Muskox (*Ovibos moschatus*) Habitat Associations and Interactions with Caribou (*Rangifer tarandus*)

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Abstract

Muskox (*Ovibos moschatus*) are a large-bodied arctic herbivore that occupy habitats used seasonally by migratory caribou (*Rangifer tarandus*). Muskox were reintroduced to the North Slope of Alaska in 1970 and mixed-sex groups have been reported in the Yukon North Slope and the Richardson Mountains since 1985. Their reintroduction has sparked concerns from local hunters and community members worried about the impact of muskox on caribou populations and vegetation. This thesis represents an ecological assessment of competition potential and habitat segregation among two arctic ungulates and community-based research that addresses local concerns and knowledge priorities. In the first part of the thesis, I use satellite collar data from muskox and caribou to analyze their spatial and habitat overlap through range overlap, encounter rates, and resource selection functions. Range overlap was at its highest in the spring and summer months, but less than 1% of collared caribou encountered a muskox during that period. Habitat overlap was minimized through differential selection of elevation, distance to water, and abundant tussock habitat. In the second part of the thesis, I use ground-based vegetation sampling to characterize fine-scale muskox-vegetation associations, determining whether there are positive or negative associations between muskox use and vegetation presence and abundance. Positive associations between muskox use and vegetation attributes were deemed to reflect a pattern of fine-scale selection, and negative associations were deemed to be the reflection of muskox herbivory impacts. Positive associations were found between muskox use and lichen, willow, and graminoid abundance and presence, an indication that within land covers, the relationship between muskox use and vegetation is mostly driven by selection rather than by herbivory. Collectively, this research reveals that in the Yukon North Slope and Richardson Mountains, the reintroduced and expanding population of muskox i) has low encounter rates and

differential habitat use with caribou and ii) has selection patterns that are quantifiable at a large and at a fine-scale.

Résumé

Le bœuf musqué (*Ovibos moschatus*), un grand herbivore habitant l'arctique, a été réintroduit dans le Nord du Yukon et les montagnes Richardson à la fin des années quatre-vingt. Sa réintroduction a donné suite à des préoccupations des membres des communautés de la région qui s'inquiètent des interactions entre le bœuf musqué et le caribou ainsi que des impacts du bœuf musqué sur la végétation. Dans cette thèse, je caractérise les interactions entre le bœuf musqué et le caribou ainsi que les associations entre le bœuf musqué et son habitat afin de répondre aux préoccupations de la communauté. D'abord, j'utilise des données GPS de colliers satellites qui ont préalablement été posés sur des bœufs musqués et des caribous afin d'analyser le chevauchement spatial et le chevauchement d'habitat entre les deux espèces grâce à des analyses d'aire de répartition, des taux de rencontres, et la modélisation de la sélection d'habitat. Le chevauchement des aires de répartition s'avère être à son plus fort au printemps et l'été. Durant cette période, moins de 1 % des caribous Porcupine rencontrent un bœuf musqué. Le chevauchement d'habitat entre les deux espèces est minimisé grâce à différents taux de sélection d'élévation, de distance à l'eau et de la toundra 'tussock'. Ensuite, utilisant des données récoltées sur le terrain, je caractérise les associations entre le bœuf musqué et la végétation à fine échelle pour déterminer s'il existe des relations positives ou négatives entre la présence de bœuf musqué et les caractéristiques de la végétation, tout ce ceci dans le but de déterminer si les tendances entre la présence de bœuf musqué et les caractéristiques de la végétation correspondent à une sélection à fine échelle ou plutôt avec de l'herbivorie. Nous trouvons des associations positives entre la présence de bœuf musqué et le lichen, les saules et les graminées, une indication qu'à fine échelle, la relation entre le bœuf musqué et la végétation est surtout dû à la sélection plutôt qu'à l'herbivorie. Mis ensemble, ces recherches

nous révèlent que les bœufs musqués et les caribous ont de faibles taux de rencontres et une sélection d’habitat différentielle dans le Nord du Yukon et les montagnes Richardson et caractérise les préférences en habitat et en végétation d’une population de bœufs musqués réintroduite et en expansion.

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Contribution of Authors

This is a manuscript-based thesis following McGill guidelines. Both chapters are intended for publication. As candidate, I was responsible for and participated in all stages of the research including developing research questions, experimental design, field work, data management and analysis, interpretation and writing.

Chapter 1 is co-authored by Murray M. Humphries, Michael Suitor, Eliezer Gurarie, David Tavares, Tracy Davison and Édouard Bélanger. Eliezer Gurarie provided advice and guidance with design, statistical analyses and interpretation. David Tavares, through Parks Canada, provided logistical and financial support, field work, and help with writing. Tracy Davison, through the Department of Environment and Natural Resources, provided logistical and financial support. Édouard Bélanger, through the Gwich'in Renewable Resources Board, provided funding, logistical support, help with field work and writing. Murray M. Humphries and Michael Suitor provided academic supervision, logistical support, input on analyses, and help with writing.

Chapter 2 is co-authored by Murray M. Humphries and Michael Suitor. Both provided input on the concept, experimental design, analyses, and general guidance.

Introduction

Species reintroduction is defined by the International Union for the Conservation of Nature (IUCN) as ‘the intentional movement and release of an organism inside its indigenous range from which it has disappeared’ (IUCN/SSC 2013). If reintroductions were initially undertaken to restock hunted populations and solve human-wildlife conflict (Fischer and Lindenmayer 2000) increasingly, they aim to promote biodiversity and ensure a restoration objective (Seddon et al. 2007). While conservation may be the main driver behind recent reintroductions, reintroductions themselves bring about a host of conservation issues. Of particular interest is the way reintroduced species will affect the ecosystem after their release (Armstrong and Seddon 2008).

Muskox (*Ovibos moschatus*), large-bodied herbivores that live in the tundra, were extirpated from their Alaskan-Yukon range in the mid 19th century (Hone 1934). Prior to their extirpation, it is speculated that the Nunamiut people used muskox when migrating caribou failed to come as expected. In these cases, the more sedentary muskox groups could be relied upon for food (Lent 1998). According to Ingstad (1951), at least one Nunamiut suggested that hunting had been responsible for the extirpation of muskox, who are also said to have ‘gone eastward’.

In 1935, muskox were transported from Greenland to Nunivak Island in Alaska, and in 1969 and 1970, 51 individuals were taken from Nunivak Island to Barter Island in Northeast Alaska. A further 13 individuals were released near Kavik River (Lent, 1998). Some of these individuals, most likely males, migrated eastwards into the Yukon where mixed-sexed groups have been reported since 1985 (Reynolds 1998). The current muskox population extends east into the Richardson Mountains of the Northwest Territories and west into the Alaskan North Slope.

Aklavik is a hamlet located in the Mackenzie Delta in the Northwest Territories. Its Gwich'in and Inuvialuit peoples are the main users of the land extending west of the Mackenzie Delta into the Northern Richardson mountain range and the Yukon North Slope where muskox now live. The muskox reintroduction has been cause for concern for members of the Aklavik community, who have expressed worries with regards to muskox-caribou interactions including potential impacts of muskox grazing on vegetation and displacement of caribou caused by muskox. These concerns were brought to the Aklavik Hunters and Trappers Committee (AHTC) and the Ehdiitat Renewable Resources Council (ERRC), who in turn shared those concerns to larger co-management bodies: the Wildlife Management Advisory Council North Slope (WMAC) and the Gwich'in Renewable Resources Board (GRRB). Similar concerns were also reported by other communities of the region.

In the fall of 2017, I interned with WMAC. During this time, I drafted the *North Slope and Richardson Mountains Muskox Research Plan*, an accompanying plan to the *Framework for the Management of North Slope Muskox* that was drafted shortly thereafter. Members of the following organizations were interviewed for their perspectives on muskox research:

- Gwich'in Renewable Resources Board
- Government of the Northwest Territories
- Parks Canada
- Wildlife Management Advisory Council North Slope
- Yukon Government

A workshop was held in Aklavik with members of the AHTC to define their priorities concerning muskox research. During this workshop, previous research completed on muskox as well as available data was presented to the members of the committee. Most of the workshop took the form of an informal conversation between participants along with pertinent presentations to provide background information.

The objective of this thesis is to characterize muskox habitat use and muskox-caribou interactions as was proposed in the *Muskox Research Plan*. In Chapter 1, I analyze spatial and habitat overlap between muskox and caribou through resource selection functions and encounter rates. In Chapter 2, I analyze muskox fine-scale habitat associations, describing and determining whether these fine-scale associations are the result of selection or muskox grazing impacts.

Literature Review

Species interactions

Niche Overlap

Species interactions, defined as the impact one species has on another, are fundamental to our understanding of species coexistence (Chesson and Kuang 2008, Mittelbach and McGill 2019). Interactions between two species can be regulated by the amount of niche overlap between the two (Durant 1998, Letten et al. 2017), with ecological niche being comprised of all conditions necessary for an organism to exist. Chesson (2000) has defined four niche axes: resources, predators, time, and space.

The competitive exclusion principle states that two species cannot stably coexist if they share the same niche, or more precisely, if they share certain niche characteristics up to a certain limit, a concept which has both been termed ‘limiting similarity’ and ‘maximum tolerable niche overlap’ (Pianka 1974). Hurlbert (1978) suggests that niche overlap measures should serve ‘as a foundation for discussion of resource utilization strategies, competition, species packing, and so on'.

Competition

Prins (2000) outlined three conditions for interspecific competition to occur : '(1) populations of the different species must share resources; (2) these resources must be limited, and; (3) the joint exploitation of those resources and/or interference interactions related to the resources must negatively affect the performance of either or both species'. Competition can be both direct, for example when a species directly interferes with the capability of another to acquire resources by displaying territorial behaviour, and indirect, for example in two herbivores who consume the same plants. The latter is referred to as exploitation competition, and the first, as interference competition (Birch 1957).

The role of both these forms of competition in shaping communities has been widely debated. Simberloff (1982), in a review of past studies of competition, suggests that competitive exclusion of one species by another is exceptional, that species sharing resources rarely affect one another, and that chance plays a major role in many competitive interactions. However, others have suggested that interspecific competition can have much greater effects on communities and can even lead to new species in a process called competitive speciation (Asbjornsen et al. 2005).

Habitat Use

Habitat Selection

Habitat use is the way an animal uses the biological and physical resources in a habitat (Krausman 1999). For example, an animal may need different resources for cover, foraging and finding mates, and these resources may or may not be found in the same habitats. Animals can balance these trade-offs by adjusting their locations in a heterogeneous space (Hebblewhite and

Merrill 2009) in a process called habitat selection. Habitat selection has been shown to be both a hereditary and a learned behaviour (Wecker 1963) and can vary seasonally and between individuals of the same species (Leclerc et al. 2016, Nielsen et al. 2003). Predicting habitat selection can be a useful tool in determining how animals might respond to habitat loss, climate change, and understanding species interactions mediated through habitat.

Habitat selection can be measured in many ways, but most include comparing characteristics of environments that are used by an animal to environments that are unused or whose use is unknown. If an animal uses a resource disproportionately to its availability, we infer selection on the part of the animal. These methodologies have been formalized in what are called resource selection functions (Manly et al. 1993, Boyce and McDonald 1999). As one might imagine, the spatial scale at which we compare used and available locations plays an important role in the outcome we will observe. Johnson (1980) describes four orders at which selection can occur: the 1st order, which is selection of a species' range, the 2nd order, or selection of an individual's home range, the 3rd order, which is selection with a home range, the 4th order, which is procurement of specific items at a site.

Herbivory and foraging

In herbivores, habitat selection is often driven by quality and quantity of available forage (Bremset Hansen et al. 2009) as herbivores must maintain sufficient caloric and nutrient intake to ensure survival and reproduction. Herbivores can affect plant communities in many ways. The most obvious of these are the deleterious effects caused by grazing and browsing, which both destroy plant capital and disrupt means of production (Brown and Allen 1989). This can lead to modified vegetation composition, productivity, and function (Gordon and Prins 2008, Bagchi et al. 2012) and have significant impact on ecosystems, leading to transitions in habitat types (Wal et al. 2006) and habitat degradation (van de Koppel et al. 1997, Adler and Morales 1999). While the great majority of herbivory is detrimental to plants (Bigger and Marvier 1998, Crawley 2009), herbivory has also been argued to produce positive effects on plants, a phenomenon called 'overcompensation' or 'compensatory growth' (Belsky 1986). Overcompensation has been demonstrated in greenhouse conditions (Paige and Whitham 1987) and in field experiments, though these studies remain controversial (Belsky 1986, Crawley 2009). Overcompensation can depend on the type of resources available to the plant and the type of plant (e.g. monocots vs dicots) (Hawkes and Sullivan 2001). Both negative and positive effects of herbivory on plants are scale-dependent in time and space (Brown and Allen 1989).

Muskox

Status and Distribution

Muskox (*Ovibos moschatus*) are large-bodied herbivores with a circumpolar distribution. Two sub-species are recognized, *O.m. wardi* and *O.m. moschatus*, respectively referred to as 'White-Faced' and 'Barren-Ground' (van Coeverden de Groot 2001). Recent studies have identified genetic separation between the two (Hansen et al. 2018). Muskox' circumpolar distribution is the result of many translocations of the *O.m wardi* subspecies (Cuyler et al. 2019). A 2019 review (Cuyler et al. 2019) estimated the global abundance of muskox to 170 000 individuals, 29 % of which were not endemic. Two of the world's largest muskox populations found on Banks and Victoria Islands are in decline (Cuyler et al. 2019).

Habitat

In the summer, muskox have been found to select for sedge-producing hydric meadows (Parker and Ross 1975), wet sedge meadow, graminoid tundra and graminoid/dwarf shrub tundra cover types (Ferguson 1991) and low, wet areas (Danks and Klein 2002). In the winter, muskox habitat has been found to be ideal in higher, drier areas (Danks & Klein, 2002), in habitats containing water sedge, *Carex aquatilis* (Schaefer and Messier 1995) and on steep slopes with *Dryas sp*. (Nellemann 1998). More recently, in Greenland, habitat suitability was consistently predicted to be highest in vegetated, flat to moderately rugged terrain at low to medium elevation close to the coast (Beumer et al. 2019).

Diet

In 1989 and 1991, muskox summer fecal samples were collected in the Queen Maud Gulf Area (Gunn, 1997). Analysis of these samples revealed that summer diet consisted mainly of sedges (*Carex spp*. and *Eriophorum spp*.) and willows (*Salix spp*.). Klein and Bay's 'Foraging dynamics of muskoxen in Peary Land, northern Greenland' (1990) provides a detailed analysis of muskox diet in the summer months. Sedges were the major food item for muskox who foraged in fens while willows were the major dietary component for muskox foraging in areas where willows are the dominant species. In 'Resource Partitioning by Mammalian Herbivores in the High Arctic' (Klein & Bay, 1994) summer and winter muskox fecal samples were analyzed to reveal that sedges and willows were the most common vegetation types used by muskox year-round. Results also show that willow intake increased in the early summer months.

Herbivory

Muskox herbivory studies have revealed that muskox removed 0.17% and 0.04% of the available forage in graminoid-dominated areas and in *Salix* snowbeds in Greenland (Mosbacher et al. 2016) and that muskox can modify the structure of sedge species through grazing (Tolvanen and Henry 2000). A study done on Unalakleet Muskox Farm in Alaska showed that following grazing, the most noticeable response was an increase in annual sedge productivity, except in cases where the soil had been destroyed, whereas lichen and shrubs decreased with grazing pressure (McKendrick 1981).

Interactions with caribou

Muskox-caribou interactions have been the subject of many interrogations from communities in the Yukon, Northwest Territories and Nunavik. Muskox-caribou interactions have mainly been studied through their dietary overlap, though some habitat selection work has been done. Diets of muskox and reindeer were analyzed on Wrangel Island, Russia (Kazmin and Abaturov 2011), where it was found that the two species had similar diet composition, forage intake rate and digestibility. On Banks Island, muskox and Peary caribou had monthly diet similarities ranging from 17.8-73.3% (Larter and Nagy 1995). Diet similarities were more pronounced when muskox densities were high. In Western Alaska, percent cover for all vegetation classes did not differ between muskox and reindeer habitat, but diet did. Muskox diet was composed of significantly more sedge and moss, and less lichen than caribou. Muskox and caribou did not select differently from each other for snow depth or hardness (Ihl and Klein 2001). Summer habitat use was studied for muskox and Peary caribou living in the High Arctic in the seventies and showed that caribou used broader habitat and moved more than muskox. Muskox selected for a sedge-producing hydric meadow whereas caribou preferred polar-desert and mesic-meadows (Parker and Ross 1975).

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CHAPTER 1: Muskox and Caribou Niche Partitioning

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Abstract

Species interactions are modulated by overlap in use of resources, time and space. The reintroduction of muskox (*Ovibos moschatus*) to Alaska and their subsequent displacement in the Yukon North Slope, where muskox have been sighted since 1985, has led to concerns about muskox-caribou (*Rangifer tarandus*) interactions and potential for competition from Indigenous hunters and community members of the region. Our objective is to characterize spatial and habitat overlap in muskox and caribou. Using GPS collar data, we determined range overlap, encounter rates and analyzed habitat overlap through resource selection functions. Range overlap was maximized in the spring and summer seasons, and encounter rates were infrequent, with less than 1 % of collared caribou encountering a muskox from May 1st to August 31st. Habitat overlap was overall minimal, with muskox exhibiting high avoidance of tussock habitat commonly used by caribou and selecting higher elevations further from water than caribou. Overlap in habitat used by the two species occurred most often in rock-lichen wetland and floodplain habitats. Muskox and caribou interactions appear to be minimal based on differential habitat selection and limited encounter rates.

Introduction

Species' interactions, defined as the impact one species has on another, are fundamental to our understanding of species coexistence (Chesson and Kuang 2008, Mittelbach and McGill 2019). Many ecologists have grappled with theories that can explain coexistence in the face of competition, and of these theories, niche separation has been recognized as a particularly important stabilizing mechanism (Durant 1998, Letten et al. 2017). Partitioning along Chesson's (2000) four niche axes: resources, predators, time, and space, can lead to minimal interactions and weak competition, whereas with highly overlapping niches, interactions between species tend to be much stronger.

Evidence of niche partitioning in the context of interspecific competition has been the subject of many studies in ungulate ecology, especially in species with seemingly highly overlapping ranges and diets. Studies with evidence for strong niche partitioning amongst coexisting ungulates include southwestern Yukon woodland bison (*Bison bison athabascae*) and caribou (*Rangifer tarandus*), where low diet and spatial overlap was observed (Fischer and Gates 2005, Jung et al. 2015*a*), and in moose (*Alces alces*) and woodland caribou habitat selection (James et al. 2004), though that partitioning was reduced in human-altered landscapes (Peters et al. 2013). Other studies have reported more ambiguous results, with potential for competition attenuated by some aspects of resource partitioning. For example, alpine chamois (*Rucicapra rucicapra*) and mouflon (*Ovis gmelini musimon*) were found to have strong niche overlap, but key differences in preferred meadow types allowed researchers to conclude to weak potential for competition (Darmon et al. 2012). Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) select similar habitats in the summer but partition their diets and their winter habitat selection (Stewart 2003; Stewart et al. 2010).

Muskox (*Ovibos moschatus*) and caribou are large-bodied herbivores that live in the Arctic. Muskox are relatively sedentary and for the most part live in mixed-sex groups whereas barren-ground caribou are a migratory species, moving long distances from their calving grounds to their wintering range. These two species niches can overlap, and they can be found in the same habitat. It is not, however, fully understood how these two arctic ungulates coexist and the extent to which they interact. Muskox habitat selection has been studied across the Arctic with varied results. In Alaska, suitable summer habitat for muskox was in low, wet areas and, suitable winter habitat was in higher, drier areas (Danks and Klein 2002). In Norway, it was found that muskox preferred *Dryas sp.* located on steep slopes with little snow accumulation (Nellemann 1998). More recently, in Greenland, habitat suitability was consistently predicted to be highest in vegetated, flat to moderately rugged terrain at low to medium elevation close to the coast (Beumer et al. 2019).

As Arctic species, muskox and caribou rely heavily on building fat stores during the summer when high-quality forage is abundant (Adamczewski et al. 1998, Chan-McLeod et al. 1999). However, we know little about muskox-caribou niche overlap during this critical time of the year. Studies contrasting muskox-caribou niche overlap have for the most part focused on diet, identifying that the two species had similar diet composition, forage intake rate and digestibility (Kazmin and Abaturov 2011). On Banks Island, in the Northwest Territories, muskox and Peary caribou had monthly diet similarities ranging from 17.8-73.3% and diet similarities were more pronounced when muskox densities were high (Larter and Nagy 1995). In Alaska, muskox diet was composed of significantly more sedge and moss, and less lichen than caribou (Ihl and Klein 2001).

The Yukon North Slope, in Yukon, Canada stretches from the Beaufort Sea inwards, including all Yukon's mainland whose waters drain into the Beaufort Sea, where caribou and muskox now coexist. Muskox are thought to have been present in the Yukon North Slope until the mid to late 1800s when they were extirpated, most likely due to human activity (Hone 1934; Lent 1998). In the late sixties and early seventies, muskox were reintroduced to the Alaskan North Slope and subsequently, some individuals migrated eastwards into the Yukon North Slope and Richardson Mountains of the Northwest Territories where mixed-sexed groups have been reported since 1985 (Reynolds, 1998). The current muskox population extends east into the Richardson Mountains of the Northwest Territories and west into the Alaskan North Slope. This area is also home to the Porcupine caribou, a migratory barren-ground caribou herd of 218, 000 individuals (Porcupine Caribou Technical Committee, 2018). In post-calving summers, their range spans the Yukon North Slope and adjacent areas, and in the winter, it spans north-central Alaska and northern Yukon. The Arctic National Wildlife Refuge (ANWR) in Alaska is where most of the calving occurs (Russell et al. 1993). Both populations are currently extensively monitored through GPS collaring programs.

The muskox reintroduction has been concerning for some community members of the Northwest Territories, especially in the hamlet of Aklavik, who worry about the impact of reintroduced muskox on caribou. Concerns about muskox-caribou interactions, focusing on possible exploitation and interference competition, have been brought to the attention of local organizations and co-management boards.

In this study, we characterize muskox and caribou interactions through analysis of their spatial and habitat overlap. We predict that muskox and caribou interactions will be minimal due to limited spatial overlap and differential patterns of habitat use due to long periods of coexistence between the two species. We take advantage of the high percentage of muskox groups having a collared individual to calculate encounter rates between the two species and use resource selection functions to quantify habitat use. The results of this study will provide useful management tools for communities and co-management Board of the region.

Methods

Study Area

Our study was conducted in the Yukon North Slope, the northern Richardson Mountains, and northern parts of Vuntut National Park (Fig. 1.1). This 26, 850 km^2 region spans all Canadian territory occupied by over 300 muskox that were first reintroduced in the Alaskan North Slope (Lent 1998; WMAC 2017). It is bordered to the West by the Yukon-Alaska border, to the North by the Beaufort Sea, and to the East by the Mackenzie Delta. Mountain ranges are present in the western and eastern parts of the study area, and gentle slopes cover the central parts.

The climate is characterized by extreme temperature fluctuations, with minimums reaching -50°C in the winter, and maximums of 30°C in the summer. Most of the study area is found in the Arctic Bioclimate Subzone E where vegetation is dominated by low birch, willow and alder shrubs over 40 cm tall, though tall shrubs (>2 m) and patches of spruce forest can be found along riparian corridors (CAVM Team 2003).

Muskox and Caribou Location Data

Twenty-five female muskox were collared from 2015 to 2018 (8 in 2015, 6 in 2016, and 11 in 2018). Because the 2015 collaring happened in the fall, and the spring and summer months were of interest, the 2015 data was not used in this study. Muskox were outfitted with Iridium collars with frequencies taken every hour from May to October, and every 5 hours from November to April. The collars were distributed in different muskox groups, such that most groups had at least one collared individual. All muskox location data were obtained from Yukon Government.

Satellite collars have been deployed on Porcupine Caribou since 1998. In this study, we focus on the 179 collared individuals who entered the Yukon North Slope from 2016 to 2019, of which 47 were male and 132 were female. Satellite collars were programmed to provide locations every 2.5 hours for females with Iridium collars and every 13 or 25 hours for males. Eighty-eight Iridium and 91 Globalstar collars were deployed. All location data was obtained from the Porcupine Caribou Management Board.

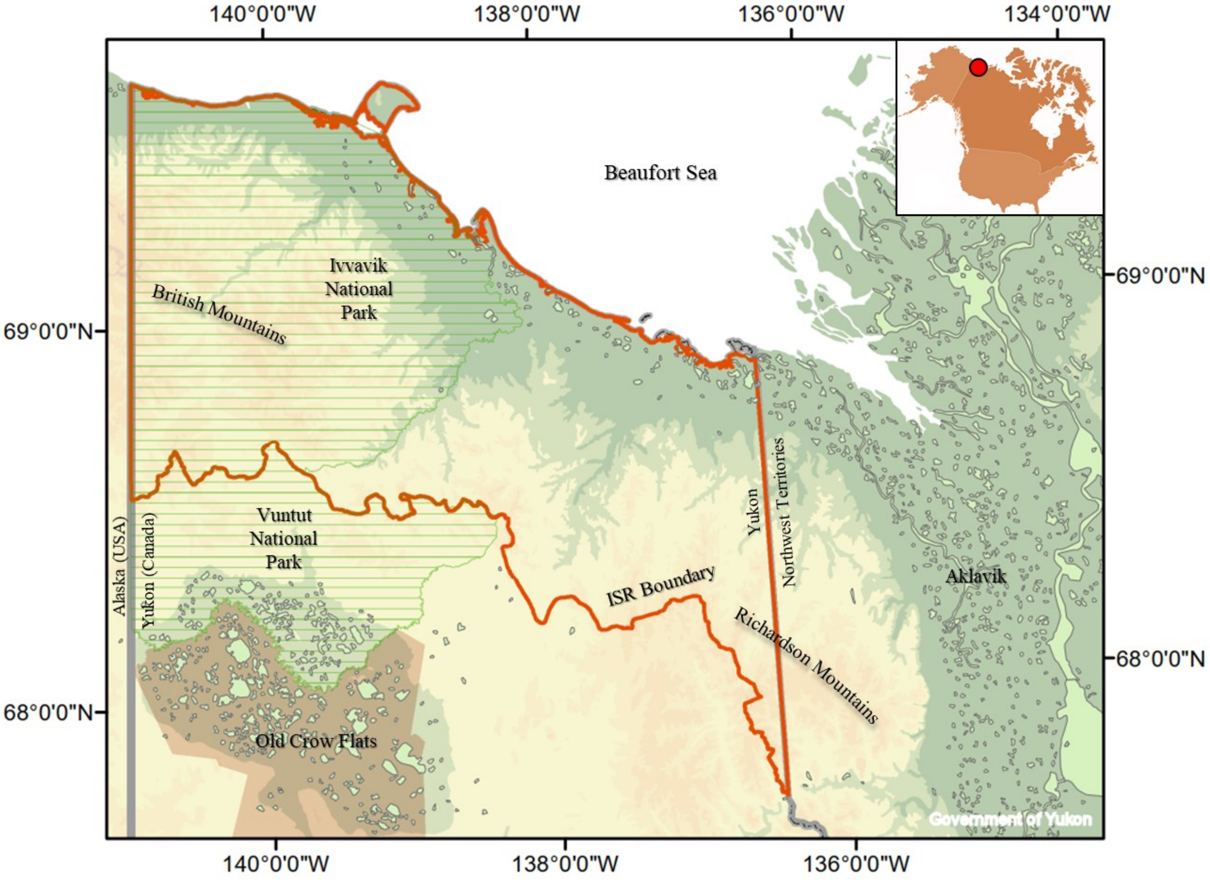

Figure 1.1 Yukon North Slope, Inuvialuit Settlement Region (in red), Richardson Mountains, National Parks and surrounding areas.

Spatial Overlap

To define muskox-caribou spatial overlap at a coarse scale, we calculated a 100% minimum convex polygon around the muskox locations taken between 2016 and 2019 (hereby referred to as the muskox range), and determined the percent of caribou collars found within the range daily between those same years. For fine-scaled analyses, we only considered caribou who had entered muskox range and with collar frequencies every 2.5 hours (all female). Among this group, we calculated the proportion of caribou who encountered a muskox, daily. Encounters were defined as two fixes (one muskox, one female caribou) that had occurred within a 2-hour window and a 2-km threshold. For those female caribou who had had an encounter with muskox, we calculated the number of contact hours.

Habitat Overlap/Resource Selection

Landscape Covariates

Resource selection models were developed with 4 environmental covariates; these included a habitat land-cover classification (PEM), a vegetation index (max-NDVI), a digital elevation model (DEM), and distance to water. The Predictive Ecosystem Mapping layer (PEM) is a high resolution (6x6 m) raster map of land cover classes covering the entire Yukon Territory (Yukon Environment, 2016). Because the 6 m PEM resolution is finer than the error on the GPS transmitters, and much finer than the other covariates that were available, we reduced the resolution to 60x60 m, where the mode of the 6x6 m cells within each 60x60 m area was identified as the dominant land cover. In addition, to facilitate interpretation, the 24 PEM land-cover types were aggregated into the following 9 classes: Beach, Floodplain, Non-Vegetated, Rock-Lichen, Tundra, Shrub Tundra, Tussock, Wetland, and Woodland (Table. 1.1, Appendix). Using MODIS imagery (Huete et al. 2002), we obtained annual maximum normalized vegetation index (NDVI) at 250-m resolution. We averaged the max-NDVI data from 2016 to 2019 to obtain a single NDVI layer containing all years under study. The digital elevation model (DEM) was obtained from NASA's Shuttle Radar Topography Mission (SRTM) at 30-m resolution from the USGS Earth Explorer. Distance to fresh water was obtained using the CanVec - Hydro Features product developed by Natural Resources Canada. All landscape covariates were scaled to a 60-m resolution to match the PEM landcover layer. In doing, distance to water was transformed from a vector to raster type, with 60-m cells containing a fresh water source given a value of zero.

Resource Selection by Muskox and Caribou

Resource selection models were developed with a used-available design (Manly et al. 2002). The Yukon North Slope (see Figure 1.1) was defined as 'available' given the high number of collared muskox and caribou found in the area and access to the PEM. Moreover, the adoption of the Yukon North Slope as the study area allowed us to define the same available region for muskox and caribou models and improved our ability to compare results. Caribou and muskox GPS locations were defined as 'used'. For every model, we generated twice as many random locations as GPS points within the study area.

Models were developed for the two periods of time with the greatest spatial overlap between muskox and caribou: spring, from May 1st to June 30th and summer, from July 15th to August 31st (Fig. 1.2). The spring season corresponds to the Porcupine caribou's pre-calving migration, and the summer to its post-calving season. Prior to the analysis, we tested for correlations between covariates using Pearson's R with a threshold of 0.7 (Dorman et al. 2013). No covariates were removed from consideration following this procedure. To avoid autocorrelation in our data, we parsed the dataset to only include one location per individual per day and removed duplicate muskox observations belonging to animals found in the same group. Data was removed in instances where locations belonging to more than one muskox were found within one kilometer over the course of four days.

We used a logistic-type generalized linear mixed-model to generate four resource selection models (Muskox-Spring, Caribou-Spring, Muskox-Summer, and Caribou-Summer). We scaled continuous variables and included a random intercept effect for individuals. The distance to water variable was log-transformed prior to scaling. 'Shrub tundra' was used as a reference class in all models because it had a selection ratio close to 1 for all season-species combinations. We generated four global models that included all habitat variables including second-order elevation to account for preference of intermediate elevations. We calculated the sum of AICs for our four global models and used a backwards selection procedure to drop variables that increased the sum of AIC and selected the model with the lowest AIC (Burnham and Anderson 2002). When the difference of AIC was less than two, we selected the model with the least number of variables (Burnham and Anderson 2002).

We fit models using the 'glmmTMB' package (Brooks et al. 2017) in R (R Core Team, 2020). In addition to the four models, we generated annual spring and summer models for both muskox and caribou, using the same parameters. In these models, the annual NDVI-max data was included in the models rather than the averaged value across all years.

We used the RSF models to generate maps of muskox and caribou occurrence and co-occurrence for the spring and summer seasons. To do so, we predicted the RSFs over the map of our covariates, subtracted the intercept and placed it in the intercept, dividing the whole by its sum and pixel size. This was then multiplied by the number of muskox (300) or caribou (53,213 for spring, 64,712 for summer). The caribou number estimate was set by calculating the proportion of caribou that entered the Yukon North Slope in spring and summer, annually, based on the collar data. Finally, muskox and caribou predicted occurrences were then multiplied to obtain maps of co-occurrence. Furthermore, we generated maps of annual predicted occurrences for all season-species combinations and used these to map inter-annual variation using the same process as for the grouped annual data.

Models were validated using K-fold cross validation and Spearman rank correlation (Boyce et al. 2002). To do so, we withheld 20 percent of the data (test set) and estimated model parameters on the remaining 80 percent (training set). Model parameters of the training set were used to predict with the withheld test set. We then split the test set into 10 bins based on quantiles of the predicted probabilities of use. Low-ranking bins have data with low relative probability of selection and high-ranking bins have data with high relative probability of selection. We assessed model performance using spearman rank-correlation between bin-rank and the count of used locations in each bin.

Results

Spatial Overlap

In the study area, spatial overlap between muskox and caribou was most likely to occur from May to August with occasional overlap in the early fall. From May 1 to August 31, on any given day, 0 to 65 % of collared caribou were within the muskox range, and across this, the average was 27 %, with a standard deviation of 19 % (Fig. 1.2). A break in overlap corresponding to the calving period occurred in early June. The year-round average of collared caribou found within muskox range was 10.84 %.

Encounters (< 2 km) between muskox and female caribou were much more likely to occur in the spring and summer months. From May 1st to August 31st, among caribou who were within muskox range, 0.81 % encountered a muskox. A peak of encounters occurred July 15, 2019, when 20 % of collared caribou encountered a muskox. For caribou who encountered a muskox, the average number of contact hours was 5.2, with 25 % of caribou having more than 5.2 contact hours and 75 % who had less than 5.2 (Fig. 1.3). Overall, there were fewer encounters in 2018 than in other years (Fig. 1.3).

Habitat Overlap

We obtained 74, 332 muskox GPS locations and 72 ,842 caribou locations during the 2016-2019 spring and summer seasons. The average number of GPS locations per muskox (n = 25) was 2,973, whereas the average number of GPS locations per caribou (n = 160) was 455. The combination of variables that minimized AICs included all considered variables (land cover, elevation, elevation-squared, NDVI, and distance to water) for all models, except muskox-summer, where NDVI was excluded, and muskox-spring, where DEM^2 was excluded (Table 1.2, Appendix).

In spring, muskox selected higher elevations, further from water but with similar greenness to caribou. In the summer, muskox and caribou differentiated even more when it comes to elevation and distance to water, with muskox selection selecting even higher elevations and caribou being closer to water than in the spring (Fig. 1.4).

Muskox selected fewer locations with Tussock, the most dominant land cover class (32%), than caribou in both seasons, with starker selection differences in the summer. Rock-Lichen, the second most abundant land cover class (15%), is more highly selected by muskox than caribou in the spring, where selection overlaps between the two species. The Tundra land cover class (15%)

is selected similarly by both species in the spring, whereas Wetland (13%) and Floodplain (8%) are selected at similar rates in the summer. Differences in selection are also present in less abundant land cover classes such as Beach (1%), which muskox select more than is available on the landscape, and that caribou avoid (Fig. 1.4). The k-fold cross-validation of the caribou and muskox RSF models indicated that strong correlations exist between predicted and actual occurrence of both species in both spring and summer (Muskox-spring: $R_s = 0.84$, Muskox-summer: $R_s = 0.92$, Caribou-spring: $R_s = 0.96$, Caribou-summer: $R_s = 0.99$, $p < 0.05$ for all models).

The estimated among-individual standard deviations for muskox are 1.13 and 1.17 for spring and summer, respectively. These numbers are greater than the magnitude of the largest parameter estimates, including the intercept. For caribou, spring and summer among-individual standard deviations are 1.08 and 1.18, also indicating wide variation in selection according to individuals.

Though overall co-occurrence probabilities on habitat selection are very low, it is possible to highlight areas of greater and lower habitat overlap, which vary greatly with the seasons. In spring, the British Mountains of Ivvavik National Park and parts of the coast are areas of higher co-occurrence. In summer, areas of higher co-occurrence are found in the southern parts of the study area, whereas the entire coast has the lowest co-occurrence probabilities. Areas with higher probability of co-occurrence tend to have less inter-annual variation than places with low probabilities of co-occurrence (Fig. 1.5).

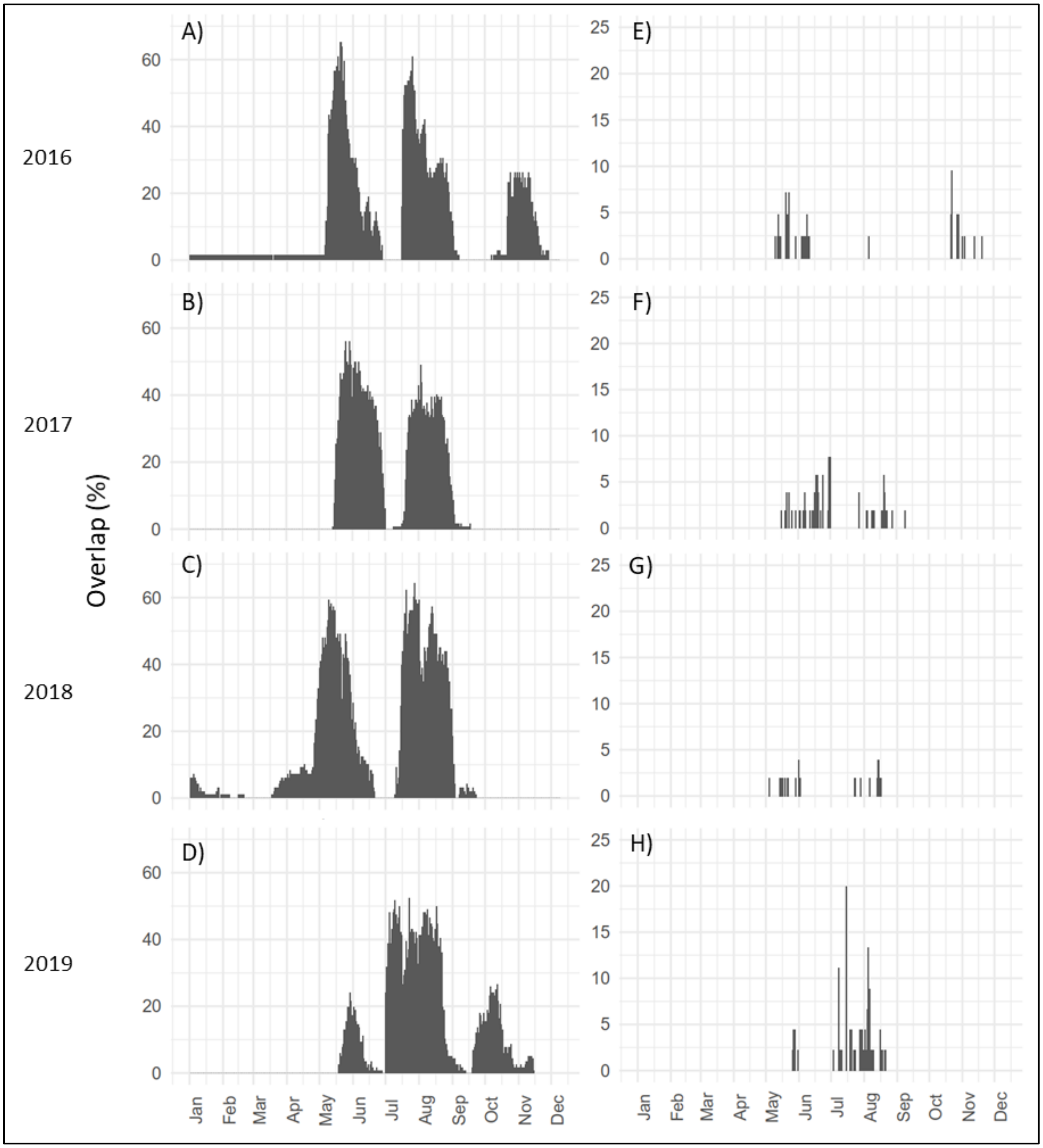

Figure 1.2. Coarse (A-D) and fine (E-H) scale spatial overlap between muskox and Porcupine caribou from 2016 to 2019 in the Yukon North Slope and Northern Richardson Mountains, Canada. Panels A to D show the percent of Porcupine Caribou collars found within muskox range, and panel E to H show the percent of caribou that entered the range who were found within 2 km of a muskox in a two-hour window. Both percentages were calculated daily.

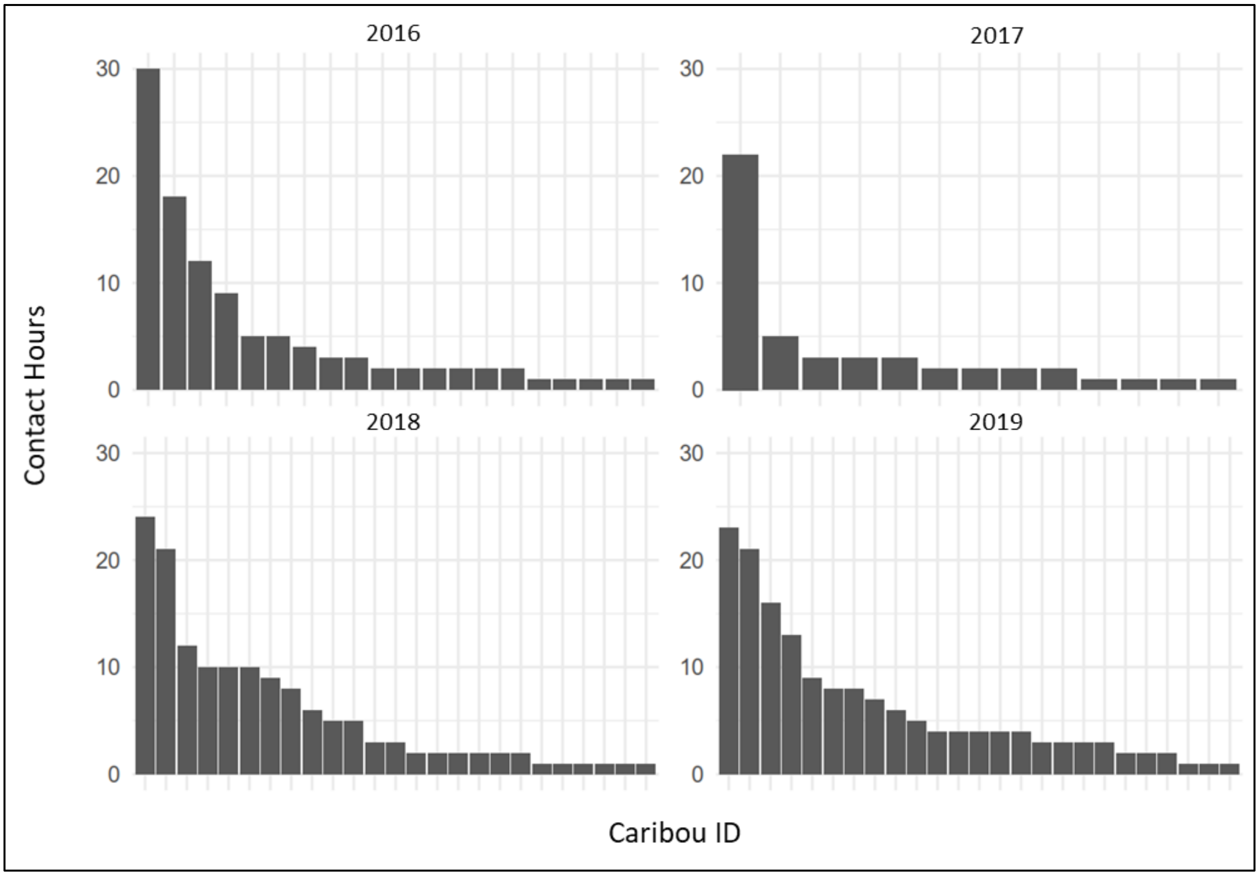

Figure 1.3. Number of contact hours between Porcupine caribou and muskox for every caribou who encountered (< 2 km) a muskox from 2016 to 2019 in the Yukon North Slope and Northern Richardson Mountains, Canada.

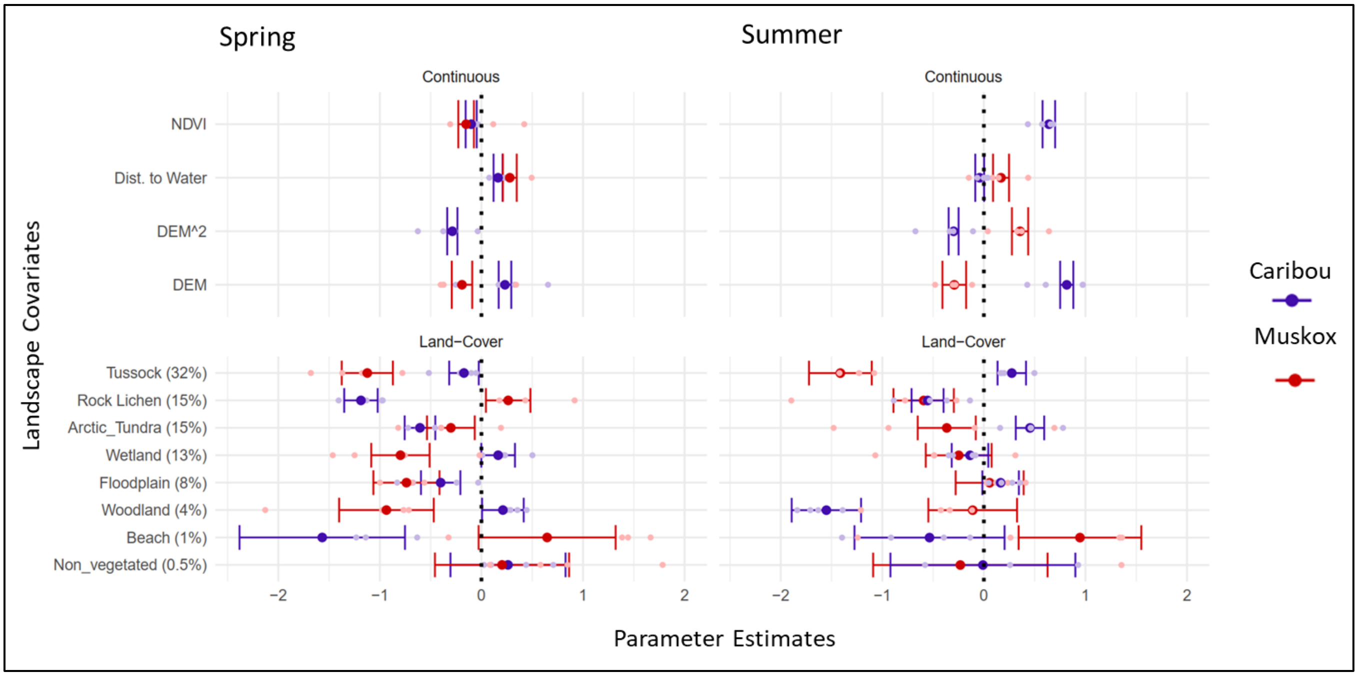

Figure 1.4. Parameter estimates and 95% confidence intervals from muskox (dark red) and caribou (dark blue) for the best resource selection models in spring (May 1st – June 30th) and summer (July 15th – August 31st) in the Yukon North Slope from 2016 to 2019. Shrub Tundra (not shown) was used as the reference class. Light red and blue dots show estimates for annual models (2016 to 2019). Landscape covariate percentages indicate the proportion of the study area covered by each land cover class.

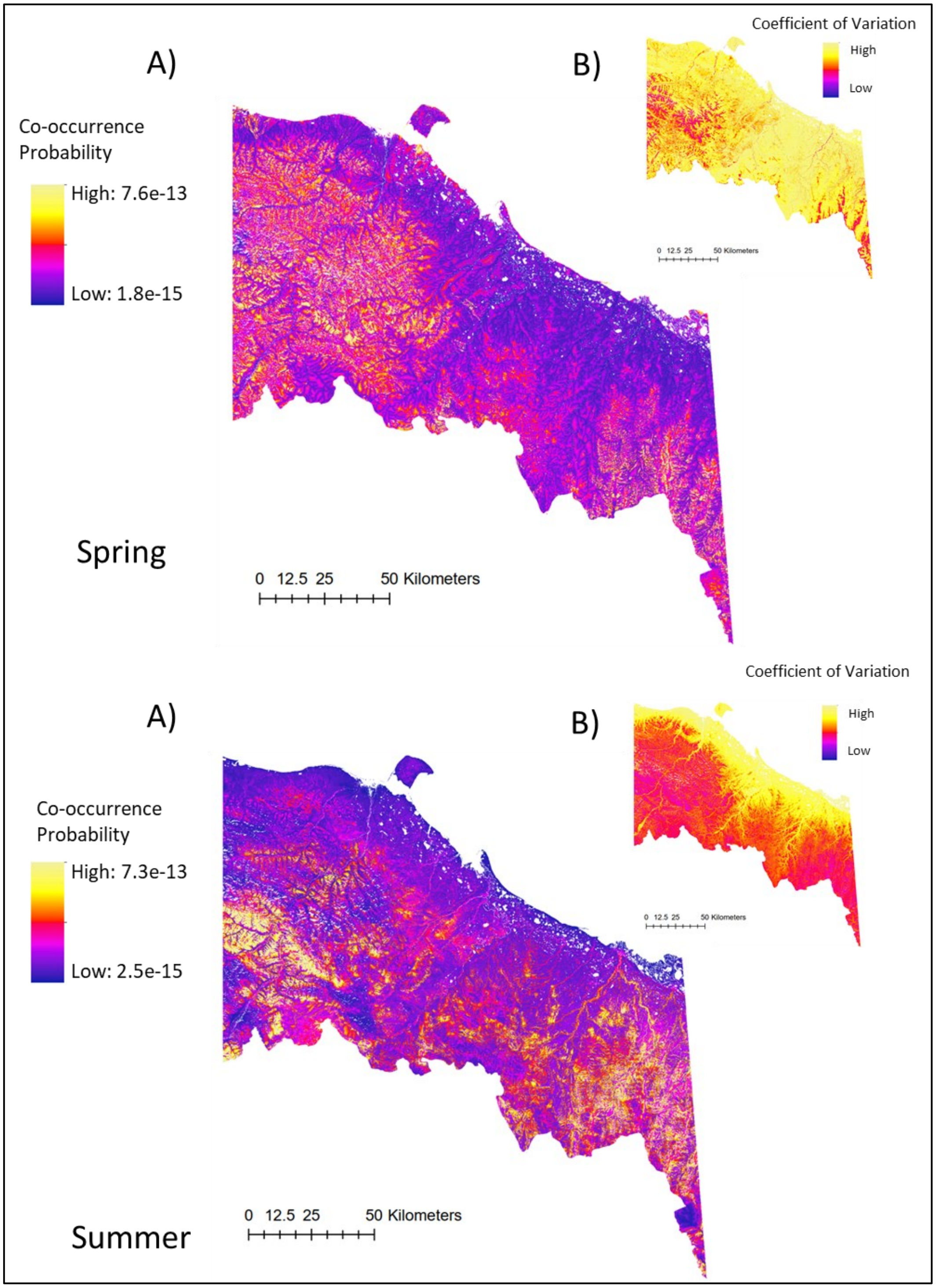

Figure 1.5. Spring and summer muskox-caribou co-occurrence probabilities in the Yukon North Slope from 2016 to 2019 (A). Insets (B) show the annual coefficient of variation for co-occurrence probabilities. Regions in yellow have high inter-annual variation and regions in purple, low inter-annual variation.

Discussion

Muskox and caribou co-occur across the Yukon North Slope and surrounding areas in the spring and summer seasons, with fine scale overlap patterns mimicking those that occur at a large scale. To our knowledge, this is the first attempt at describing spatial overlap between the two species using collar data. Our spatial overlap results indicate some habitat overlap between the two species, consistent with a potential for competition in the Yukon North Slope in the spring and summer months. However, our habitat overlap analysis indicates muskox and caribou select different attributes on the landscape. Muskox exhibited high avoidance of tussock habitat commonly used by caribou and selected higher elevations further from water than caribou. Species differences in habitat use were most marked in the summer, when they differentiate in selection for greenness, elevation, distance to water, and tussock habitat.

Shared use of habitats and resources is a pre-requisite for direct competition between interacting species. Despite a proliferation of research on ungulate space use and movement patterns facilitated by GPS collar technology, direct comparisons of inter-specific encounter rates and habitat selection remains uncommon. Seemingly, collars are rarely deployed on more than one ungulate species at the same time and in the same region or, if they are, data from different species are rarely analyzed in relation to each other.

Encounter rates in wildlife populations have most often been assessed through camera traps (Macdonald et al. 2004, Aguiar-Silva et al. 2017) or, increasingly, with proximity loggers (Drewe et al. 2012). Using GPS fixes has several limitations for assessing encounters, particularly if movement rates are high relative to fix rates and brief encounters are ecologically important. In our study, 0.81 % of caribou encountered a muskox during spring and summer. These results serve as a rare example of a study calculating interspecific encounter rates using GPS collars. As such, our encounter results are challenging to put into context, with a major challenge in assessing the encounter rates as ‘low’ or ‘high’. Based on our encounter rate and resource selection results, we believe that this encounter rate represents a low potential for direct competition. Modelling an expected encounter rate between the two species (in the absence of avoidance or attraction behaviour) would have helped us to qualify the encounter rates but this was beyond the scope of this project. We believe more exploration of this potential analytical opportunity is warranted, especially with the widespread use of GPS collars.

Nonetheless, our results in the Yukon North Slope are consistent with muskox-caribou niche partitioning through differential habitat use. We found that muskox used dry habitats, especially in the spring, whereas caribou were more likely to be found in tussock habitat and in lower elevations. Most importantly, in both spring and summer, habitat types that were selected by one species were avoided by the other. Beach habitat was selected by muskox and avoided by caribou. Among more dominant land cover types, tussock and tundra habitats were selected by caribou in the summer but avoided by muskox during that same period. The niche partitioning results are consistent with other work done on muskox-caribou, who have found muskox and caribou to use habitat differently (Schaefer and Messier 1996; Larter and Nagy 2001; Parker and Ross 1975).

Niche overlap is often used for evaluating competition potential because species that use the same resources at the same time will compete if those resources are limited. Niche overlap has been used in many studies to characterize species interactions (Cody 1974, Pianka 1975, Darmon et al. 2012, Jung et al. 2015*b*). However, it will never be an exact proxy for competition. The pitfalls of using of niche overlap as a proxy for competition have been discussed by Abrams (1983) and Holt (1987), who mention that competition is possible even though niche overlap in a multidimensional niche space is zero, and that there is no limit to similarity in resource use patterns that is consistent with the coexistence of two species. The habitat partitioning we observe in the two ungulates could be the result of present-day competition leading to displacement of one or both species, rather than species-specific preferences. However, given the long history of coexistence of these two ungulates, it is likely that current partitioning is the result of past competition, the so-called ghosts of competition past (Rosenweig 1979).

Muskox and caribou have lived in Arctic Yukon and Alaska since the Pleistocene but were extirpated by the mid to late1800s (Hone, 1934). Though this long history of coexistence might lead us to conclude that niche differentiation is inevitable between the two species, accounts and concerns shared throughout the Canadian Arctic about muskox-caribou interactions should give pause to such steadfast interpretations. For example, on Banks Island, demographic accounts (Gunn et al. 1991, 2000) and Inuvialuit traditional knowledge (Nagy 2004) suggest that muskox and caribou populations fluctuate in opposing cycles. From the 70s to the early 21st century, the muskox population increased, reaching a high close to 70 000 individuals (Davison et al. 2013) while the caribou population simultaneously declined. It is unclear whether these patterns are the result of competition or environmental variability (Gunn et al. 2003, Tyler 2010) but they do warrant our attention.

We currently estimate there to be a minimum of 300 muskox in the study region (WMAC North Slope 2017). It will be interesting to follow the population and re-assess habitat and spatial use of both muskox and caribou if muskox numbers increase. If increases in populations in one or the other species leads to differing habitat selection in the other, a competition hypothesis could be supported. For the moment, though, we believe that interactions that may arise from range overlap and encounter rates are offset by differing habitat selection.

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Appendix

Table 1.1. Original land cover classes from the Predictive Ecosystem Mapping layer (Yukon Environment, 2016) and the grouped classes used for muskox and caribou resource selection.

Original PEM Classes	**Grouped Classes**
Tussock	Arctic_Tundra
Heather_Nivation_Slope	Arctic_Tundra
Mesic_Sparse_Low_Shrub_Tundra	Arctic_Tundra
Coastal_Beaches	Beach
River_Beaches	Beach
Dense_Low_Med_Shrub	Floodplain
Herb_Willow_Riparian	Floodplain
Dense_Med_Tall_Shrub	Floodplain
Alluvial_non_vegetated,_fine_texture	Non_vegetated
Non_vegetated_peat	Non_vegetated
Slumps	Non_vegetated
Ocean	Ocean
Rock_Lichen	Rock_Lichen
Subxerix_Sparse_Dwarf_Shrub_Tundra	Shrub_Tundra
Shg_Sparse_Med_Tall_Shrub_Herb_Moss	Shrub_Tundra
Willow_Horsetail	Shrub_Tundra
Water	Water
Hydric_Sedge	Wetland
Shrub_Sedge_Fen	Wetland
Shrub_Sedge_Tussock	Wetland
Alder_Cottongrass_Tussock	Wetland
Subhygric_Spruce_Tussock	Woodland
Subhygric_Spruce_Horsetail	Woodland
Sub_mesic_Spruce	Woodland
Mesic_Spruce	Woodland
Spruce_Alder_Willow	Woodland

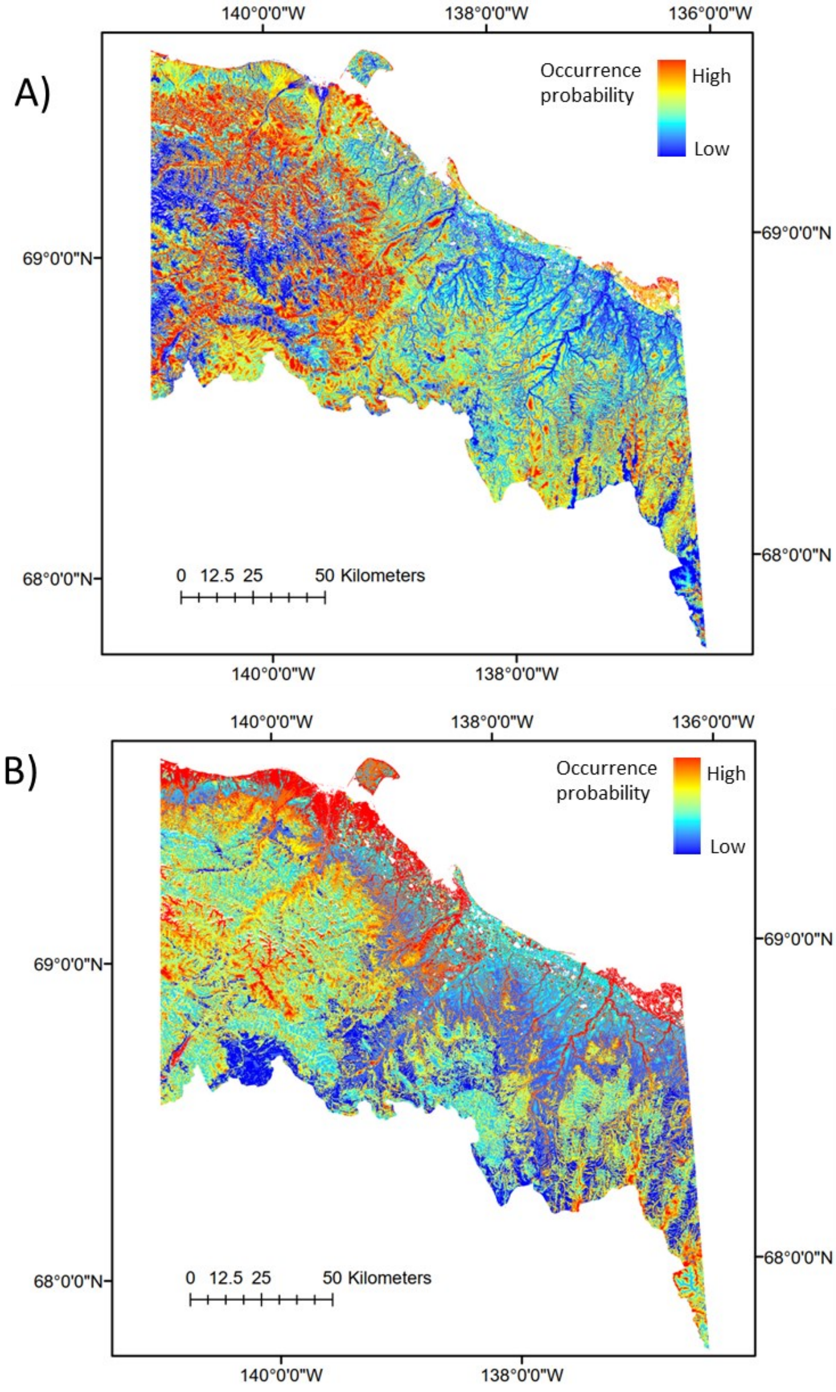

Figure 1.6. Muskox spring (A) and summer (B) predicted occurrence based on habitat selection with data from 2016 to 2019 in the Yukon North Slope. Probability of occurrence was separated into 10 bins (red to blue), with areas in red showing high probability of occurrence, and areas in blue, low probability.

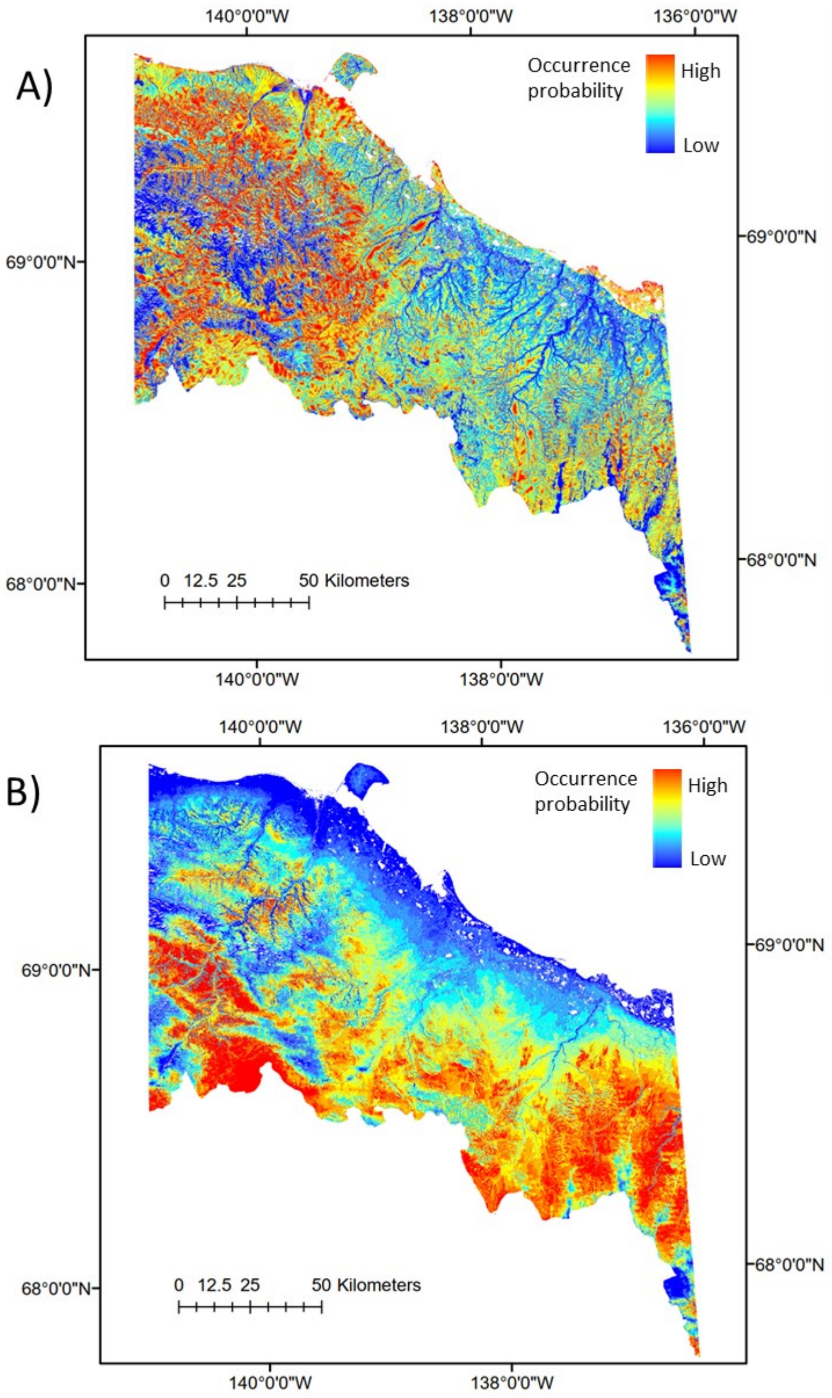

Figure 1.7. Porcupine caribou spring (A) and summer (B) predicted occurrence based on habitat selection with data from 2016 to 2019 in the Yukon North Slope. Probability of occurrence was separated into 10 bins (red to blue), with areas in red showing high probability of occurrence, and areas in blue, low probability.

Table 1.2. AIC values of the models with PEM (Predictive Ecosystem Mapping), DEM (digital elevation model) NDVI (Normalized Differential Vegetation Index), and distance to water covariates for the four species-seasons resource selection functions.

Covariates	AIC	dAIC
Muskox-Spring		
PEM + DEM + NDVI + DIST. TO WATER	5930.4	0.0
PEM + DEM + DEM2 + NDVI + DIST. TO WATER	5931.1	0.7
PEM + DEM + DEM2 + DIST. TO WATER	5932.0	1.6
PEM + DEM2 + NDVI + DIST. TO WATER	5937.6	7.2
PEM + DEM + DEM2 + NDVI	5991.9	61.5
DEM + DEM2 + NDVI + DIST. TO WATER	6224.5	294.6
PEM + DEM + DIST. TO WATER	6232.9	302.5
Muskox-summer		
PEM + DEM + DEM2 + DIST. TO WATER	4318.6	0.0
PEM + DEM + DEM2 + NDVI + DIST. TO WATER	4320.0	1.4
PEM + DEM2 + NDVI DIST. TO WATER	4334.0	15.3
PEM + DEM + DEM2 + NDVI	4378.7	60.0
PEM + DEM + NDVI + DIST. TO WATER	4380.8	62.2
DEM + DEM2 + NDVI + DIST. TO WATER	4650.6	332.0
Caribou-spring		
PEM + DEM + DEM2 + NDVI + DIST. TO WATER	15394.5	0.0
PEM + DEM + DEM2 + DIST. TO WATER	15405.8	11.2
PEM + DEM2 + NDVI + DIST. TO WATER	15446.3	51.7
PEM + DEM + NDVI + DIST. TO WATER	15528.4	133.0
PEM + DEM + DEM2 + NDVI	15534.4	139.9
DEM + DEM2 + NDVI + DIST. TO WATER	15939.9	545.6
Caribou-summer		
PEM + DEM + DEM2 + NDVI + DIST. TO WATER	16625.5	0.0
PEM + DEM + DEM2 + NDVI	16640.9	15.4
PEM + DEM + NDVI + DIST. TO WATER	16777.9	152.3
PEM + DEM + DEM2 + DIST. TO WATER	17066.5	441.0
DEM + DEM2 + NDVI + DIST. TO WATER	17066.5	479.7
PEM + DEM2 + NDVI + DIST. TO WATER	17267.0	641.5

Table 1.3. Parameter estimates, standard error and p-values from muskox and caribou best resource selection models in spring (May 1st – June 30th) and summer (July 15th – August 31st) in the Yukon North Slope from 2016 to 2019. Shrub Tundra (not shown) was used as the reference class.

	Muskox-Spring			Muskox-Summer		
Term	*Estimate*	*Std. Error*	*Pr(>|z|)*	*Estimate*	*Std. Error*	*Pr(>|z|)*
Continuous variables						
DEM	-0.19	0.05	0.0002	-0.29	0.06	9.87e-07
DEM^2	-	-	-	0.36	0.04	< 2e-16
NDVI	-0.15	0.04	0.0001	-	-	-
Dist. To Water	0.28	0.03	9.12e-16	0.17	0.04	2.48e-05
Land Cover						
Tundra	-0.3	0.12	0.0121	-0.37	0.15	0.0121
Beach	0.65	0.34	0.0603	0.95	0.31	0.0021
Floodplain	-0.74	0.17	8.68e-06	0.06	0.17	0.7386
Non_vegetated	0.2	0.34	0.5475	-0.23	0.44	0.5972
Rock_Lichen	0.26	0.11	0.0184	-0.59	0.15	9.27e-05
Tussock	-1.12	0.13	< 2e-16	-1.41	0.16	< 2e-16
Wetland	-0.8	0.15	5.32e-08	-0.25	0.17	0.1344
Woodland	-0.94	0.24	8.28e-05	-0.11	0.22	0.6215

	Caribou-Spring			Caribou-Summer		
Term	*Estimate*	*Std. Error*	*Pr(>|z|)*	*Estimate*	*Std. Error*	*Pr(>|z|)*
Continuous variables						
DEM	0.23	0.03	2.10e-13	0.82	0.03	< 2e-16
DEM^2	-0.29	0.03	< 2e-16	-0.3	0.03	< 2e-16
NDVI	-0.1	0.03	0.0003	0.64	0.03	< 2e-16
Dist. To Water	0.16	0.02	5.90e-13	-0.04	0.02	0.0645
Land Cover						
Tundra	-0.61	0.08	3.88e-15	0.45	0.07	2.00e-10
Beach	-1.57	0.42	0.0002	-0.54	0.38	0.1558
Floodplain	-0.4	0.1	4.99e-05	0.16	0.09	0.0722
Non_vegetated	0.26	0.29	0.3656	-0.01	0.46	0.9837
Rock_Lichen	-1.19	0.08	< 2e-16	-0.55	0.08	5.68e-12
Tussock	-0.17	0.07	0.0204	0.27	0.07	0.0001
Wetland	0.16	0.08	0.0519	-0.14	0.09	0.138
Woodland	0.21	0.1	0.0438	-1.55	0.17	< 2e-16

Connecting Statement

Results from the first chapter suggest that muskox and caribou interact infrequently. However, their selection rates for Wetland, Floodplain, and Rock-Lichen land cover classes do overlap in the summer. In the following chapter, I characterize muskox habitat associations within land cover classes where muskox-caribou use overlaps with the intention of determining if muskox herbivory has quantifiable impacts on the vegetation caribou also rely on.

CHAPTER 2: Fine-Scale Muskox-Vegetation Associations

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Abstract

Fine-scale associations between herbivores and vegetation can be the result of both selection, in which herbivores select or avoid certain micro-environments, and herbivory, in which herbivores remove biomass and in so doing can change vegetation composition. Here, we study fine-scale habitat associations in a reintroduced muskox (*Ovibos moschatus*) population in the Yukon. In the summers of 2018 and 2019, we sampled 205 plots in three habitat types in Ivvavik National Park, recording species height and cover, and number of muskox fecal samples at each site. Vegetation height and cover were used to estimate biomass, and muskox fecals as a proxy for muskox use at a given site. Muskox use did not explain total plant biomass and species richness in the three sampled habitats. However, we found positive associations between muskox use and lichen and graminoid biomass, and positive associations between muskox use and presence of willow. The positive associations between muskox use and lichen, graminoids, and willow are an indication that within land covers, the relationship between muskox use and vegetation is mostly driven by selection rather than by herbivory. Overall muskox impacts on vegetation are low.

Introduction

Studies on associations between plants and large-bodied herbivores tend to fall within two broad categories. Firstly, ecologists often want to know what attributes on the landscape are being selected by the animal under study. Many frameworks exist to investigate this type of question, most popular of which are resources selection functions and species distribution modelling, which predict species' occurrences based on environmental variables at used and available locations (Hegel et al. 2010). These frameworks assume that at a large-scale, the association between an animal and its environment is driven by the selection of landscape attributes by the animal. Secondly, ecologists take a different approach, asking what impact an animal has on its environment. For example, it is well documented that herbivores can modify vegetation composition, productivity, and function (Gordon and Prins 2008, Bagchi et al. 2012). The impact this modification of vegetation can have on ecosystems is significant and can lead to transitions in habitat types (Wal et al. 2006) and habitat degradation (van de Koppel et al. 1997, Adler and Morales 1999). In these studies, the association between an animal and its environment is the result of grazing and browsing by the animal.

In the first scenario, an animal selects vegetation types suitable for its needs, and that environment is unresponsive to the presence of the animal, and in the second, selection has already come to pass, and an animal modifies its environment. Though these two frameworks make sense, one could seek to ask opposing questions. Do herbivores modify landscape-level vegetation patterns? And do animals display selection behaviour at a very fine, habitat-patch scale? In this study, we focus on the latter, turning our attention to an arctic herbivore, the muskox (*Ovibos moschatus*).

Muskox are large-bodied herbivores with a circumpolar distribution. Their diet is mainly composed of sedges and willow (Klein and Bay 1990, Gunn 1997, Kristensen et al. 2011), though they have also been found to consume forbs and lichen (Ihl and Klein 2001, Rozenfeld et al. 2012). At a large scale, studies on resources selection patterns show that muskox select low and wet areas in summer and, in winter, higher and drier areas (Nellemann 1998, Danks and Klein 2002). Highly vegetated, wet meadows at low to medium elevation are also selected (Schaefer and Messier 1995, Beumer et al. 2019). Muskox herbivory studies have shown that muskox removed 0.17% and 0.04% of the available forage in graminoid-dominated areas and in *Salix* snowbeds in Greenland (Mosbacher et al. 2016) and that muskox can modify the structure of sedge species through grazing (Tolvanen and Henry 2000).

Muskox are thought to have been present in the Yukon North Slope, an area stretching from the Beaufort Sea inwards into the Yukon Territory, until the mid to late 1800s when they were extirpated (Hone, 1934; Lent, 1998). In the late sixties and early seventies, muskox were reintroduced to the Alaskan North Slope and subsequently, some individuals migrated eastwards into the Yukon North Slope and Richardson Mountains of the Northwest Territories where mixed-sexed groups have been reported since 1985 (Reynolds, 1998). This reintroduction has been cause for concern for local community members, who worry about the impact of muskox herbivory on vegetation, and how diminished vegetation may affect caribou (*Rangifer tarandus*) (WMAC, 2018).

Our overall objective was to describe the relationship between muskox and its environment at a fine, habitat-patch scale. To do so, we first documented those associations at a fine-scale, and secondly, we determined which, of muskox selection or muskox herbivory, would be the driving force behind associations that guide muskox and vegetation within varying habitats. If muskox selection is the driver behind those relationships, we expected to see a positive relationship between muskox use and attributes reflective of forage abundance, and no relationship between those variables and time elapsed since muskox use. If muskox herbivory determines the associations between muskox and its environment, we expected to see a negative relationship between muskox use and attributes reflective of forage quantity and quality. To research muskox-habitat associations at a fine-scale, we first determined what habitats are selected by muskox at a large, landscape scale, and conducted field sampling within three of those habitat types.

Methods

Study Area

This study was conducted in Ivvavik National Park, a 10 170 km^2 park located in the Yukon's Northwestern most corner, bordered to the West by the Alaska border and to the North by the Beaufort Sea (Figure. 1). The climate is characterized by extreme temperature fluctuations, with minimums reaching -50°C in the winter, and maximums of 30°C in the summer. Snow covers the ground from September to June. Most of the study area is found in the Arctic Bioclimate Subzone E where vegetation is dominated by low birch, willow and alder shrubs over 40 cm tall, though tall shrubs (>2 m) and patches of spruce forest can be found along riparian corridors (CAVM Team 2003).

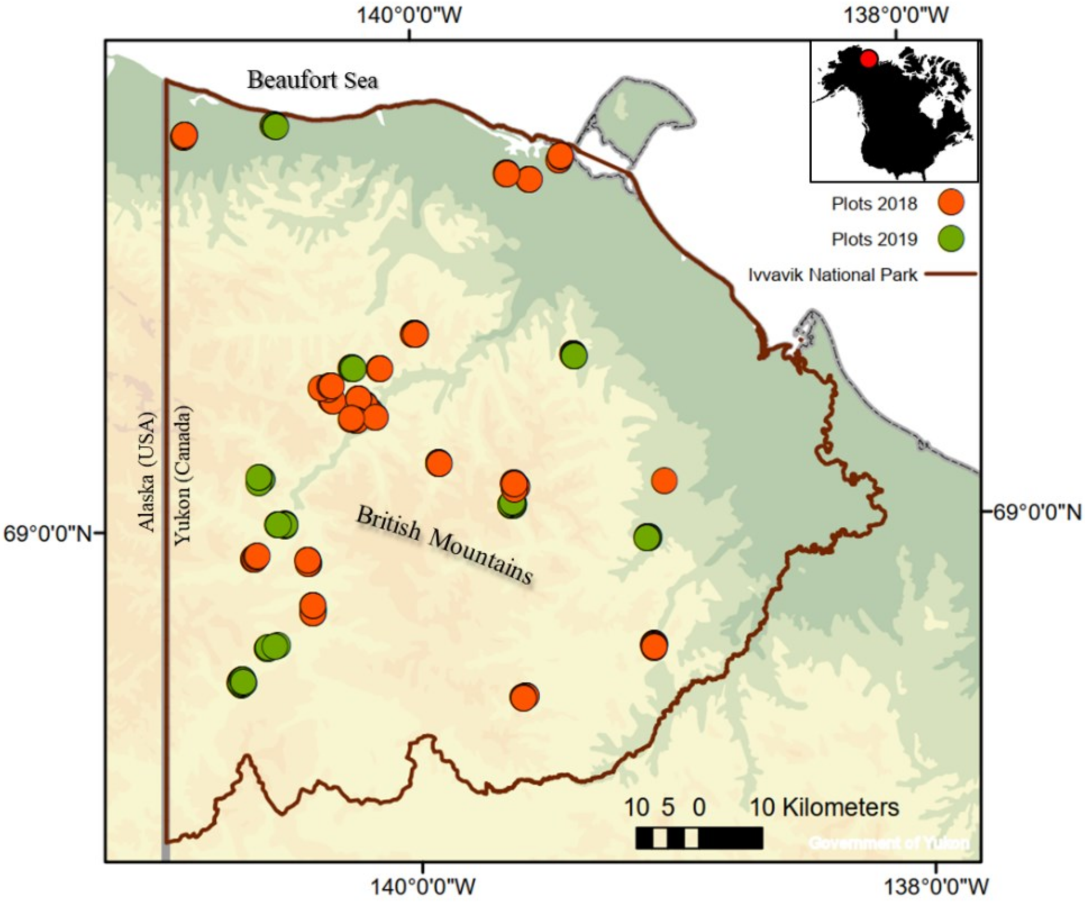

Figure 2.1. Vegetation sampling plots in Ivvavik National Park, Yukon, Canada. Plots sampled in 2018 are in orange and plots sampled in 2019, in green.

Predictions

We generated a series of predictions that would allow us to determine what guides the associations between muskox and vegetation at a fine-scale (Table 1). If muskox selection is the driver behind those relationships, we expect to see a positive relationship between muskox use (defined here as the presence or absence of muskox and the intensity of muskox use) and total plant biomass, and in particular graminoid, sedge, and lichen biomass. Furthermore, we would not expect to see any relationship between vegetation attributes and time elapsed since muskox use.

Opposite predictions are expected if muskox herbivory is the driver behind vegetation-muskox associations. In this scenario, we would expect to se a negative relationship between muskox use and plant biomass as well as species richness. However, we would expect to see vegetation recover after time elapsed since muskox use. For simplicity's sake, muskox use was entered as a predictor variable and vegetation data as our response variable in all our models, but we did so recognizing that the models themselves do not imply directionality. The models were used to reflect correlations between our variables, and the direction of the correlation was used to assign causation through our prediction table.

Table 2.1. Predicted relationships (positive [+], negative [-], null [0] and unknown [?]) between environmental variables and muskox use, if a) muskox selection is the driving force behind those relationships or b) muskox herbivory drives the relationship between muskox and its environment.

Driving Force	Variables			
	Total plant biomass	Species Richness	Graminoid, willow, and lichen biomass	Time since use
a) Muskox selection	+	?	+	0
b) Muskox herbivory	-	-	-	+

Site Selection and Vegetation Sampling

Sites were selected according to muskox use and land cover. Eighteen muskox were outfitted with Iridium collars from 2015 to 2018, with locations taken every hour from May to

October, and every five hours from November to April. These collars were distributed in different muskox groups, such that most groups had at least one collared individual. All muskox location data were obtained from Yukon Government, and were used along with the Predictive Ecosystem Mapping layer (PEM), a high resolution (6x6 m) raster map of land cover (Yukon Environment, 2016) to determine muskox selection ratios. Selection ratios were calculated for winter (November 1st to March 31st) and summer (June 1st to August 31st) by dividing the percentage of muskox locations found within a land cover class by the percentage of land the class occupies in the Park.

Using the selection ratios (Table 2, Appendix), we chose to sample in three land cover classes: Rock-lichen, Riparian Herb-Willow, and Hydric Sedge. These land classes were selected because of a) wide coverage area in the Park (for Rock-lichen), b) heavy use by muskox relative to land cover's availability (for Riparian Herb-Willow), and c) a combination a widespread coverage and heavy use (Hydric Sedge) (Table 2, Appendix). Within these land cover classes, sampling sites were chosen to represent a gradient of muskox use, time since a site was last occupied, and accessibility.

Each sampling site consisted of four 20 x 20-meter plots in an 80 x 80-square formation. In the few cases where we sampled more or less than four plots in one location, we kept an 80-meter distance between plots. Four 1 x 1-meter quadrats were randomly positioned in each corner of every plot (Figure 2). In every quadrat, an observer visually estimated cover at every layer for every plant species or group. The height of three individuals from every species or group was then measured by selecting a tall, a low, and a plant of average height and measuring the distance between the base of the plant to the top leaf. If a plant could not be identified, the genus or family was listed in lieu of the species. Willow, lichen, moss, sedge, and grass were never identified to the species. Observers walked transects across the 20 x 20-meter plots to count all muskox fecal piles.

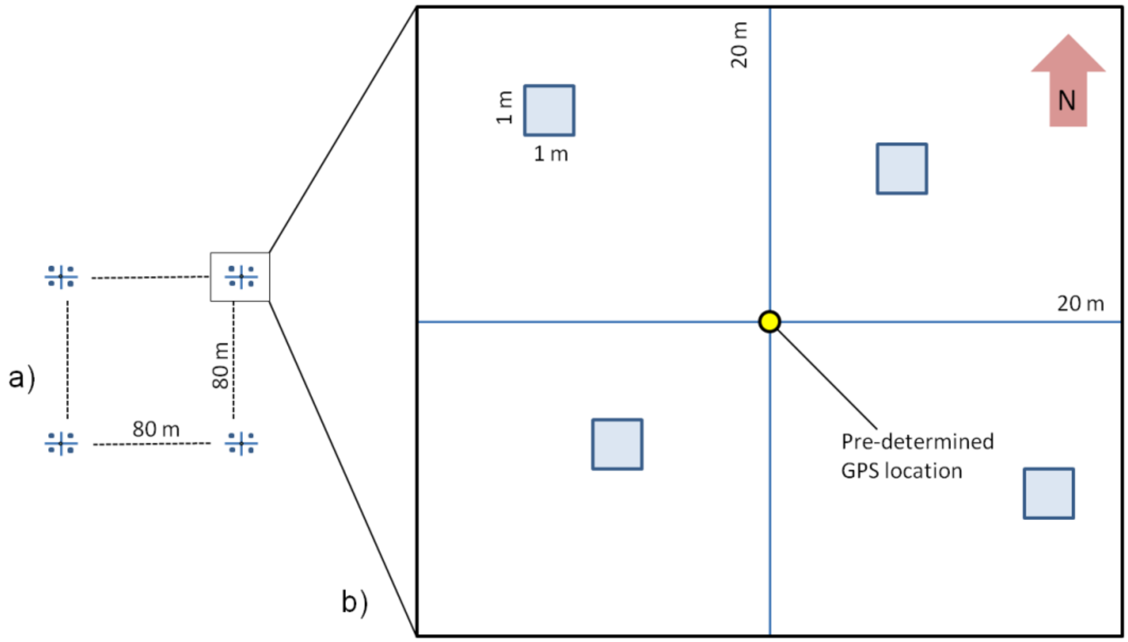

Figure 2.2. Vegetation sampling design showing a) a site consists of many plots and b) every plot consists of four 1x1-meter quadrats within which cover and heights were estimated for every species.

Statistical Analyses

Cover and height were multiplied by factors developed by Chen (2014) to estimate biomass for every species. This estimated biomass was then used in our modelling. We developed linear mixed-models to evaluate the relationship between muskox use and total plant biomass and species richness. Biomass data was square root transformed to linearize the relationship between biomass and species richness. Fixed effects included land cover, year of sampling, and days since a plot was last occupied by a collared muskox. For each of these response variables, we developed two sets of models, one with muskox presence-absence data (as determined by muskox fecals) and another with presence-only data, using the number of muskox fecals per plot as our explanatory variable. For every model, site was the random effect. One outlier was removed from the total biomass analyses as its value was more than 5 standard deviations away from the mean and it was influencing the behaviour of models disproportionately. Model heteroscedasticity was analysed through a Levene test (Garson, 2012), and qqplots were used to verify normality. To further explore the relationship between muskox use and species richness, we created a species-site matrix for each of the three land classes, showing the relationship between number of muskox fecals and the biomass of every plant species.

To test the relationship between muskox use and the biomass of willow, graminoids, and lichen we developed gamma hurdle models (Potts and Elith 2006), which allowed us to model our zero-inflated biomass data. The data were first modelled as a binary response – presence/absence of the vegetation group using logistic mixed-models. Zero values were then removed, and biomass data was modelled using a gamma distribution. As with the total biomass and species richness models, we developed two sets of models, one with muskox presence-absence data (as determined by muskox fecals) and another with presence-only data, using the number of muskox fecals per plot as our explanatory variable. For every model, site was the random effect. Fixed effects included land cover, year of sampling, and days since a plot was last occupied by muskox. Models were assessed by analysing the residual plots.

For both the linear and the gamma models we determined the optimal fixed effects structure by creating models with all possible combinations of fixed effect terms. Interactions between land cover and all other variables were also tested. We then calculated the AICc value for each model and selected the model with the lowest AICc. For models with an AICc difference of less than 2, we kept the model with the lowest number of variables (Burnham and Anderson 2002). Analyses were conducted using the glmmTMB package in R (Brooks, 2017).

Results

One hundred and thirty-nine plots were sampled in 2018 and 66 in 2019, for a total of 56 sampling sites. The number of muskox fecal pellets that were found in one 20 x 20-meter plot ranged from 0 to 80. Fifty-one % of plots were sampled in Rock-Lichen habitat, 30 % in Hydric Sedge, and 19 % in Riparian Herb Willow.

Total Biomass and Species Richness

Muskox presence was weakly positively associated to total available biomass ($\beta = 2.21$, CI from - 0.62 to 5.05), though the 95 % confidence intervals did slightly overlap with zero. The best model for muskox presence impact on biomass did not include an interaction effect between muskox and land cover, indicating a similar relationship between muskox presence and biomass across the sampled habitat types. Models including only land cover and year sampled performed better at modelling biomass than those that also included presence-only muskox intensity of use.

Muskox presence was also weakly associated with species richness in our presence-absence model ($\beta = 0.8803$, CI from -0.15 to 1.92) (Fig. 3-5, Appendix), with confidence intervals once again overlapping with zero. It should be noted that this model did not have the lowest AICc, but we choose to present its results because of the weak AICc difference (0.03) between it and the best model, which included only land cover and year sampled. Species richness was not associated with muskox use when only factoring the number of muskox fecal pellets when those were greater than zero.

Species Composition

Muskox use was not associated with the presence or absence of graminoids. However, muskox presence was associated with higher graminoid biomass in Rock-Lichen habitat, when those graminoids were already at the site. In Hydric Sedge and Riparian Herb Willow, the opposite relationship was observed, with muskox presence being associated with 64 and 100 grams less per meter square, respectively, though those values were not statistically significant (p = 0.27, and p = 0.33) (Table 2.2). Muskox presence was associated with willow presence regardless of habitat type (Fig. 3-5, Appendix). The odds of there being willow at a site where muskox were present increased by a factor of 5.12. However, muskox presence was not associated with greater willow biomass when those willow were already present (Table 2.2). Lichen was 5.14 times more likely to be present when muskox were present in Rock-Lichen habitat (p = 0.014). However, as with graminoids, the opposite relationship was observed in Hydric Sedge and Riparian Herb Willow, with 18 % (p = 0.057) and 58 % (p= 0.452) less chance of there being lichen with presence of muskox, respectively. Muskox presence had a positive effect on lichen biomass. When lichen was present, muskox presence was associated to an increase of 192 g and 67 g per meter square in 2018 and 2019 respectively, regardless of land cover type (p = 0.0304). The land cover, muskox, and vegetation relationships are summarised in Table 2.3.

Though muskox presence and absence were associated with vegetation groups, our modelling did not reveal any associations between muskox intensity of use and vegetation groups. None of our best models included number of muskox fecal pellets nor date since a plot was last occupied by muskox.

Table 2.2. Predicted values of graminoid, willow, and lichen according to muskox use in three habitat types in the Yukon North Slope, Canada, between 2015 and 2019. Muskox use was first used to predict a vegetation group's presence or absence using binomial logistic models. When a vegetation group was present in a plot, we then modelled its biomass according to muskox presence using a gamma distribution. We report predicted values (in grams per square meter for gamma models, 0-1 probability for the logistic models), standard errors, and p-values of the best mixed-models with site as a random effect.

	Rock Lichen			Riparian Herb Willow			Hydric Sedge		
Vegetation Group	Muskox Presence Pred ± SE	Muskox Absence Pred ± SE	P-value	Muskox Presence Pred ± SE	Muskox Absence Pred ± SE	P-value	Muskox Presence Pred ± SE	Muskox Absence Pred ± SE	P-value
Graminoid Presence	-	-	-	-	-	-	-	-	-
Graminoid Biomass	11.51 ± 2.65	6.35 ± 1.41	0.0252	69.51 ± 21.72	169.60 ± 61.04	0.3263	137.50 ± 42.50	201.59 ± 52.45	0.2749
Willow Presence	0.75 ± 0.08	0.38 ± 0.09	0.002	0.99 ± 0.01	0.96 ± 0.03	0.002	0.99 ± 0.01	0.97 ± 0.04	0.002
Willow Biomass	-	-	-	-	-	-	-	-	-
Lichen Presence	0.99 ± 0.01	0.87 ± 0.07	0.0138	0.45 ± 0.19	0.63 ± 0.15	0.0566	0.02 ± 0.02	0.59 ± 0.23	0.4515
Lichen Biomass (2018)	488.75 ± 126.72	297.15 ± 64.92	0.0304	488.75 ± 126.72	297.15 ± 64.92	0.0304	488.75 ± 126.72	297.15 ± 64.92	0.0304

Table 2.3. Relationships (positive (+), negative (-), none (0)) between muskox and vegetation in three land classes. Red symbols indicate relationships that were statistically significant.

Muskox Use	Total plant biomass	Species Richness	Graminoid	Willow	Lichen	Time Since Use
Rock-Lichen	+	+	+	+	+	0
Riparian Herb Willow	+	+	-	+	- and +	0
Hydric Sedge	+	+	-	+	- and +	0

Discussion

At a fine-scale, muskox selection seems to play a greater role in muskox-vegetation associations than muskox herbivory impacts. Most of the associations between muskox and vegetation in the supported models were positive, with greater vegetation biomass being associated with muskox presence. The lack of any relationship between time elapsed since muskox use and vegetation is also indicative of herbivory not being a significant factor in muskox-vegetation associations as we would expect vegetation recovery (Henry and Gunn 1991, Sjögersten et al. 2011), or as has been observed in certain cases, a decrease in the biomass of certain vegetation groups (Ravolainen et al. 2011) following an intense herbivory event.

The relationship between muskox use and vegetation varied across the three land covers. It is interesting to note that muskox use was linked to a decrease in willow biomass in the two most productive habitat types, Riparian Herb Willow and Hydric Sedge, but the opposite relationship was observed in the much less productive Rock-Lichen habitat. This is an indication that muskox selection is the more noticeable driver in low productivity habitat, but that in areas of higher productivity muskox herbivory may stand out as that driver. In other words, even when muskox remove graminoid biomass from Rock-Lichen habitat, that biomass removal is less than the breadth of biomass variation already existent in Rock-Lichen habitat. However, in more productive habitats, we may notice a decrease in biomass associated with herbivory because the breadth of vegetation biomass in these productive habitats is not sufficient for muskox selection to be at play. This is not to imply that only selection or herbivory are playing out in an instance, we cannot deny that both herbivory impacts and selection are processes that occur at the same time, and that as both their effects can subdue the other's impact, we are noticing the most prominent of the two processes.

Our best models only featured muskox use as a presence/absence variable. Once muskox were present, intensity of use did not explain vegetation structure. One might conclude that this is further evidence of muskox selection being an important factor in fine-scale habitat associations. For example, one can argue that selection is more at play when comparing sites where muskox choose to be rather than sites where they choose to be for a longer period of time. It highlights that the observed associations between muskox and vegetation are moderate, and that no extreme associations were found at this fine a scale.

Overall, the results point to minimal muskox impacts on vegetation. This is similar to what was found in Zackenberg, Greenland, where muskox grazing had small effects on vegetation biomass, removing 0.17% and 0.04% of biomass at high muskox densities (Mosbacher et al. 2016). It is unsurprising then, that at lower densities, we would find less evidence of muskox grazing pressure, and no significant relationship between muskox use and total vegetation biomass. The positive association between muskox and lichen we find in this study is contrary to McKendrick (1981), who found that lichen biomass decreases with muskox grazing pressure. Muskox have been found to consume lichen (Ihl and Klein 2001, Rozenfeld et al. 2012), and we suppose our positive association is the result of muskox selection, though the muskox-lichen association has not been highlighted by selection studies at a larger scale.

This project brings together the worlds of selection and herbivory, and highlights ways in which both processes can occur simultaneously. The observed relationships at a fine-scale imply there is sufficient variation in vegetation within land cover classes to allow for selection, something that is rarely discussed or considered in traditional resource selection studies. Our results highlight a scale of selection that goes beyond the traditional regional-home range-within home range orders of selection (1st, 2nd, and 3rd order of selection, respectively) (Johnson 1980), and allow us to consider habitat associations within land cover types. When used in resource selection functions, land cover classifications are tools that can be at times quite coarse. Even very detailed land cover classes, such as the one used in this study (6 x 6 meters), with dozens of land classes, cannot fully capture the variation in vegetation communities. Though we are not suggesting that habitat use studies turn to extremely fine and detailed land classes, we believe diving deeper into the tools made available to scientists can further our understanding of animal behaviour. For example, a few studies on muskox have shown that muskox select barren, high-altitude, sparsely vegetated areas (Danks and Klein 2002). Though this true, our study highlights how muskox will actually select the more vegetated, graminoid and lichen-covered of those barren habitats.

When it comes to herbivory studies, this study highlights the importance of interpreting changes to vegetation caused by herbivores with an eye on landscape changes. Herbivores may have quantifiable impacts on vegetation composition or biomass, but it is important to regard those data in relationship with the broader landscape and determine impacts at a landscape-level. In this study, muskox herbivory impacts were not quantifiable at within land cover classes.

Regarding concerns brought forward by communities of the region and in terms of management of reintroduced species, it will be important to monitor the muskox population in the Yukon North Slope and adjacent regions. Muskox densities are still low but may increase in the following decades as the population continues to establish itself and possibly extend its distribution. This study did not specifically target areas of high use by muskox focusing instead on a landscape approach to studying muskox herbivory. Of possible interest would be a more traditional exclosure-type study in areas of high use.

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Appendix

Table 2.4 Muskox winter and summer selection ratios in Ivvavik National Parks from 2015 to 2019. Highlighted in bold are the three land classes in which we sampled vegetation. Selection ratios greater than 1 indicate positive selection.

Land cover class	Land cover in Park %	Muskox Winter Selection Ratio	Muskox Summer Selection Ratio
Rock-Lichen	**17.5**	**1.8**	**0.8**
Hydric sedge fen	**2.4**	**1.9**	**2.0**
Riparian Herb-willow	**0.1**	**21.6**	**5.8**
Tussock	20.0	0.4	0.6
Shrub Sedge Tussock	10.0	0.5	1.1
Sparse Med Shrub	6.8	1.7	1.6
Shrub Sedge Fen	5.9	0.5	1.1
Dense Low Shrub	3.2	0.1	2.2
Other classes	34.2	0.7	1.2

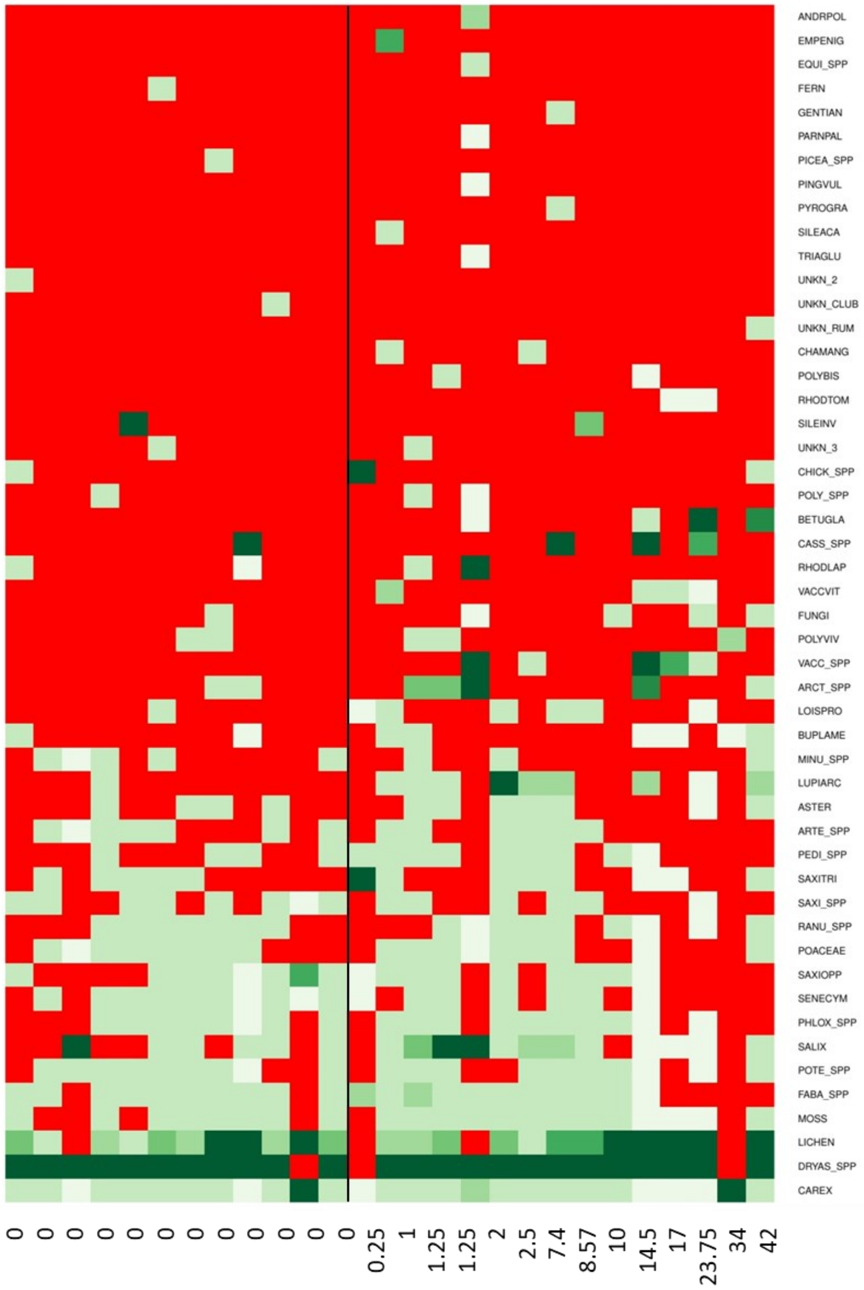

Figure 2.3. Site-species matrix showing vegetation species (or groups) vertically and average number of muskox fecal piles per site in Rock-Lichen habitat. Red indicates absence of the species at the site, and the white-green scale represents the weight of a species at a particular site, with dark green indicating the species represent a high proportion of the total biomass at any given site. The black line delineates sites with recorded muskox presence and no recorded presence.

Figure 2.4. Site-species matrix showing vegetation species (or groups) vertically and average number of muskox fecal piles per site in Riparian Herb Willow habitat. Red indicates absence of the species at the site, and the white-green scale represents the weight of a species at a particular site, with dark green indicating the species represent a high proportion of the total biomass at any given site. The black line delineates sites with recorded muskox presence and no recorded presence.

Figure 2.5. Site-species matrix showing vegetation species (or groups) vertically and average number of muskox fecal piles per site in Hydric Sedge habitat. Red indicates absence of the species at the site, and the white-green scale represents the weight of a species at a particular site, with dark green indicating the species represent a high proportion of the total biomass at any given site. The black line delineates sites with recorded muskox presence and no recorded presence.

General Discussion

This thesis characterizes muskox habitat use and muskox-caribou interactions. In Chapter 1, I analyzed spatial and habitat overlap between muskox and caribou through resource selection functions and encounter rates. In Chapter 2, I analyzed muskox fine-scale habitat associations, describing and determining whether these fine-scale associations were the result of selection or muskox grazing impacts.

Habitat and Spatial Overlap

In the Yukon North Slope and Richardson mountains, muskox and caribou ranges overlap in the spring and summer, with 0.81 % of collared caribou encountering a muskox during that time. These results are the first estimates of encounters between muskox and caribou across the Arctic, and a rare example of a study calculating interspecific encounter rates using GPS collars. Our results highlight that though overlap of ranges is considerable, only a minimal proportion of caribou encounter muskox at a fine-scale, but that for caribou encountering muskox, the number of contact hours is significant, with an average of 5.2 hours.

Our results point to muskox-caribou habitat partitioning in the Yukon North Slope. In both spring and summer, habitat types that were highly selected by one species were not highly selected by the other. This was noticeable in dominant land cover types such as ‘Tussock’ and ‘Tundra’, which are highly selected by caribou in the summer, but not highly selected by muskox during that same period, but also in less dominant land classes, such as ‘Beach’. These results are consistent with other work on niche partitioning in muskox and caribou, such as Schaefer and Messier (1996) who found muskox to be associated with lowland habitat and caribou with upland habitat use, and Biddlecomb (1992), who found that muskox and caribou used moist sedge tundra types, but their dietary and spatial overlap was overall minimal. This study was the first comparing muskox and caribou habitat selection in the Yukon North Slope.

Assessing competition between species is never an easy task. Indirect and observational research measures such as spatial and habitat overlap cannot demonstrate with certainty that competition is occurring in the species studied (Holt 1987, de Boer and Prins 1990). Nonetheless, measuring niche overlap is used in many studies to characterize species interactions (Cody 1974, Pianka 1975, Darmon et al. 2012, Jung et al. 2015b), as it does give associations and points to the possibility of competition. An experimental approach would be necessary to arrive to firm conclusions on competition. However, we hope that our study will give wildlife managers and Aklavik community members information they need to discuss interactions between muskox and caribou.

Herbivory and Fine-Scale Selection

Within land cover classes, we found mostly positive associations between muskox presence and vegetation. There were no negative associations between muskox presence and willow presence, as well as no negative associations between muskox presence and vegetation biomass in Rock-Lichen habitat. This is the first study to characterize muskox-vegetation associations at a fine-scale in the Yukon North Slope. The results point to minimal muskox impacts on vegetation, though they do not exclude muskox having more localized impacts. This is consistent with other muskox herbivory studies, such as Zackenberg, Greenland, where muskox grazing had small effects on vegetation biomass, removing 0.17% and 0.04% of biomass at high muskox densities (Mosbacher et al. 2016).

Our study was conducted by comparing vegetation found within three distinct habitat types ('Rock-Lichen', 'Riparian Herb Willow', and 'Hydric Sedge') in sites that were on a continuum of heavy use by muskox to no muskox use. Assessing associations between muskox with the vegetation found within the land classes was complicated by the inherent variation in vegetation within habitat types. This variation is not caused by muskox, and can be the result of varying soil conditions, other sources of herbivory, light and wind exposure, and randomness in seed deposition. As such, it can be difficult to ascribe the associations found between muskox and vegetation are the result of herbivory on the part of muskox (e.g., we find less willow where there are muskox because muskox remove willows through grazing) or selection (e.g. we find less lichen where there are muskox because lichen is not a preferential element in their diet). To make the process clearer, we developed an a-priori set of hypotheses that described the vegetation characteristics we would expect to attribute to herbivory and the characteristics we could expect to result from selection. We believe this method led us to make correct inferences on muskox-vegetation associations, but the lack of an experimental approach does limit the strength of our conclusions.

Future Directions

This thesis gives us a better understanding of the reintroduced muskox's role in the Yukon North Slope and Richardson Mountains by characterizing interactions with caribou and muskox-vegetation associations. It also opens the door to other research projects. Some community members and hunters in Aklavik have stated that caribou may be avoiding areas occupied by muskox. To further explore this scenario, an analysis of caribou movement patterns in relationship to muskox occurrence would be particularly interesting. An analysis of dietary overlap between muskox and caribou through fecal pellets would allow us to determine if these species eat the same plants and would further allow us to characterize their niche overlap. When it comes to muskox-vegetation fine-scale associations, an experimental design that uses exclosures would allow for finer characterization of muskox herbivory impacts. Also of importance will be the monitoring of the muskox population size as the decades since their reintroduction go by and muskox further implant themselves into their reintroduced range.

Conclusion

The objective of this thesis was to characterize muskox habitat use and muskox-caribou interactions as was proposed in the *Muskox Research Plan* developed by the Wildlife Management Advisory Council North Slope. This objective was achieved by analysis of spatial and habitat overlap between muskox and caribou through resource selection functions and encounter rates, and an analysis of muskox fine-scale habitat associations, which included describing and determining whether the fine-scale associations were the result of selection or muskox grazing impacts.

We found that range overlap between muskox and caribou was at its highest in the spring and summer months, but less than 1% of collared caribou encountered a muskox during that period. Habitat overlap was minimized through differential selection of elevation, distance to water, and an abundant tussock land cover class. Positive associations were found between muskox use and lichen, willow, and graminoids within land cover classes. These findings imply low potential for competition between muskox and caribou, and that the relationship between muskox use and vegetation is mostly driven by selection rather than by herbivory.

We hope this data will open the door to further discussions about the role and the impact of reintroduced muskox in the Yukon North Slope and Richardson Mountains.

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