage of significant positive slopes greatly outweighed the percentage of significant negative slopes for each herd; EVI had significantly increased in more than half the pixels in the Cape Bathurst's range. The increase in productivity detected here is consistent with multiple studies that have examined Arctic vegetation productivity, all of which indicate a greening of the Arctic that is generally associated with increased growing season length, particularly in spring (Stow et al., 2004; Raynolds et al., 2008; Bhatt et al., 2010; Guay et al., 2014). Importantly, this productivity signal was detected using only Landsat imagery avoiding any issues of data compliance between sensors which may occur when combining data across sensors such as AVHRR and MODIS (Fontana et al., 2012).

Measured productivity responses were not, however, uniformly consistent across the landscape. Vegetation productivity increased more rapidly and had a greater percentage of positive significant slopes in the western herd ranges. Increases in productivity were most pronounced in shrub habitats in the western herds, while grassland habitats displayed the largest increases in productivity in the more eastern herds. Bhatt et al. (2010) and Post et al. (2013) linked increases in Arctic vegetation productivity to earlier sea ice melt, and the western herds are closer, on average, to the Arctic Ocean than the eastern herds. Macias-Fauria et al. (2012), however, detected a link between sea ice melt and vegetation productivity in early spring only and attributed increased Arctic vegetation productivity more to increasing early summer air temperatures. There is a marked divide in the surficial materials present on the eastern edge of Great Bear Lake (Shaw et al. 2010), which also generally divides the Bluenose West and Cape

Bathurst herds from the three more eastern herds. The majority of the surficial materials west of Great Bear Lake in the Taiga Plains Ecozone are made up of thick continuous surface till, while east of Great Bear Lake the Taiga Shield Ecozone is predominantly ancient bedrock rock and thin, divided till. The higher rates of vegetation productivity increase could be linked to more abundant surficial materials found in the more western herd ranges. Macias-Fauria et al. (2012) detected depressed levels of vegetation productivity in *Salix lanata* in nutrient poor, sand dominated substrates. Similarly, Myers-Smith et al. (2015) detected elevated shrub productivity in soils with greater soil moisture retention capacity. Additionally, the continentality, resulting in colder temperatures, of the eastern herd ranges may also play a role in limiting shrub recruitment (Lantz et al., 2010). The higher rate of increase in shrub and tundra habitats is consistent with the multiple studies documenting shrub proliferation in tundra habitats (Stow et al., 2004; Lantz et al., 2013), whereby low productivity lichen/moss/grass land cover types are shifting towards birch- and alder-dominated land cover types, becoming more productive in the process (Fraser et al. 2014). Myers-Smith et al. (2015) found that shrub expansion was greatest at the northern margins of shrub communities indicating that climatic warming is indeed affecting some shrub communities. However, the authors also document extensive spatial variation in how Arctic shrub communities are responding to changing climatic conditions and suggest that variation in soil moisture can limit shrub communities' response to warming.

When animals forage, they tend to move slowly in a random search pattern; when they are movement focused, caribou tend to move quickly in a more linear fashion. Measuring the velocity of movement (Dodge et al., 2008; Calenge et al., 2009) allows for inferences to be made regarding whether the animal was primarily engaged in foraging behavior or movement (Zollner and Lima, 1999). However, there are numerous factors other than foraging which can affect barren ground caribou movement patterns (see Hebblewhite and Haydon 2010 for a general summary of GPS collar limitations), including but not limited to: predator and insect avoidance (Hagemoen and Reimers, 2002; Weladji et al., 2003), rutting, and landscape features such as impassable terrain and water. Therefore, while movement rates may reflect foraging behavior, we limit our assessment to movement velocities and the potential influences of vegetation productivity.

Barren ground caribou moved more slowly in more productive tundra and grassland habitats. As a foraging species, this seems intuitive, especially considering the amount of tussock cottongrass (Cerbrian at al., 2008; Jandt et al., 2008) and lichen (Bergerud, 2000) consumed as forage. While the ability of EVI to act as an appropriate proxy measure for lichens is unknown, EVI will detect elevated productivity in cottongrass species. If movement velocities in these two habitats do reflect some degree of foraging activity, increasingly levels of vegetation productivity in grassland habitats may result in increased foraging opportunities for caribou, while in tundra habitats our results indicate that any gain due to increased productivity are likely to occur only in low productivity tundra habitats.

Caribou displayed a different reaction to elevated levels of productivity in shrub habitats, traveling most rapidly through intermediately productive shrub habitats. Although caribou do selectively forage on shrub species (Hansen et al., 2007), many shrub species are not primary forage and therefore will not promote vigorous foraging activities. We suspect that shrub density may be an important (and unmeasured) factor here, with open shrub habitat supporting some lichen growth while dense shrub habitats may suppress both lichen growth and force slow movement rates. We hypothesized that insect harassment would play an important role in movement velocities in shrub habitats (Hagemoen and Reimers, 2002; Weladji et al., 2003);

however, shrub movement velocities were considerably lower than tundra or grassland movement velocities. It is possible that rather than forcing caribou to move rapidly through shrub environments, insect harassment forces caribou to exposed ridges and eskers or to north aspect slopes which have retained some snow to avoid parasitism which subsequently reduces their movement rates.

Chapter 5: Estimating changes in lichen mat volume through time and related effects on barren ground caribou movement

5.1 Introduction

Barren ground caribou represent one of the most numerous large mammals in Arctic and sub-Arctic environments (Berger, 2004; Vors and Boyce, 2009; Festa-Bianchet et al., 2011). Barren ground caribou are commonly grouped into herds based on high fidelity to calving grounds (Gunn and Miller, 1986; Bergerud, 2000; Schaefer et al., 2000). In Canada, barren ground caribou herds are important culturally, ecologically, and economically, as well as for local food security (Gordon, 2003; Parlee et al., 2005; Festa-Bianchet et al., 2011). As foragers, barren ground caribou diets are variable throughout the year depending on forage availability (Jandt et al., 2008); however, terricholous lichen mats (primarily formed by circumpolar *Cladonia* lichens) form a part of barren ground caribou diet throughout the year (Bergerud, 2000) and represent the majority of barren ground caribou forage in winter months when other forage is not available (Joly et al., 2010). Terricholous lichens are high in digestible energy, making them excellent (and highly available) winter forage when energy demands are high (Jandt et al., 2008; Joly et al., 2010). Conversely, when animals are adding fat, especially cows during spring and summer, lichen are less desirable owing to their low protein and fat content and availability of alternative forage (Cebrian et al., 2008; Joly et al., 2010).

Terrestrial Arctic and sub-Arctic environments are experiencing some of the most rapid climate driven changes on Earth (Chapin et al., 2000; Serreze et al., 2000; Kelly et al., 2013). The Arctic tundra is increasing in vegetation greenness (Euskirchen et al., 2006; Kimball et al., 2006) (i.e. the Normalized Difference Vegetation Index; used as a proxy for vegetation biomass) and wetness (i.e. the Normalized Difference Moisture Index; used as a proxy for the amount of moisture contained in vegetation biomass) which is likely a result of lengthening growing seasons and warmer summer months (Myers-Smith et al., 2011; Rickbeil et al., 2015; Ju and Masek, 2016). Shrub ingress in certain tundra environments is occurring in a rapid fashion, replacing forb/moss/lichen dominated communities with shrub dominated ones which can overtop and out-compete the lower forb/moss/lichen communities (Lantz et al., 2010; 2013; Fraser et al., 2014). Additionally, there is evidence of lichen mat declines in certain tundra regions that have experienced high barren ground caribou densities, where overgrazing and trampling led to reduced lichen abundance (Skogland, 1985; Manseau et al., 1996; Hansen et al., 2007; Tveraa et al., 2013). Understanding the spatial patterns and temporal dynamics of terricholous lichen biomass is a critical piece of information for barren ground caribou conservation and management; as such, considerable effort has been focused on this question. Colpaert et al. (2003) mapped both terricholous lichen and arboreal lichen resources across Finland while Théau et al. (2005) tested multiple methods for classifying lichen land cover across barren ground caribou herd ranges.

Historically, acquiring remotely sensed data in Arctic environments has been challenging owing to issues with short growing seasons, snow/ice, and weather. These challenges have been addressed in the past by using coarse spatial resolution imagery (250 m to 1 km spatial resolution) from sensors such as MODIS with rapid (1 – 2 day) revisit times. Finer spatial resolution satellite programs such as Landsat (30 m spatial resolution) have been less commonly utilised in Arctic environments due to the challenge of acquiring images free of cloud (related shadow), haze, and smoke from Boreal fires. This challenge is exacerbated by longer revisit times between image acquisitions for Landsat (16 days when only 1 sensor is in operation). However, following the 2008 opening of the United States Geological Survey Landsat archive (Woodcock et al., 2008; Wulder et al., 2012), rapid developments in the application of Landsat TM, ETM and OLI, have taken place (Wulder et al., 2012; Wulder and Coops, 2014). Recent advances in Landsat data processing have included the production of large area annual pixel-based composites (Roy et al., 2010; White et al., 2014), and seamless gap free surface reflectance composites of Canada (Hermosilla et al., 2015; 2016). The developments surrounding Landsat compositing are making assessments of barren ground caribou habitat, including lichen condition, possible at spatial scales appropriate for individual barren ground caribou movement analyses (Rickbeil et al., 2016).

Recently, Falldorf et al. (2014) developed an algorithm (the lichen volume estimator or LVE) for estimating lichen volume from Landsat data, which was successfully applied to Landsat imagery in Norway and is the first ever successful attempt at estimating lichen volume using remotely sensed spectral data. The LVE was built using an in-situ data set of 1345, 50x50 m plots which measured lichen mat volume and were designed to match Landsat spatial resolution (30x30 m) and avoid mixed pixel issues. The LVE is based off two previously developed metrics, the normalized differenced moisture index (NDMI; Wilson and Sader, 2002) and the normalized differenced lichen index (NDLI; Nordberg, 1998), both of which have been previously shown to effectively assess lichen’s spectral signatures. The LVE had an average adjusted R squared of

0.67 using ten-fold cross validation of two dimensional Gaussian regression (Falldorf et al., 2014).

The objectives of this study were to (1) apply the lichen volume estimator developed by Falldorf *et al.* (2014) across the ranges of five barren ground caribou herds in northern Canada from 1985 to 2011, allowing for (2) an assessment of changes in lichen mat volume both spatially and temporally for five barren ground caribou herds and to (3) assess how changes in lichen mat volume are associated with barren ground caribou movement rates across different seasons. The opening of the Landsat archive allows for the extension of the work of Falldorf et al. (2014) both spatially and temporally. Moreover, the current barren ground caribou telemetry data sets occurring within the Northwest Territories (with over 300 000 individual data points for five barren ground caribou herds from 2006 to 2011) allowed for an assessment regarding how LVE values associate with barren ground caribou movement metrics. I expect an overall decrease in lichen mat volume to have occurred since 1985, especially across the ranges of the more western herds, which have experienced significant expansion of shrubs (Lantz et al., 2010; 2013; Fraser et al., 2014). I also expect that barren ground caribou will exhibit more foraging type behavior in locations with higher lichen mat volume estimates as lichen mats for a critical portion of barren ground caribou diets throughout the year (Bergerud, 2000; Joly et al., 2010).

5.2 Methods

5.2.1 Study area

For details of the study area see Section 2.1. The five herds examined in this Chapter are: the Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Ahiak/Beverly.

5.2.2 Landsat spectral data

For details of the NTEMS project and the Landsat spectral data product produced, see Section 2.3.2. The lichen volume estimate (LVE) was computed using the NTEMS dataset (Figure 2b) on an annual basis by applying the algorithm developed by Falldorf et al. (2014). The LVE product was developed in Norway on an extensive in-situ lichen volume data set on a single Landsat scene (34 225 km^2). The algorithm employs a multi-dimensional Gaussian curve and two Landsat indices: the Normalized Differenced Lichen Index (Nordberg, 1998) ([Band 5 - Band 2] / [Band 5 + Band 2]; Band 2 representing reflectance in the green portion of the spectrum while Band 5 represents shortwave infrared reflectance) and the Normalized Difference Moisture Index (Wilson and Sader, 2002) ([Band 4 – Band 5] / [Band 4 + Band 5]; Band 4 representing reflectance in the blue portion of the spectrum). These two indices were combined in the LVE algorithm using the mean parameters calculated by Falldorf et al. (2014) through ten-fold cross validation. The caribou range-wide mean NDMI and NDLI values required in the LVE algorithm were calculated by masking all non-lichen pixels and taking a mean of each index across all combined herd ranges. Lichen tundra pixels were identified using the Canada Center for Remote Sensing's annual MODIS land cover product, which describes 19 land cover classes across Canada at 250 m spatial resolution from 2001 to 2011 (Pouliot et al., 2014). The 2011 year was used to represent current conditions and tundra classes (tundra grassland and tundra moss/lichen/sparse vegetation classes) were aggregated to produce a tundra containing lichen product at 250 m spatial resolution which was then resampled to a 30 spatial resolution to match the Landsat data (Figure 5.1a). The LVE algorithm was applied across more than 700 000 km^2 of barren ground caribou habitat (that is, the spatial equivalent of approximately twenty 185 x 185 km Landsat scenes) for every year from 1984 to 2012.

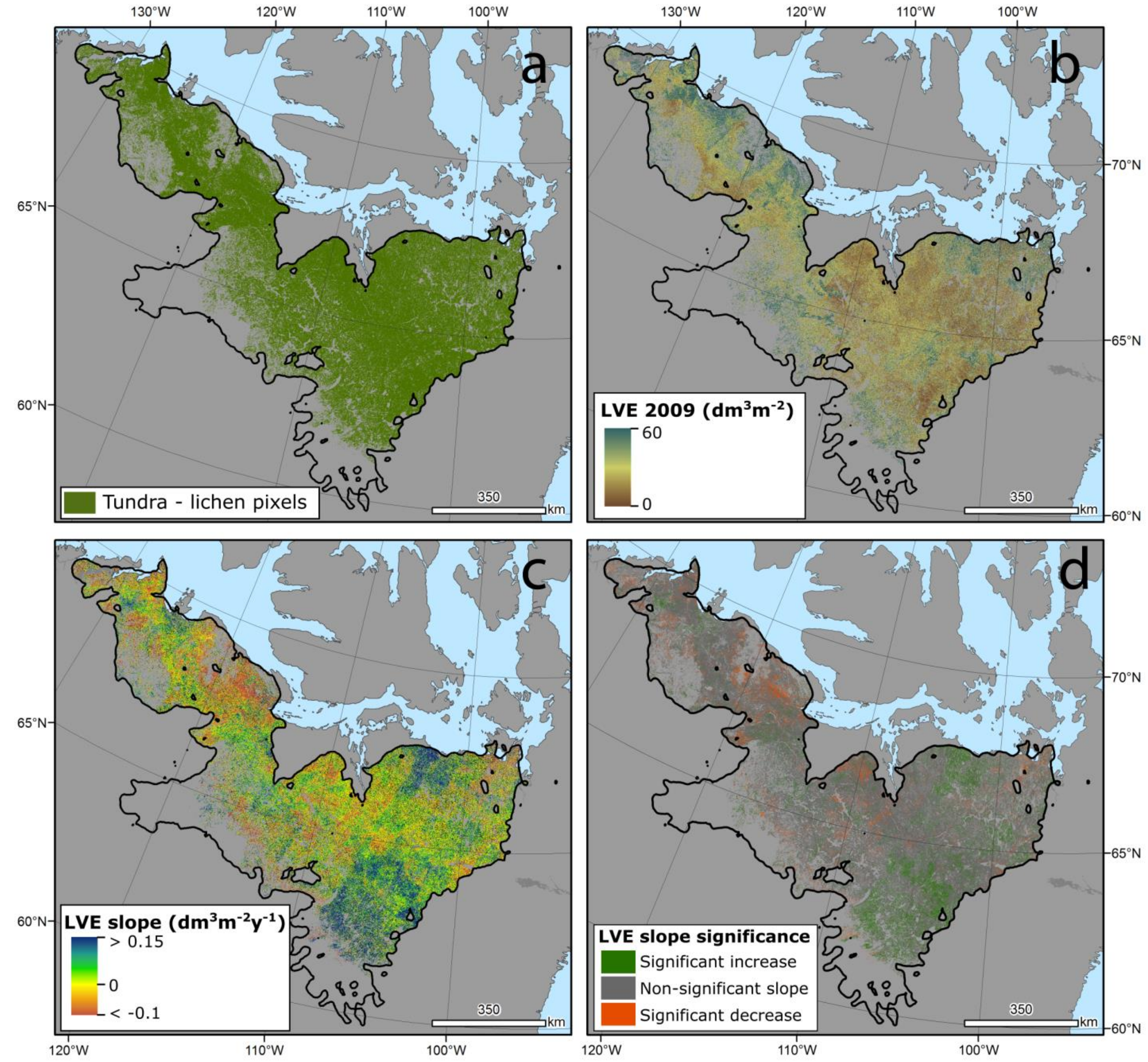

Figure 5.1 (a) The tundra – lichen map derived from the Canadian Centre for Remote Sensing MODIS land cover data set. (b) 2009 LVE estimates for the five herd ranges. (c) the Theil-Sen slopes estimating change per year for each pixel. (d) significant increases, decreases, and non-significant slopes determined using Mann-Kendall tests.

I caution against interpreting the LVE estimates as absolute values of lichen mat volume across our study area, as no in-situ data was available for parameter estimation or validation. However, even using the mean coefficients (which were shown to be stable through cross-validation) established by Falldorf et al. (2014) should provide useful information when evaluating the LVE values spatially or through time as potential directional biases resulting in over or underestimation of actual lichen mat volumes should be consistent. Additionally, Scandinavian and Canadian tundra ecosystems share dominant lichen types (genus *Cladonia* primarily) which are expected to have largely similar spectral reflectance characteristics in the different environments and both indices employed in the LVE (NDMI and NDLI) have been shown to be associated with lichen cover. Despite this, I recommend treating our application of the LVE as a relative index of lichen mat condition rather than a direct, absolute, measurement of volume.

5.2.3 Barren ground caribou telemetry data

For details of GPS telemetry data see Section 2.2.1.2. By relating velocity (used here due to the use of two different time steps (5 hour and 8 hour intervals); Dodge et al., 2008; Calenge et al., 2009) to lichen volume estimates I was able to characterize how differing lichen conditions influence barren ground caribou movement and make inferences regarding possible effects of lichen mat conditions on caribou movement.

5.2.4 Analysis approach

5.2.4.1 Temporal changes in lichen mat volume

Changes in annual LVE were examined using Theil-Sens (TS) non-parametric regression (Sen, 1968; Michaud et al., 2012; Fraser et al., 2014) (Figure 2c). The TS analysis calculated all pairwise slopes for the LVE through time for each pixel throughout the image stack (1984–2012), returning the median slope as the estimate of yearly LVE change. TS slopes are less sensitive to outliers than traditional linear regression and, as a result, are becoming more commonly used in time series analyses at the pixel level (Michaud et al., 2012; Rickbeil et al., 2015). Slope significance was determined using non-parametric Mann-Kendall tests (Figure 2d) (Kendall, 1975; Fraser et al., 2014).

5.2.4.2 Local spatial autocorrelation characteristics of temporal changes in lichen mat volume

The Getis-Ord G_i* statistic (Getis and Ord, 1992; Anselin, 1995) was used to assess the spatial dependence of the LVE Theil-Sen's slope pixels. This allowed me to determine whether pixels representing change in change in LVE over time were spatially organized into local groupings of positive or negative change, and whether or not the degree of spatial clustering observed in the LVI Theil-Sen's slope raster is less than or greater than chance (Getis, 1994). The G_i* statistic evaluates a particular pixel against neighbouring pixels and calculates a weighted variate value for the group of pixels which is expressed as a proportion of the sum of the entire data set's variate value, derived in this case from the entire LVE TS slope raster. This can be compared against an expected value under the assumption of no local spatial autocorrelation (Wulder and Boots, 1998; 2001). Here, I applied a Queen's case kernel, with all neighbouring pixels considered, including diagonals. The G_i* analysis produces "a standardized value which indicates both the degree of [spatial] autocorrelation in the values of the digital numbers centered on a given pixel and the magnitude of these values in relation to those of the entire image" (Wulder and Boots, 1998, p. 2224). This can be considered a z score, and statistical significance can be assessed using the area under the z curve. The end result is an assessment of all pixels relative to their neighbours to determine whether each pixel is centered in a cluster of more positive or negative values than would likely occur randomly, or conversely, whether the pixel is centered in a cluster displaying no spatial organization.

5.2.5 Temporal changes in lichen mat volume across herd ranges

To examine spatial variation in LVE TS slopes by herd, 1000 random samples were taken from each herd's range ensuring a spatially stratified random sample. This sample was then analyzed in single factor generalized least squares regression (GLS) with a maximum-likelihood iterator, built using the package “nlme” (Pinheiro *et al.*, 2013) in R (R Core Team, 2013). GLS was used, as it allows for the inclusion of spatial autocorrelation functions to account for issues with spatially structured model residuals (Zuur et al., 2009). The GLS model, built using the randomly sampled data, was assessed for spatially structured residuals using a semi-variogram which did indeed indicate spatial structuring of residuals. A Gaussian spatial correlation structure was added to the GLS model and the model was subsequently re-examined using Likelihood Ratio test with the best model being retained (Zuur et al., 2009). If significant differences between groups were detected in the final model, a Tukey’s HSD test (Day and Quinn, 1989) was used to assess where differences were significant (an alpha value of 0.05 was used for all statistics).

5.2.5.1 Lichen mat volume estimates and barren ground caribou behavior

Barren ground caribou behavior was inferred using velocity estimates derived from the telemetry data which were, in turn, associated with LVE values based on the year in which the telemetry data were collected. Models were built for each season (seasons were defined using a generalized version of Nagy’s (2011) analysis of differing movement rates of barren-ground caribou throughout the year) with the same randomly sampled data set used for the herd range analysis described in the section above. Generalized additive mixed models (GAMM) with a negative binomial link were built to account for over-dispersion in the data. GAMMs allow for non-linear responses to be appropriately estimated while assigning unique animal identifiers as a random effect accounted for repeated measures per animal (Cuiti et al., 2012; Rickbeil et al., 2016). All model residuals were examined for spatial autocorrelation using semi-variograms (Zuur et al., 2009). Since all models displayed evidence of spatially autocorrelated residuals, Gaussian spatial correlation structures were added to the GAMM models (Zuur et al., 2009).

5.3 Results

The Ahiak/Beverly herd was found to have the largest percentage of land with increasing lichen volume estimates (17.1 %, Table 5.1). The Bathurst and Bluenose West were found to have relatively similar percentages of increasing and decreasing lichen containing tundra (7.7 vs. 8.0 % and 6.7 vs. 7.2 % respectively). The Bluenose East had slightly more than double the percentage of decreasing than increasing lichen containing tundra (10.9 vs. 5.4 %) while the Cape Bathurst had almost five times the percentage of decreasing vs. increasing lichen containing tundra (13.0 vs. 2.9 %).

Table 5.1 The percentage of significantly increasing, significantly decreasing, and no significant change lichen containing tundra pixels detected by herd range over all lichen containing tundra.

Change	Ahiak/Beverly	Bathurst	Bluenose East	Bluenose West	Cape Bathurst
Increasing	17.0	7.7	5.4	6.7	2.9
Decreasing	4.0	8.0	10.9	7.2	13.0
No Change	79.0	84.3	83.7	86.1	84.1

Our analysis of the local spatial autocorrelation contained within the LVE TS slope raster (Figure 5.2a) revealed that the Bluenose West herd had the largest percentage of its lichen containing tundra pixels centered in clusters of increasing LVE slopes (18.5 %; Table 5.2, Figure 5.2b), followed closely by the Ahiak/Beverly herd (16.3 %). The Cape Bathurst, Bluenose East, and Bathurst herds all had more than 20 % (21.0, 20.9, and 20.9 % respectively) of their lichen containing tundra pixels centered in clusters of declining LVE slopes.

Table 5.2 The results of the G_i* analysis, showing the percentage of pixels which were centered in significant clusters of increasing and decreasing LVE TS slope values, as well as pixels displaying no slope clustering, by herd range.

Change Cluster	Ahiak	Bathurst	Bluenose East	Bluenose West	Cape Bathurst
Increasing	16.3	8.4	13.2	18.5	7.4
Decreasing	12.8	20.9	20.9	12.1	21.0
No Change	70.9	70.8	65.9	69.4	71.6

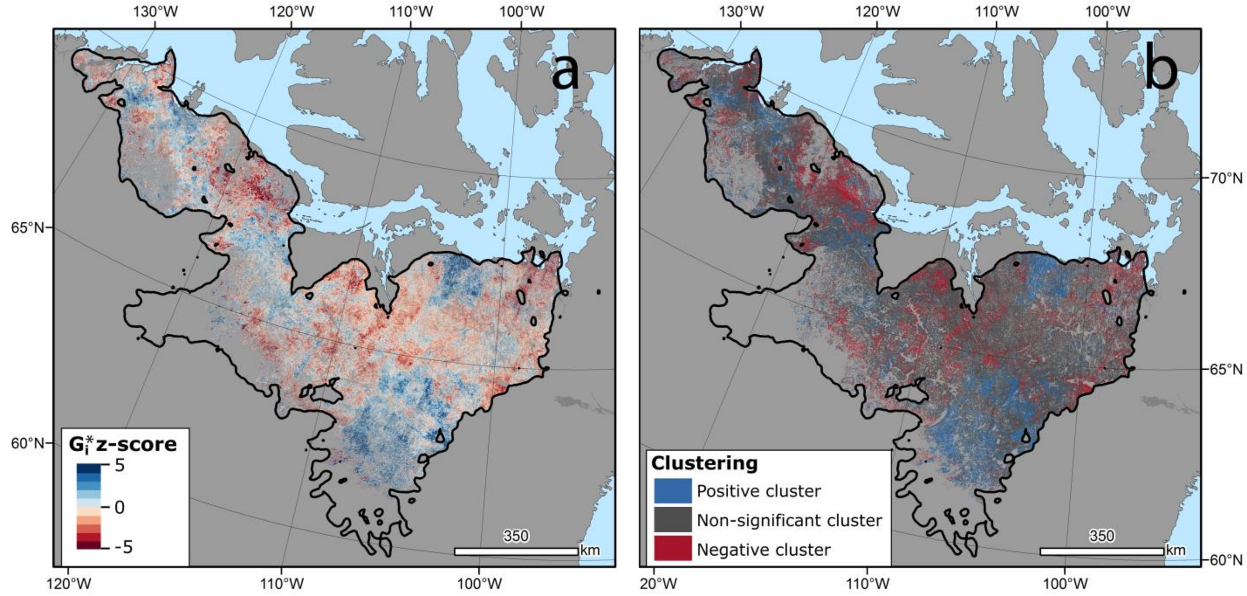

Figure 5.2 (a) The G_i* z scores for the LVE Theil-Sen's slopes. (b) Significant positive, negative, and non-significant G_i* z score values indicating a pixel was centered in a cluster of positive, negative, or non-significant LVE Theil-Sen's slope values.

The LVE slopes by herd range model that incorporated a Gaussian spatial correlation structure out-performed the model lacking one (L. Ratio = 262.84; P < 0.001). A significant difference between classes was detected (F = 4.27; P = 0.002). The Ahiak/Beverly herd range was found to have more positive slopes than all other herd ranges save the Bathurst (Figure 5.3).

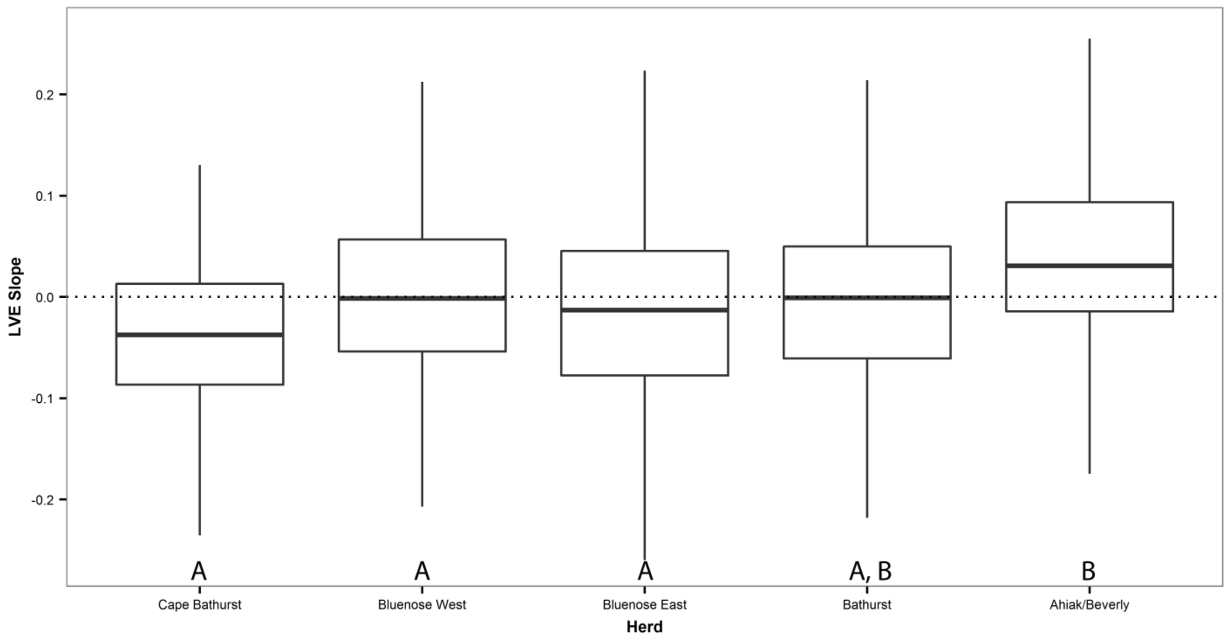

Figure 5.3 Boxplot of the lichen volume estimate Theil-Sen's slopes by herd range (west to east). Shared letters indicate non-significant differences.

Movement velocities varied by herd and season (Figure 5.4). Caribou moved fastest in summer (except for the Ahiak/Beverly herds which had slightly higher movement rates in Fall) and slowest in winter across all herds. Fall movement rates were faster than spring movement rates in all herds except the Bathurst. Herds with smaller overall range sizes and lesser distances between their winter habitat and calving grounds (i.e. the Cape Bathurst) tended to move more slowly than herds with large distances between their calving and winter grounds and larger herd ranges (i.e. the Ahiak/Beverly and Bathurst herds).

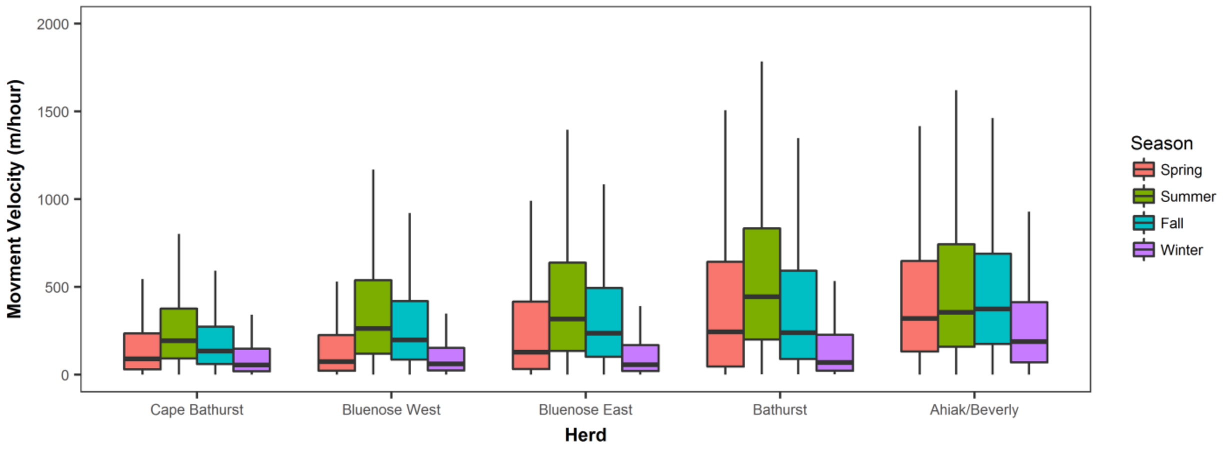

Figure 5.4 Boxplot of barren ground caribou movement velocities by herd (west to east) and season.

Significant smoothing terms were detected across all seasons for the movement velocity versus LVE GAMMs (Figure 5.5). A nearly linear negative association between mean movement velocity and LVE was detected in spring (F = 5.121; P = 0.02). In summer, a reduction in mean movement velocities was detected at LVE values of approximately 16 and then again after LVE values of 45 (F = 5.92; P < 0.001). In fall, mean movement velocity reached a minimum at LVE values of 25 (F = 10.52; P < 0.001). Mean movement velocities remained relatively constant in winter until LVE values of 25 after which mean movement velocities declined rapidly (F = 3.17; P = 0.02).

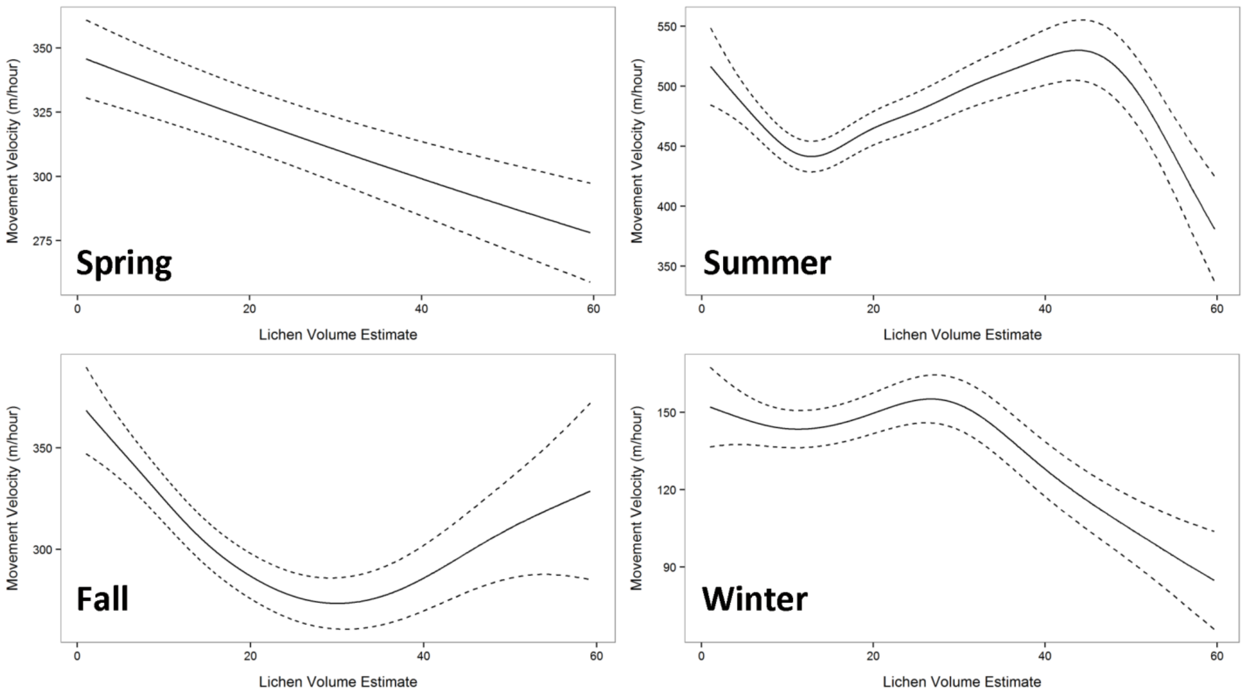

Figure 5.5 Mean predicted movement velocities (m/hour) predicted using LVE values by season. Dashed lines represent one standard error.

5.4 Discussion

In this research, I applied the lichen volume estimator across more than 700 000 km^2 of barren ground caribou habitat in northern Canada, providing unique information on lichen mat condition and potential barren ground caribou habitat quality. By accessing data available in the Landsat archive and applying novel processing techniques to generate gap-free, time series, reflectance composites I was able to evaluate change in LVE across multiple decades. I detected significant temporal changes in lichen mat volume across the study area and identified significant spatial clusters of positive and negative changes in lichen mat volume. Finally, by incorporating an extensive barren ground caribou telemetry data set I was able to detect subtle changes in barren ground caribou movement rates relative to LVE values.

The Ahiak/Beverly herd experienced significantly larger temporal increases in LVE values when compared with all other herds expect the Bathurst. Conversely, the Cape Bathurst herd experienced the largest overall decline in LVE values, although not statistically different from the Bluenose East, Bluenose West, and Bathurst. The Cape Bathurst herd has declined from 12 516 (SE = 3504) individuals in 1987 to 2427 (a complete herd census therefore no SE estimate is provided) individuals in 2012 (see Boulanger et al. (2014) for details of herd count methods). Both Stow et al. (2004) and Lantz et al. (2010; 2013) documented shrub proliferation in the Mackenzie delta/Tuktoyaktuk Coastlands which occur in the western portion of the study area and corresponds with our documented declines in LVE values. This is a product of low productivity lichen/moss/grass communities shifting towards birch- and alder-dominated communities and becoming more productive in the process (Fraser et al., 2014). Conversely, the continentality of the eastern herd ranges, which results in colder temperatures, may play a role in limiting shrub recruitment (Lantz et al., 2010; Myers-Smith et al., 2015).

Assessing the LVE TS slope raster for spatial clusters of slope values offers a complementary analysis for assessing LVE changes through time. While the results of the Theil-Sen’s test are pixels occurring in space, the analysis is purely temporal in nature in that the only consideration is one particular pixel. And while this approach is likely of more interest to ecologists examining changing environmental conditions which may be driving changes in lichen mat condition, testing pixels for evidence of local clustering of positive or negative LVE TS slopes allows managers to move beyond the 30x30 m Landsat pixel. As a data capture technology, remote sensing, by nature, partitions the earth’s surface into a grid of regularly sized and shaped cells. When considered independently, ecological and contextual information can be lost. The detailed depiction of landscapes available from the 30 x 30 m spatial resolution of Landsat may be too fine to inform on the larger landscape conditions present. Meaningful spatial aggregation of pixels based upon spatial dependence allows for trend insights that are sized and shaped based upon the conditions present. As an example, spatial clusters of declining LVE values could indicate zones of shrub proliferation (Lantz et al., 2010; 2013) or intensive barren ground caribou grazing (Manseau et al. 1996; Tveraa et al. 2013). In a more applied sense, assessing the landscape by individual Landsat pixel may be a prohibitively small spatial scale for management across herd ranges and testing changes for spatial clustering may identify larger zones of positive or negative change indicating a likely change in barren ground caribou habitat condition.

LVE values were associated with variation in barren ground caribou movement rates in all seasons and these associations changed throughout the year, supporting the need to assess LVE – movement associations by season. Winter movement velocities were lower for all herds, likely a result of individuals moving through snow and having to crater for terricholous lichens. In contrast, summer movement velocities, when cows and calves are moving from calving grounds to summer ranges, were among the highest velocities for each herd.

Summer and winter displayed relatively consistent movement velocities across low and medium LVE values followed by declining movement rates at high LVE values. The summer association did have a reduction in movement velocities that occurred at mean LVE values of 18. When investigated further it was apparent that the summer telemetry points with slow movement rates (velocities less than 450 m/hour) are associated with low LVE values (between LVE = 10 to 25) occurred on calving grounds in the northern portion of each herd's range. Barren ground caribou use calving grounds primarily as a predator avoidance tactic as these locations are not overly productive or nutritious (Heard et al., 1996). This decline in movement at low LVE values is likely associated with calving – barren ground caribou cows with recently dropped calves slow considerably for up to a week or more post calving– and likely does not represent foraging type behavior.

The points during summer and winter where movement velocities slowed consistently identified thresholds at which increasing LVE values may result in improved forage conditions at these times of year (LVE values greater than 45 in summer and 25 in winter). Since lichens make up a greater proportion of barren ground caribou diet in winter (Joly et al., 2010) it is perhaps not surprising that improved foraging conditions in winter occur at lower LVE values when compared with summer. Spring movement velocities were nearly linearly negatively associated with LVE values, indicating consistent improvement in forage conditions with increasing LVE values. Surprisingly, barren ground caribou movement reached a minimum at intermediate LVE values in fall and movement rates increased at high LVE values. The increased rate of movement through areas with high estimated lichen mat volume is unexpected and unexplained at this point.

Barren ground caribou movement rates are, however, undoubtedly affected by more than lichen availability. Seasonal spring, post-calving, and fall migrations to and from calving grounds can result in elevated movement rates (Nagy, 2011), while snow and difficulties accessing terricholous lichens in winter can result in lowered movement rates. Insect harassment, which tends to peak in July, can force individuals to more wind prone areas like eskers and ridges, or north aspect slopes which may have retained snow, and in both cases this can reduce move rates (Hagemoen and Reimers, 2002; Weladji et al., 2003). These factors support our decision to assess movement by season, eliminating a potentially confounding factor in movement variation. I do acknowledge, however, that binning by season will not address factors affecting movement on shorter time frames (i.e. snow depth, insect harassment, calving) nor address spatial variation in these factors.

Access to spatially and temporally expansive Landsat composites allowed for the extension of Falldorf et al.'s (2014) assessment of lichen mat volume across five herd ranges for 26 years. Statistically significant temporal changes were detected in lichen mate volume estimates, and these changes varied depending on the herd in question. Temporal LVE TS slopes formed clusters of positive or negative change across the study area, revealing more spatially expansive patterns in increasing and decreasing LVE values when compared with the temporal assessment. Barren ground caribou movement velocities were shown to significantly associate with LVE values, with foraging type behavior occurring in a manner consistent with our knowledge regarding barren ground caribou dietary requirement throughout the year; the increase in movement velocities at high fall LVE values being the only exception to this. The lichen volume estimate proved to be a promising method for assessing potential lichen mat volume changes through time across expansive herd ranges and warrants further use. Furthermore, as a relative indicator the LVE showed potential as a predictor of barren ground caribou behavior; future work describing how landscapes affect how barren ground caribou movement and foraging should incorporate this estimate.

The application of the LVE algorithm here highlights both the strength and weakness of using remote sensing for terrestrial ecosystem assessment in northern environments. The ability to collect synoptic remotely sensed terrestrial data repeatedly through time at a reasonable cost is undoubtedly a benefit to northern research. Conversely, the lack of appropriate in-situ data makes the transition from an index to an estimate challenging. In this case, the spectral responses being measured here led to a valuable assessment of spatial and temporal patterns in lichen mat condition. However, if I wish to fully utilize the LVE and produce lichen mat volume estimates, an in-situ ground campaign with a data collection design appropriate for remotely sensed data needs to be carried out, which is an expensive and challenging endeavour.

Chapter 6: Barren ground caribou movement after recent fire events; integrating caribou telemetry data with Landsat fire detection techniques

6.1 Introduction

Disturbance regimes in Canada's north are changing in a more rapid fashion than estimated historical rates of change (Kasichke and Turetsky, 2006). Boreal fire regimes in particular are changing with fire seasons becoming longer and having higher temperatures leading to more severe fires and more area burned annually (Joly et al., 2010; Kelly et al., 2013). In the western North American Boreal forest, the area burned by wildfire has doubled from the 1960/1970s to the 1980/1990s (Kasichke and Turetsky, 2006) and this pattern is projected to continue in the future (de Groot et al., 2013). Consumption of organic materials during fire events in the Boreal has been linked to melting permafrost (Johnstone et al., 2010a), reductions in organic layers and conversions of spruce dominated stands to deciduous dominated stands (Johnstone et al., 2010b). Historical information regarding fire regimes across the North American tundra is less well documented; however, some evidence suggests that tundra fires were more widespread than previously thought (Jones et al., 2013).

The effects of changing fire regimes in the Boreal forest and tundra are widespread (McGuire et al., 2006) and can influence the animal species that utilize these environments (Joly et al., 2010). Barren-ground caribou are the most numerous large mammal in the Canadian Arctic (Bergerurd, 2000; Festa-Bianchet et al., 2011) and are critical to northern ecosystems and cultures (Gordon, 2003; Parlee et al., 2005). Currently, the majority of barren-ground caribou herds worldwide are in decline, with some herds having lost more than an order of magnitude of their population sizes in less than 30 years (Vors and Boyce, 2009). Barren-ground caribou have been shown to react negatively to fire in the forested areas of their range (Joly et al., 2010). Fire removes important food species such as terricholous lichens and cottongrass leading to a reduction in forage for caribou (Jandt et al., 2008). Fire can also remove cover which serves to offer concealment from predation. Recovery times for caribou forage can vary from three to four years for tussock cottongrass (Bret-Harte et al., 2013) to more than a century for lichens (Zouaoui et al., 2014) leading to uncertainty regarding how rapidly caribou habitat recovers post-fire.

Currently, the majority of analyses examining the effects of fire on caribou foraging ecology compare used locations versus random locations (Joly et al., 2010), since true negatives (i.e., areas that are not utilized by caribou) are difficult to identify reliably for herds that commonly have tens of thousands of members. Moreover, there are a number of shortcomings with a random location approach. Random locations will undoubtedly result in false negatives, adding noise to habitat use models. Additionally, estimating habitat use as a binary use/non-use metric oversimplifies the complex ways in which caribou interact with their environment. It is conceivable that caribou would avoid foraging in a recently burned area while still using the area for travel. Expectations regarding how caribou react to fire events varies with traditional users as well, with some elders predicting caribou will completely avoid recent burns and others arguing that some movement will still occur immediately post-fire (Kendrick et al., 2005). Incorporating caribou behaviour into analyses regarding habitat use post-fire would help address the multiple ways in which caribou interact with their habitat. Additionally, habitat use is not uniform throughout the year, with parts of the year more dedicated to foraging (i.e. increasing fat stores) and other parts more dedicated to movement (e.g. traveling to calving grounds in spring) (Bergerud, 2000).

As foragers, caribou diets vary throughout the year depending on forage availability and nutritional needs (Jandt et al. 2008); however, terricholous lichen mats (primarily *Cladonia* type lichens) form a portion of caribou diet throughout the year (Bergerud, 2000) and represent the majority of caribou forage in winter months (Joly et al., 2010). Terricholous lichens are high in digestible energy, making them excellent (and highly available) winter forage when energy demands are high (Jandt et al., 2008; Joly et al., 2010). Terricholous lichens are also readily destroyed by fire owing to their low moisture content and location on the ground (Jandt et al., 2008). Conversely, when animals, especially cows during spring and summer, are gaining fat, lichens are less desirable owing to their low protein and fat content (Cebrian et al., 2008; Joly et al., 2010).

Predicting the impacts of future fire on caribou habitat has, to this point, employed successional ecosystem forecasting incorporating global emission scenarios and global circulations models with stochastic fire events (see Joly et al., 2012; Gustine et al., 2014). Habitat gain/loss is examined at the end of the model run as the amount of habitat remaining that is defined as being favourable for caribou, such as spruce-lichen dominated communities which have long estimated rates of recovery (more than 55 years; Joly et al., 2012; Gustine et al., 2014), versus initial habitat availability. The effects of recent burns (i.e. immediately post-fire and in the following years) on caribou behaviour, however, has not been tested directly and remains unknown.

Considering the lack of integration of behaviour into post-fire-caribou analyses and uncertainty regarding caribou reactions to recent fire events, this Chapter presents two key analyses. Firstly, I assess how the size and severity of fires have changed over the past 26 years across five barren-ground caribou herd ranges. Secondly, I examine how the behavioural metrics of individual barren-ground caribou change during the 26 year time period in burned locations. To provide context for our interpretations, I expect the burned area to have increased over the past 26 years in concert with recent findings (Kasichke and Turetsky, 2006; Kelly et al., 2013). I expect fire to result in a complete elimination of foraging-focused behaviour (Joly et al., 2010); however, I expect some movement-focused behaviour to remain (Kendrick et al., 2005; Anderson and Johnson, 2014). I expect behaviour to shift from movement-focused behaviour towards foraging-focused behaviour as time since fire increases and as fire severity decreases.

6.2 Methods

6.2.1 Study area

For details of the study area see Section 2.1. The five herds examined in this Chapter are: the Cape Bathurst, Bluenose West, Bluenose East, Bathurst, and Ahiak/Beverly.

6.2.2 Barren ground caribou telemetry data

For details of GPS telemetry data see Section 2.2.1.2. By relating velocity (used here due to the use of two different length time steps (five hour and eight hour); Dodge et al., 2008; Calenge et al., 2009) and relative turning angle (i.e. the angle of deflection from the previous linear segment of a GPS trajectory; Marsh and Jones, 1988; Calenge et al., 2009) to time since fire and fire severity, both movement metrics were associated with fire disturbance characteristics.

In order to quantify how caribou move in absence of fire, velocities and relative turning angles of GPS relocations were also calculated for non-burnt areas. These values are presented with the burnt values in the Results section to compare expected movement in absence of fire with movement values in burnt areas. To avoid including GPS relocations which fell in areas with fires occurring prior to the Landsat time series used here (which begins in 1985; see Methods – Fire Detection) the fire record was extended prior to 1985 using the Canadian National Fire Database (Stocks et al., 2002; Canadian Forest Service, 2015) which provides spatial polygons of fires dating back to 1966 in this study area. However, the reliability of the data set deeper in the time series is unknown and likely contains false negatives.

6.2.3 Fire detection

Remotely sensed optical imagery has been used for fire detection for decades (Haume and Rust, 1995; Hall et al., 2008; Roder et al., 2008); however, gaps in data archives, image perturbations (cloud, shadow, haze), and coarse spatial resolution, among other issues, have hampered documenting fires at high latitudes at a scale that can be related to individual animals. To address these issues, the NTEMS data set (see Section 2.3.2) was used to identify forest disturbances. Random Forests (Liaw and Wiener, 2002) was used to classify change events based on spectral, temporal, geometrical data into an agent of change: fire, harvest, road, and non-stand replacing changes (e.g., vegetation stress) (Hermosilla et al., 2015b). This product is built using an augmentation of Canadian Landsat archive data (White and Wulder, 2014) with that of the United States Geological Survey where analysis ready image products are available on a free and open basis (Wulder et al., 2012). The resultant Landsat image composites provide a temporally dense and spatially detailed source of data for comprehensive (most recent) fire detection across caribou habitat from 1985 to present (Figure 6.1a; b) at a spatial resolution that is appropriate for use with highly spatially accurate GPS telemetry data.

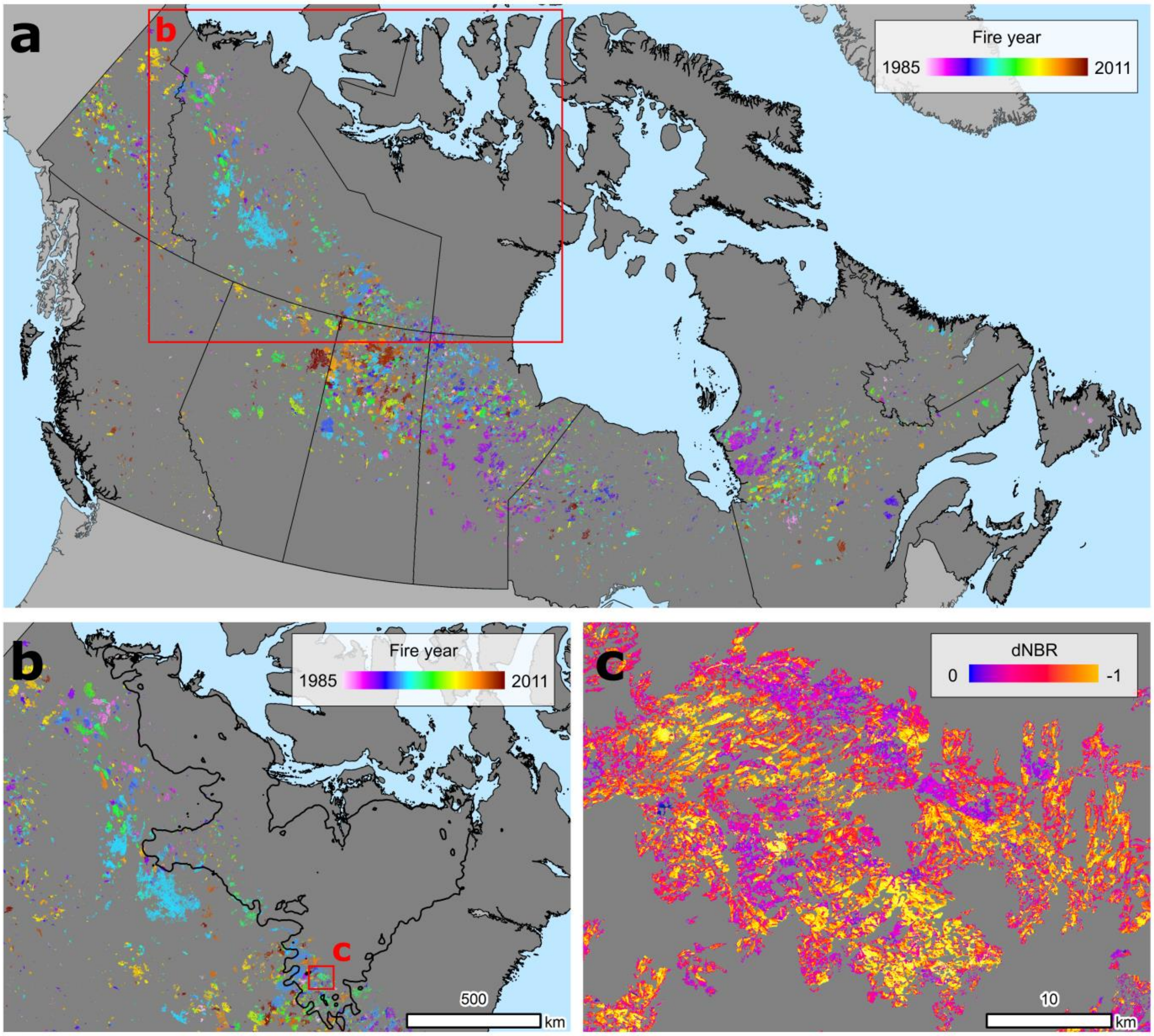

Figure 6.1 Most recent fire detection from composite Landsat imagery across (a) Canada and (b) the study area, with the cumulative herd range outline of the five herds examined here shown in black. (c) Estimated burn severity (dNBR) across a fire complex.

Landsat data has been used extensively to assess fire disturbances through time (e.g., Vogelmann et al., 2011). Most commonly, Landsat data is used to measure time since fire and estimate burn severity (Lentile et al., 2006; Eidenshink et al., 2007); however, a single universal measurement of burn severity has yet to be defined and usually depends on ecological conditions as well as project objectives (Lentile et al., 2006; Hall et al., 2008). The difference in pre- and post-fire normalized burn ratio, dNBR (Key and Benson, 2006; Figure 6.1c), is now the most often used Landsat index to estimate burn severity and is the index I used to estimate burn severity (NBR = [Band 4 – Band 7]/[Band 4 + Band 7]). dNBR values range from 0 dNBR to -2 dNBR, depending on amount of removal of plant biomass; -2 dNBR is the maximum possible value of burn severity although values below -1 are rare. Positive, i.e. 2 - 0 dNBR values, do not represent a disturbance and are therefore not included here (Brewer et al., 2005; Lentile et al., 2006; Roy et al., 2006; Eidenshink et al., 2007; French et al., 2008). Hall et al. 2008 detected a strong association between dNBR and burn severity; however, it is not a perfect estimate as time since fire, ecosystem characteristcs, and the definition of burn severity used can all affect how well dNBR describes burn severity in any one location (Epting et al., 2005; Wulder et al., 2009).

6.2.4 Analysis approach

Area burned (km2) and mean burn severity were summarized for each herd range through time and assessed using least squares regression. Animal movement velocity and absolute turning angle (in radians) were related to time since fire and burn severity using negative binomial generalized additive mixed models built with the "mgcv" package (Wood, 2011) to account for over-dispersed data and non-linear associations (Zuur et al., 2009). The generalized additive portion of the GAMM model employs cubic regression splines to estimate non-linear associations between the dependent and independent variables (Wood, 2006). Unique animal identifiers were used as a random factor to account for repeated measures across the same individual (Cuiti et al., 2012). Models were built with an interaction term between burn severity and time since fire (Model 1 below). Model selection used the Akaike Information Criterion (AIC) score as well as the significance of the interaction term; if the interaction term was found to not improve the model it was removed. Time since fire and fire severity were related to both movement metrics independently (Model 2 below).

$$Model\ 1{:}\ Movement\ Metric_i = \alpha + f_1(Time\ Since\ Fire)_i * f_2(Burn\ Severity)_i + \varepsilon_i$$

$$Model\ 2{:}\ Movement\ Metric_i = \alpha + f_1(Time\ Since\ Fire)_i + f_2(Burn\ Severity)_i + \varepsilon_i$$

$$where\ \alpha\ is\ the\ intercept, f_1 and\ f_2 are\ spline\ functions, and\ \varepsilon\ represents\ model\ error$$

All models included Gaussian spatial autocorrelation structures to account for potential spatial dependence issues. This model procedure was used for an overall model (all seasons, although summer was not included owing to the lack of summer GPS fixes occurring in burnt areas) as well as for fall (September to November), winter (December to March), and spring (April and May) to examine how associations change with time of year. Seasons were defined using a generalized version of Nagy's (2011) analysis of differing movement rates of barren-ground caribou throughout the year. An alpha value of 0.05 was used for all significance tests. All statistical analyses were carried out in the R software package (R Core Team, 2015).

6.3 Results

6.3.1 Area burned and burn severity through time

Neither area burned nor mean burn severity showed significant trends through time, save for the Bluenose West herd that had a significant decrease in both area burned ($p = 0.002$) and burn severity ($p = 0.02$) from 1985 to 2011 (Figure 6.2). However, both relationships were driven by one exceptional fire year in 1987 that was almost equivalent to the sum of area burned in all other years for this herd. In general, area burned was driven more by extreme fire years rather than a linear increase through time.

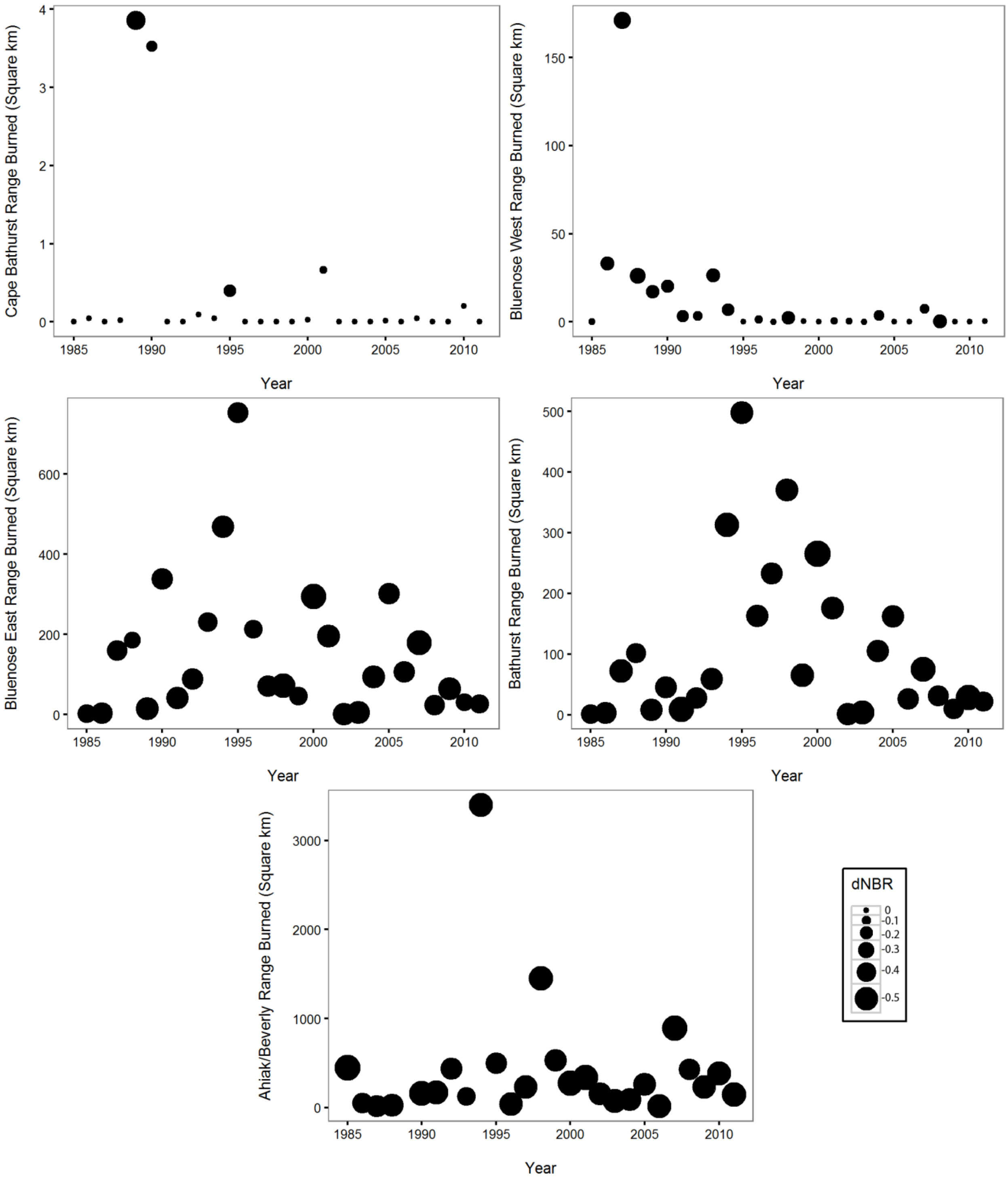

Figure 6.2 Annual area burned and mean burn severity (mean dNBR) for each herd from 1985 to 2011. Please note area burned scales differ between panels.

6.3.2 Caribou behaviour

6.3.2.1 All seasons

The final overall movement velocity model had no interaction term (two variable no interaction model AIC = 4479.7; two variable interaction model AIC = 4481.1; interaction term F = 2.32, p = 0.07) and included only burn severity as a significant predictor of movement velocity (F = 6.90, p = 0.009) (Figure 6.3). A slightly non-linear relationship between movement velocity and burn severity was detected, with increasing burn severity resulting in larger mean velocities. Overall mean predicted velocities exceeded the median overall velocity (119.6) in non-burnt areas across the entire range of dNBR values.

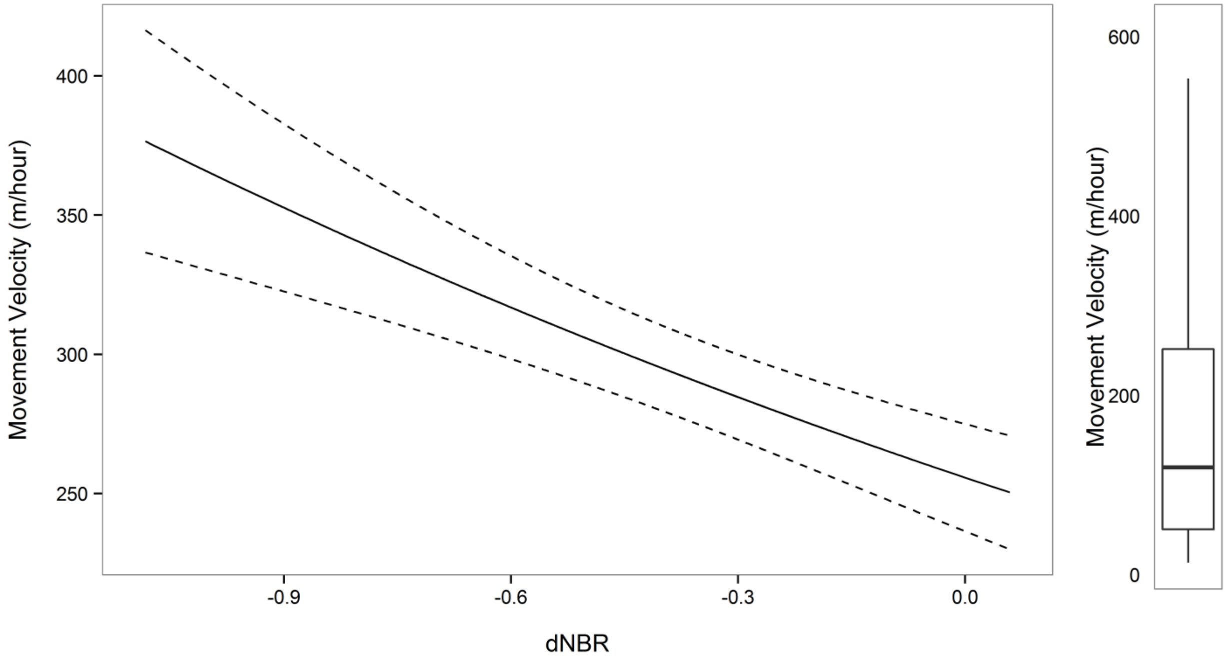

Figure 6.3 Burn severity (dNBR) as a predictor of mean movement velocity for individual caribou across seasons. Dotted lines represent one standard error. Boxplot shows the distribution of overall velocities in absence of fire (median = 119.6).

The final overall turning angle model incorporated both time since fire and burn severity along with an interaction term (two variable interaction model AIC = 3732.8; two variable no interaction model AIC = 3736.2; interaction term F = 2.317, p = 0.03). Turning angles were largest in < 5 years old high severity fires and > 20 years old low severity fires (Figure 6.4). The smallest turning angles were in found previously burnt areas aged 10 to 20 years with moderate levels of burn severity. Similar to the overall velocity analysis, mean overall turning angles were higher than the median overall turning angle (0.94) in absence of fire except in moderate severity fires aged 10 to 20 years.

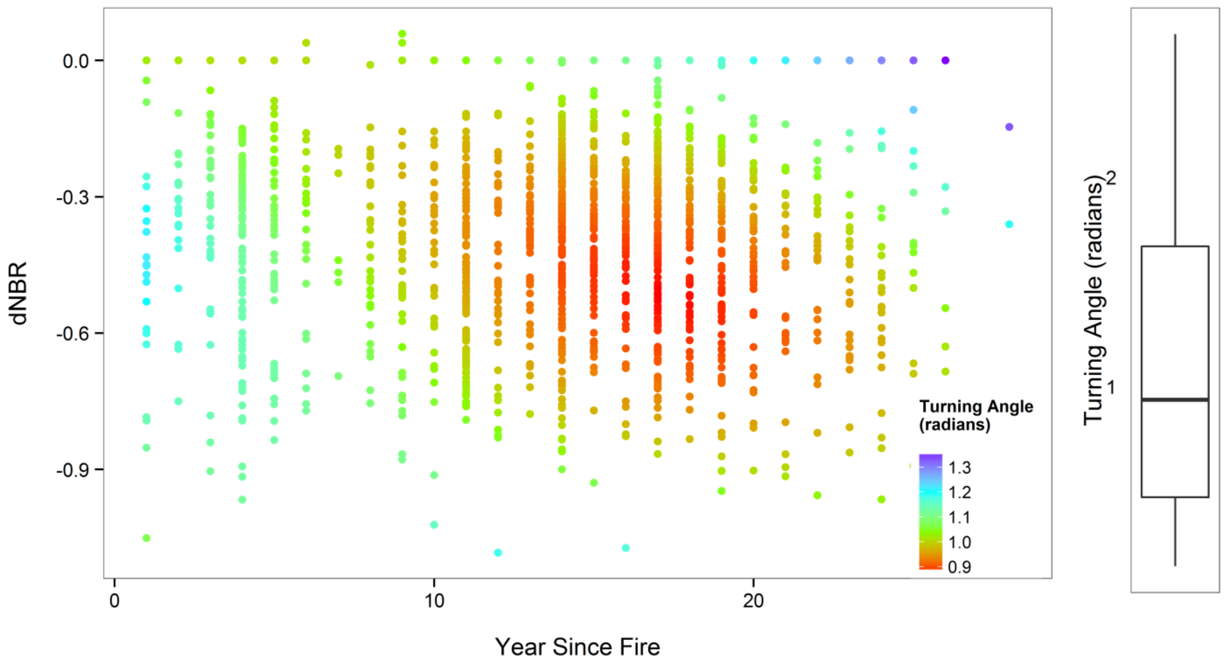

Figure 6.4 Interaction plot of burn severity (dNBR) and time since fire as predictors of individual turning angles of caribou across all seasons. Boxplot shows the distribution of overall turning angles in absence of fire (median = 0.94).

6.3.2.2 Fall

The fall movement velocity model did not include an interaction term (two variable with no interaction model AIC = 794.0; two variable with interaction model AIC = 797.2; interaction term F = 1.15, p = 0.33) nor was any relationship detected between turning angle and time since fire (F = 0.90, p = 0.34) or burn severity (F = 1.08, p = 0.30).

The fall turning angle model did not include an interaction term (two variable no interaction model AIC = 806.8; two variable interaction model AIC = 807.7; interaction term F = 2.03, p = 0.06) and only contained time since fire as a predictor of turning angle (F = 5.23, p = 0.01). This resulted in a non-linear relationship between turning angle and time since fire with a minimum predicted turning angle occurring at 18 years post-fire (Figure 6.5). Mean predicted turning angles in fall were higher than the median turning angle (0.90) in absence of fire until approximately 10 years since fire and then again beyond 22 years.

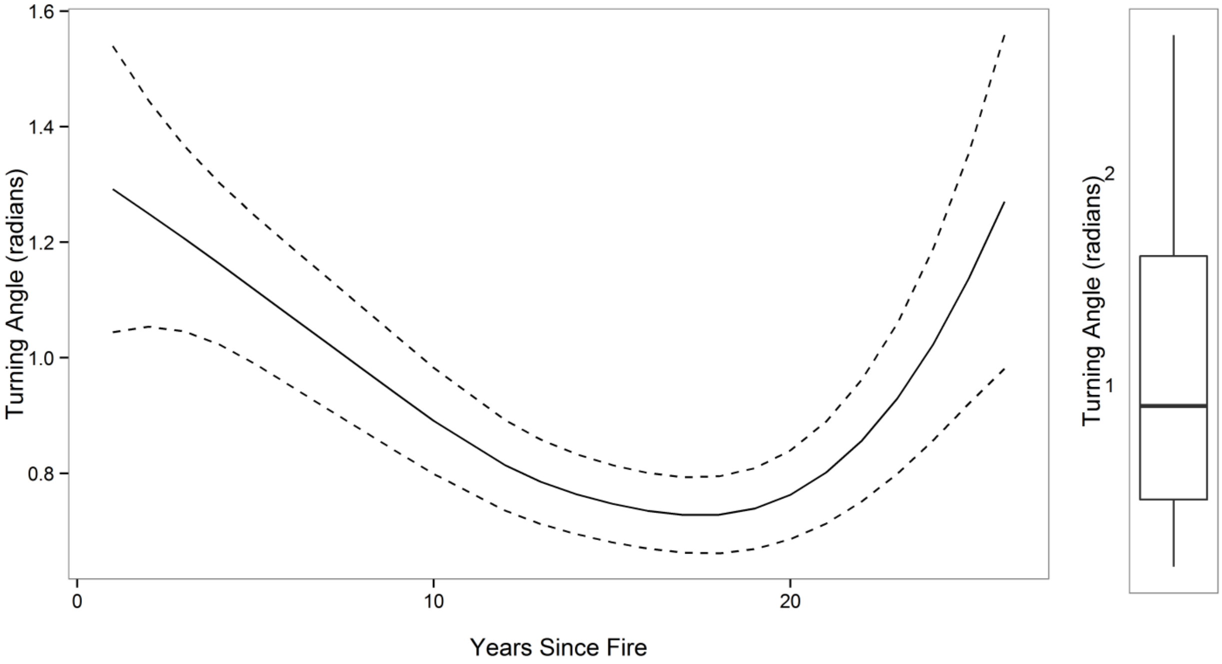

Figure 6.5 Time since fire as a predictor of individual turning angles of caribou during fall. Dotted lines represent one standard error. Boxplot shows the distribution of fall turning angles in absence of fire (median = 0.90).

6.3.2.3 Winter

The final winter movement velocity model contained both time since fire (F = 3.28, p = 0.01) and burn severity (F = 4.92, p = 0.027) with no interaction term (two variable no interaction model AIC = 2559.7; two variable with interaction model AIC = 2565.7; interaction term F = 2.16, p = 0.06). The result was a non-linear relationship between predicted movement velocity and time since fire with a peak in movement velocity at 8 years and a negative relationship between movement velocity and burn severity (Figure 6.6). Mean predicted winter velocities in burnt areas exceeded the median winter velocity (72.4) in non-burnt areas across the entire range of time since fire and dNBR values.

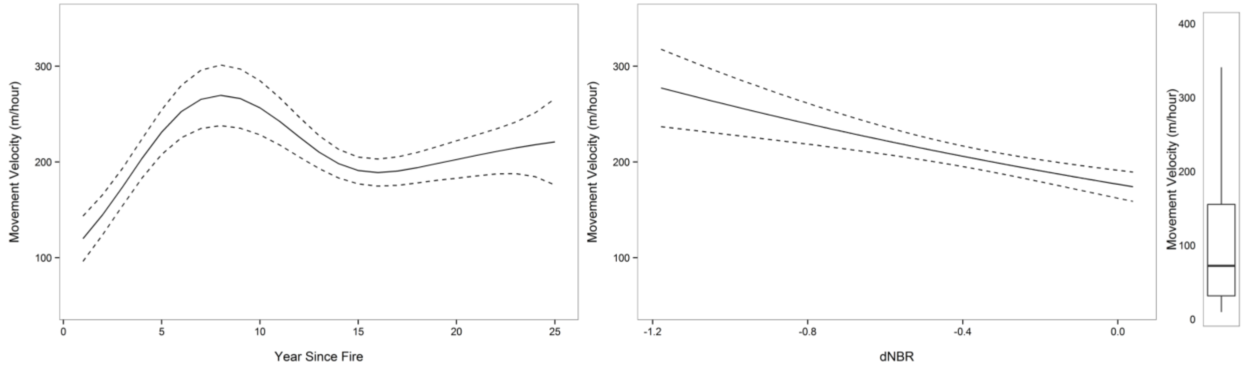

Figure 6.6 Time since fire (right panel) and burn severity (dNBR; left panel) as predictors of individual turning angles of caribou during winter. Dotted lines represent one standard error. Boxplot shows the distribution of winter velocities in absence of fire (median = 72.4).

The winter turning angle model did not include an interaction term (two variable with no interaction model AIC = 1660.6; two variable with interaction model AIC = 1661.3; interaction term F = 1.10, p = 0.41) nor was any relationship detected between turning angle and time since fire (F = 0.55, p = 0.46) or burn severity (F = 0.13, p = 0.72).

6.3.2.4 Spring

The spring movement velocity model did not include an interaction term (two variable with no interaction model AIC = 711.2; two variable with interaction model AIC = 714.9; interaction term F = 1.15, p = 0.33) nor was any relationship detected between turning angle and time since fire (F = 0.76, p = 0.39) or burn severity (F = 0.58, p = 0.45).

The spring turning angle model did not include an interaction term (two variable no interaction model AIC = 721.7; two variable interaction model AIC = 722.4; interaction term F = 1.47, p =

0.17) contained only time since fire as a predictor of turning angle (F = 8.91, p = 0.003). The result was a slightly non-linear negative relationship between movement velocity and time since fire (Figure 6.7). Mean predicted spring turning angles were higher than the median spring turning angle (0.82) in absence of fire until approximately 10 years since fire.

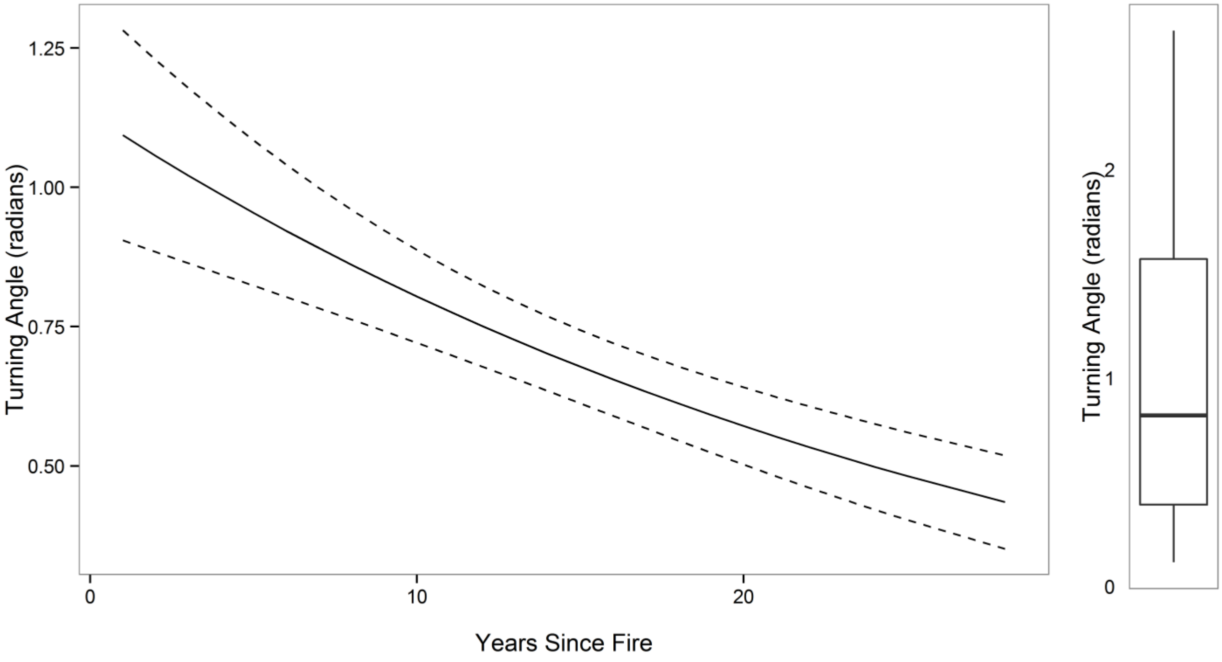

Figure 6.7 Time since fire as a predictor of individual turning angles of caribou during spring. Dotted lines represent one standard error. Boxplot shows the distribution of spring turning angles in absence of fire (median = 0.82).

6.4 Discussion

No increase in annual area burned was detected for any of the herds (except the Bluenose West, where the observed decrease in area burned was the result of one large fire year early in the time series). Multiple analyses of Boreal fire regimes have demonstrated that area burned is increasing across the Boreal (Kelly et al., 2013; Joly et al., 2010), especially in the western portion of the Canadian Boreal where some of these herds are located (Kasischke and Turestsky, 2006; de Groot et al., 2013). Whereas these studies examined much larger areas and/or longer time frames (e.g. Kasischke and Turestsky, 2006 examined 40 years of data form 1959 to 1999 across the entire Boreal), our study encompassed only a small portion of the northern extent of the western Canadian Boreal forest. Across each herd range, what was evident is that annual area burned is highly variable, primarily as a result of extreme fire years, rather than the result of a consistent increase in annual area burned. Despite this, our results are useful for herd managers concerned with how influential fire may be for the five herds examined here. The Cape Bathurst herd's largest area burned from 1985 to 2011 was less than 4 km^2 indicating that, at present, fire is likely not a major concern for this herd. Alternatively, the Ahiak/Beverly herd range experienced one fire year (1994) where over 3000 km^2 of habitat burned; fire may be a major concern for this herd at present and moving forward. In general, fires remain somewhat uncommon across the northern extent of the Boreal forest and the intersection of tracked caribou in recently burned locations is a relatively infrequent occurrence.

Despite the rarity of obtaining collar locations in previously burnt areas, the large amount of data available did still allow for an assessment of how fire events affect caribou movement patterns. The results presented here demonstrate that caribou respond to recent fires in different ways depending on the time since fire, fire severity, and season. When considering all seasons, caribou moved more slowly through burned areas with lower estimated burn severity. At no point, however, did the predicted mean overall velocities drop below the median overall velocity in unburnt areas, indicating that even after 26 years caribou were selecting these areas as movement habitat rather than foraging habitat. This result supports our initial hypothesis predicting an earlier return of foraging type behaviour after less severe fires, as movement rates slowed significantly in less severely burned areas. As such, I posit that low severity fires should result in a faster recovery of foraging in-spite of how much time has passed since the fire occurred.

Conversely, predicted overall turning angles were larger than median turn angles in new (aged ten or less years) high severity burned areas and low severity burned areas aged >20 years since fire, indicating some level of foraging-focused behaviour may occur in certain circumstances. The result seen in newly burned areas may be due to initial encounters of individuals moving into burned areas that they previously used without issue and then reversing course to avoid an area (Thomas et al., 1998), while the low severity burned areas aged >20 years may have retained some lichen and/or allowed for some recovery of high quality forage.

Jandt et al. (2008) found that terricholous lichens burned even during low severity fires; therefore, burn severity may be less important to caribou forage than time since a fire event occured. Multiple studies have documented slow recovery of lichens post-fire (Hart et al., 2006; Bret-Harte et al., 2013; Zouaoui et al., 2014) and it is unlikely that lichen communities recovered during the 26-year time frame examined here. Zouaoui et al. (2014) documented a highly non-linear recovery rate for lichens that increased rapidly at approximately 100 years post-fire. If lichen recovery rates are minimal immediately following fire then caribou movement is likely being influenced by other factors such as vegetation recovery rates or changes in forest structure. Hart et al. (2006) documented rapid recovery rates of understory vegetation species in the Boreal forest; specifically fire-adapted species and deciduous species, neither of which forms a major portion of caribou diet (although some selective foraging on deciduous shrubs does occur). An increase in non-forage or less preferred forage species at the expense of premium forage species may be driving this decline in caribou foraging activity post-fire.

Time since fire and fire severity’s effects on caribou behavior differed according to season. Caribou reaction to time since fire in fall was similar to that detected in the overall model, with mean predicted turn angles falling below the median fall turning angle between 10 and 22 years post-fire. This age range may result in forested communities with particularly poor forage conditions for caribou or a forest structure which is particularly difficult for travel (see Bolton et al., 2015) resulting in the use of established trails (Thomas et al., 1998).

A statistically significant decline in foraging behaviour and then a slow increase towards the end of the study period was detected, although it occurred slightly earlier (from 5 to 15 years) than the overall and fall models. Winter movement velocity displayed a nearly linear negative relationship with burn severity indicating more foraging occurred in less severely burned areas regardless of time since fire. In all cases, predicted winter movement velocities remained greater than the median winter movement velocity indicating that during these months burned areas were primarily used for movement. Anderson and Johnson (2014) also detected limited use by barren-ground caribou in early seral forests across their winter range, commonly at the boundaries between burned and non-burned areas, which supports the findings described here.

In spring caribou displayed a nearly linear negative relationship between turning angle and time since fire, with increasing time since fire resulting in more linear, movement behaviour regardless of burn severity. Similar to fall, mean predicted spring turning angles were lower than the median turning angle in absence of fire at ten years; however, no recovery was documented and caribou continued to move more linearly through burned areas in spring as time since fire increased. Spring is one of the more movement-focused times of year for barren-ground caribou (Bergerud, 2000); however, it is also a time for gaining fat, primarily through access to nutritious young forage such as tussock cottongrass (which can make up 70% of caribou diets in spring; Cebrian et al., 2008). Tussock cottongrass can recover quickly post-fire (in some cases within a few years post-fire, although this was measured in tundra ecosystems; Racine et al., 2004; Bret-Harte et al., 2013). The rapid recovery of an important spring forage species supports our findings of large turning angles in the first years following fire; however, the trend of increasingly linear movements post-fire is unexpected.

Bolton et al. (2015) recently assessed post-fire Boreal forest structure using light detection and ranging data (LiDAR) within Landsat detected burned areas finding that a substantial amount of residual biomass is left immediately following fire. In addition, Johnstone et al. (2004) found that tree establishment in Alaskan and Yukon Boreal forests took 3-7 years. The retention of residual biomass and delay in tree requirement results in canopy height being lowest and forest structure being most homogenous approximately 10 to 15 years post-fire, with height and structural complexity slowly increasing after this time (Bolton et al. 2015). Considering the location of Bolton et al. (2015)'s study (the Canadian Boreal Shield) is substantially further south than the study area examined here, it is likely the structural recovery rates of the forests examined here are at the low end of their findings (i.e. closer to 15 years). Both Harper et al. (2002) and Bartels et al. (2016) found that tree growth post fire was limited to less than 2 m in the first 10 years post fire. The marked increase detected in movement type behaviour across multiple seasons at a similar time post-fire could be driven by a lack of cover owing to the loss of residual biomass which occurs at this 10 -15 year interval or increasingly impassable terrain resulting in certain established trails being used for movement.

It is important to note several limitations of this study. First, the impact of fire on the probability of use was not assessed; rather, behaviour post-fire given use was evaluated. It is likely that overall caribou avoidance of burnt areas did transpire, as only 1369 individual telemetry points occurred within burnt areas out of the more than 100,000 GPS relocations in forested areas. Additionally, 26 years of fire data is clearly an insufficient temporal record with which to document the full recovery of Boreal barren-ground caribou habitat (Bartels et al., 2016);

however, movement rates were shown to change significantly even within the first 26 years post-fire. As remote sensing data sets increase in temporal length and as caribou telemetry data are accumulated, our ability to refine our understanding of caribou behavioural responses to fire will continue to improve. Additionally, the ability of remote sensing data to not only identify fires but also estimate the magnitude of disturbance was shown to be a useful predictor of caribou behavioural metrics. Thus, I propose that the analysis approach applied in this study provides a robust framework for moving forward with similar investigations in the future.

Chapter 7: Conclusions

7.1 Significance of research

In this Dissertation I linked barren ground caribou movement and population data with newly developed remotely sensed products describing barren ground caribou habitat. Specifically, in this research I:

- Developed an assessment of the effects of barren ground caribou herd density on summer range productivity (Chapter 3)
- Assessed spatio-temporal changes in vegetation productivity across the entirety of herd ranges and evaluated how vegetation productivity changes result in changes in barren ground caribou movement (Chapter 4)
- Assessed spatio-temporal changes in lichen mat condition across herd ranges considered tundra and evaluated how these changes result in changes in barren ground movement (Chapter 5)
- Summarized fire disturbances across the southern portion of herd ranges for 26 years and evaluated recovery in terms of barren ground caribou behavioral indices post-fire and likely causes of changes due to time since fire (Chapter 6)

This Dissertation presents a number of methods and findings which are, to the best of my knowledge, novel in terms of approach and results. Specifically, I developed novel methods for assessing:

- Grazing pressure on tundra vegetation productivity (Chapter 3)

- Fine scale habitat effects (vegetation productivity (Chapter 4) and lichen mat condition (Chapter 5) on barren ground caribou movement metrics
- The effects of fire on caribou behavior and habitat recovery directly measured from barren ground caribou movement data instead of employing assumptions regarding habitat recovery and time

These novel approaches led to new findings regarding how barren ground caribou influence and are influenced by their environment. Specifically, I found that:

- While herd densities do have an effect on summer range vegetation productivity, it is unlikely that this effect is a cause of herd population cycling (Chapter 3)
- Both vegetation productivity and lichen mat condition are changing across barren ground caribou herd ranges. Furthermore, these changes result in complex changes in barren ground caribou movement patterns depending on season, habitat type, and herd (Chapter 4 and 5)
- Fire remains a relatively rare event across barren ground caribou herd ranges; however, fire events have significant effects on barren ground caribou movement patterns. Foraging type behavior is largely eliminated by fire and structural changes post fire likely result in animals moving through fire affected areas even more rapidly (Chapter 6)

7.2 Research questions addressed

Chapter 3. Is caribou density related to summer range vegetation productivity at the landscape scale?

Approach: I estimated summer range productivity using MODIS and AVHRR 1 km fPAR data and the DHI approach outlined in Coops et al. (2008) and then corrected for climate by using residual productivity from the growing season length – productivity relationship. Herd density was related linearly to one year lagged residual summer range productivity.

Main findings: barren ground caribou density was associated with the following year’s overall residual productivity and seasonality. This indicates that there may be some effect on vegetation productivity due to changing grazing pressure (and possibly trampling effects). However, the Bathurst herd had the least negative association between herd density and vegetation productivity while having the densest herd estimates by a factor of three. This led to the conclusion that while there appears to be some effects from herd densities, they are likely not limiting or I would expect to see them even more strongly in the Bathurst herd.

These findings are important for the debate surrounding density dependent effects on herd sizes. There is some evidence that density dependence played a role in the George River herd declines in the 1990s and some have suggested a similar mechanism may be responsible for the Northwest Territories herd declines as well. These results led me to conclude that density dependent grazing effects are not likely the main factor governing herd size currently and that density independent climatic effects on habitat are more likely responsible for the large changes in herd size currently being documented.

Chapter 4. How do changing Arctic and Boreal vegetation productivity conditions affect caribou movement rates post-calving?

Approach: I used the NTEMS Landsat 30 m data to compute EVI yearly for the 26 year study period. Changes in EVI were assessed using Theil-Sen’s non-parametric regression. Barren ground caribou movement rates were associated with yearly EVI values during the post-calving portion of the year (July and August).

Main findings: EVI was shown to be changing significantly through time across large portions of each of the five herd's ranges. There was a distinct West – East gradient in changes, with the western herds (the Cape Bathurst and Bluenose West herds) experiencing larger positive changes in EVI on average. It is important to note that the western herds also fall closest to the Arctic Ocean and sea ice melt has been linked to increasing terrestrial productivity in multiple studies. On the whole, the majority of changes documented collectively across herd ranges were positive changes indicating an overall greening effect of the herd ranges.

Barren ground caribou movement rates were associated with measures of EVI in tundra, shrub, and grasslands habitats. Individuals moved more slowly through more productive tundra habitats to a point after which increasing productivity did not affect movement rates. Caribou movement rates declined with increasing productivity levels in grassland habitats. In shrub habitats, caribou movement rates peaked at moderate productivity levels and declined in both low and high productivity shrub habitats. Barren ground caribou movement patterns will likely change as a result of changing vegetation productivity in complex manners depending on herd, habitat type, and the magnitude of change in vegetation productivity.

Chapter 5. How do changes in lichen mat volume affect barren ground caribou movement rates across different seasons?

Approach: Lichen mat condition was estimated yearly across all tundra habitat using the Lichen Volume Estimator developed by Falldorf et al. (2014) and the NTEMS Landsat 30 m data set. LVE values were assessed for change through time using Theil-Sen's non-parametric regression slopes after which the slopes were clustered spatially using the the Getis-Ord Gi* statistic. Changes in barren ground caribou movement rates were assessed by season using GAMM models.

Main findings: Lichen mat condition changed through time at the pixel level across significant portions of each herd's range. Generally speaking, lichen mat condition was increasing in the eastern herd ranges and decreasing in the western herd ranges. LVE slopes were spatially clustered indicating that changes were not restricted to pixels but were aggregated to larger landscapes.

Barren ground caribou movement rates were associated with LVE values in ways which agreed with their known ecology. In both summer and winter I identified LVE levels at which movement rates significantly decrease and which may represent increasing levels of forage. LVE had a nearly linear negative association with movement rates. In the fall, however, an unexpected increase in movement rates at high LVE levels was detected and remains unexplained.

Chapter 6. How do fire disturbances affect barren ground caribou movement?

Approach: Area burned and fire severity were assessed across each herd's range. Barren ground caribou telemetry points occurring in previously burned areas were extracted allowing for movement rate and turning angle to be related to time since fire and fire severity using GAMM models.

Main findings: Neither area burned nor average fire severity increased during the study period. Fires remain a relatively rare event and I suggest that area burned across barren ground caribou herd ranges is driven more by extreme fire years than a consistent increase year over year.

Barren ground caribou reacted predictably to fires, with foraging behavior in those areas largely eliminated even 26 years post fire. Changes in movement rates and turning angles are likely driven by changes in forest structure post fire, with standing dead trees falling over 10-15 years post fire.

7.3 Lessons learned

7.3.1 Barren ground caribou – habitat interactions can be effectively described using remotely sensed data

Each of the four research Chapters presented here demonstrated that remotely sensed data can effectively describe barren ground caribou habitat and integrate with barren ground caribou data, be it population level herd counts or individual telemetry data. Selecting a sensor appropriate for a particular question (i.e. MODIS for inter annual variation at broad scales, Landsat for annual measurements at finer scales) is critical for project success. Lastly, acknowledging data limitations and designing analyses which can work within data limitations is crucial for arriving at credible and ecologically defensible results.

7.3.2 It is unlikely overgrazing is a leading cause of herd declines in the five herds examined here

Chapter 3 demonstrated that while there is a detectable effect of herd density on vegetation productivity, it is likely not a limiting factor for herd size. The Bathurst herd experienced densities three times that of any other herd and had far less of a negative association between herd density and vegetation productivity.

7.3.3 Barren ground caribou habitats are undergoing widespread, rapid changes

Chapters 4 and 5 both demonstrated that a large portion of each herd’s range is undergoing rapid changes in terms of vegetation and lichen condition. The western herds have seen the largest overall increases in vegetation productivity and reductions in lichen mat condition; however, all herds have seen a net greening effect and all herds except the Ahiak/Beverly herd have seen a net decline in lichen mat condition.

7.3.4 Changes in habitat have complex effects on barren ground caribou movement

These changes in barren ground habitat have detectable, complex effects on barren ground caribou movement. Barren ground caribou movement was associated negatively with increases in both tundra vegetation productivity and lichen mat condition, which is to be expected if these locations offer improved foraging conditions. This indicates that increasing vegetation productivity may not be a net negative in terms of forage for caribou in tundra and grasslands habitats; however, lichen mat degradation is undoubtedly a negative outcome for caribou given the importance of lichen in caribou diets. Shrub expansion and increases in shrub productive likely do indicate a net negative foraging outcome for barren ground caribou.

7.3.5 Fire disturbances eliminate foraging opportunities

Fire disturbance almost completely eliminated foraging behavior post fire. Movement through fires did occur as soon as one year post fire, however, these movements remained high velocity movements through fires for the entire study period.

7.3.6 Changes in movement patterns post-fire possibly due to changes in forest structure

The complex changes in movement patterns detected post fire are likely a result of changing forests structure up to 20 years post fire. Standing dead wood can stay upright post fire for approximately 20 years and I postulate that as these standing snags fall and create impassible structures on the ground, forcing caribou to use particular paths through fires.

7.4 Barren ground caribou management applications

One of the major challenges of managing barren ground caribou is the size of their ranges and the amount of habitat needed to fulfill their life-history requirements. The five herds examined here utilize over 700 000 km^2 of habitat, likely an underestimation of their historic ranges when herd sizes were much larger (Boulanger et al., 2011; 2014). The methods developed in this Dissertation present novel and useful ways to assess barren ground caribou habitat at scales relevant to entire herds; however, turning these assessments into concrete prescriptions is not easily done.

When considering large mammal habitat management, most commonly managers are looking for actionable information that can lead directly to management prescriptions aimed at improving an aspect of a species' habitat (Sinclair et al., 2006). This is challenging with some of the aspects of barren ground caribou examined here. The spatial scale of the changes in vegetation productivity and lichen mat condition means that attempts at directly addressing these changes are unfeasible, and in a sense managers are at the mercy of a changing climate. However, given that barren ground caribou habitat is changing at a rapid pace, as demonstrated here, my work allows managers to identify areas which present as high quality and stable habitat and allows for these areas to be either studied further or protected moving forward.

Some effort has been made, notably by the Government of the Northwest Territories, to ban any future development on calving grounds. This concept of protecting habitat leads into another complication however. Barren ground caribou herd ranges remain relatively intact in terms of anthropogenic disturbance when compared with more southern sub-species of caribou (i.e. woodland caribou (*Rangifer tarandus caribou*) in British Columbia and Alberta; COSEWIC 2014). The Bathurst herd has seen some road and mine development occur within its range (Boulanger et al., 2004) and some road development has also occurred in the Bluenose East range while both gas and urban development has occurred in portions of the Cape Bathurst range (Tyson et al., 2016). This does not preclude managers from protecting habitat from future development, but only highlights that providing habitat is likely not enough to conserve these herds.

One area of research presented in this Dissertation which is directly actionable is Chapter 6. Fire disturbance was shown to almost completely eliminate foraging behavior. Additionally, fire disturbances largely affect winter foraging grounds in the Boreal forest and winter is a time of food scarcity and even a population bottleneck for barren ground caribou in some circumstances. Removing high quality old spruce forests through fire disturbance, even if it is a natural process, is likely a net negative for barren ground caribou. The Government of the Northwest Territories could conceivably identify fires occurring in barren ground caribou winter range and focus firefighting resources on these fires to limit their extent, although the financial feasibility of such an action is unknown. Conversely, fires in spring migration corridors may promote the recovery of tussock cottongrass and could be left to burn.

7.5 Limitations

7.5.1 Climate corrected DHI

In Chapter 3 every effort was made to account for climate in the DHI indices, therefore isolating the effects of grazing and trampling; however, it is unknown whether climate was fully accounted for. This could confound our assessment of grazing and trampling effects given the rate and magnitude of climatic change occurring in the Arctic.

7.5.2 Caribou telemetry data and caribou behavior

A major challenge of the work presented in this Dissertation is linking movement metrics such as velocity or turning angle to behavior such as foraging or migration. There is a substantial body of work supporting movement metrics as proxies for behavior in large mammals; however, they are by no means perfect. To my knowledge, there has been no work done linking in-situ caribou behavioral data to telemetry movement metrics.

This is a real limitation in Chapters 4, 5, and 6, which all employ movement metrics as a potential proxy for caribou behavior. One reason raw metrics like velocity were used here instead of classifying metrics into behavioral classes using an algorithm like a hidden Markov model or similar is because of the ecology of caribou. In my opinion, binary classifications of foraging versus movement do not apply to this species, which commonly moves and forages simultaneously. Using velocity or turning angle allowed me to describe behavior continuously which I feel is a more appropriate method of detailing how focused an individual is on movement versus foraging.

7.5.3 In-situ lichen volume estimates

A limitation of the work presented in Chapter 5 is the lack of in-situ data to validate the lichen volume estimates presented. Consequently, the LVE is presented as an index rather than an actual measure of lichen mat volume. It still has use as an index in terms of spatial and temporal comparisons and change assessment; however, building and validating the model with in-situ data would allow for volume estimation making the LVE even more effective and promising for future caribou habitat assessments.

7.6 Future research

7.6.1 Linking barren ground behavior with telemetry data

Cementing the link between barren ground caribou telemetry movement data and in-situ behavioral data would be a major step forward, not only for the work here but for large mammal ecology as a whole. Generalities regarding rates of movement and foraging are well known, but nuances in terms of species, timing, life-history strategies, foraging strategies, and sex (this is not an exhaustive list) have not been well developed. Telemetry data presents an opportunity to gather large amounts of data on individual animals and populations; however, continued effort needs to be placed on ensuring the data are used to describe biologically sound concepts that link movement data to meaningful behavioral changes.

7.6.2 Linking changes in vegetation productivity with shrub expansion

Chapter 4 describes significant increases in vegetation productivity in areas that have large amounts of vegetation shifting from tundra to shrub. The NTEMS data set might allow for change detection between tundra and shrub and, in fact, there is some research being undertaken on land cover change by Dr. Hermosilla and co-authors. In-situ examples of pixels that have changed from tundra to shrub type vegetation during the study period would allow for remotely sensed spectral changes to be identified which exemplify this change and increase confidence that detected changes represent real ones.

7.6.3 Validating and expanding lichen volume estimates

The major limitation in Chapter 5 is the lack of ground based lichen volume plots to correct the coefficients in the Lichen Volume Estimate. As stated above, this restricted LVE use to an index of lichen mat condition rather than an assessment of the volume of lichen mats per pixel. A ground-based data collection campaign similar to Falldorf et al. (2014) would allow for the LVE to estimate actual mat volume which is a more useful measure of lichen mat condition than the index presented here. The LVE shows great promise for monitoring lichen mat condition in the Arctic and I feel that this should be a monitoring priority moving forward.

7.6.4 Updating and continuing the fire disturbance movement models

The work presented in Chapter 6 represents an important new development in assessing fire disturbance across caribou ranges and its subsequent effects on individual behavior. Since the research ended, however, there have been several severe fire seasons which may change the results of the area burned and mean fire severity through time. The work of updating the NTEMS data set is currently ongoing. The second portion of the work, linking fire metrics to behavioral metrics, will only improve as the telemetry data sets expand with new collared animals, more fires are added to the data set, and the time since identified fires lengthens allowing for longer examinations of recovery in terms of caribou movement. There should be an effort to revisit this work in the future to allow for this update to occur.

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