EFFECTS OF ABUNDANT SNOW AND ROSS'S GEESE ON ARCTIC ECOSYSTEM STRUCTURE: PLANTS, BIRDS, AND RODENTS

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By

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ABSTRACT

Migratory animals link and often have profound impacts on geographically distant ecosystems through trophic interactions and transport of nutrients, energy, toxins, parasites and pathogens. Moreover, when seasonally linked ecosystems differ in carrying capacity of migrant species, detrimental effects to biodiversity through trophic cascades can occur in ecosystems with lower carrying capacity. Access to agricultural production has increased carrying capacity of lesser snow (*Anser caerulescens caerulescens*) and Ross's geese (*Anser rossii*, collectively, 'light geese') in southern agricultural landscapes where these species winter and stage during migration to and from northern breeding regions. Rapid population growth in response to increased carrying capacity during fall, winter, and spring has caused trophic cascades in less productive subarctic and arctic ecosystems during summer. I investigated changes to plant community structure in direct response to foraging and nesting by abundant and highly concentrated light geese within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut, Canada, with particular reference to Karrak Lake, one of the largest nesting goose colonies in the world. I further studied indirect impacts of vegetation change on aspects of sympatric vertebrate response, including resident brown lemmings and ptarmigan, and migratory shorebirds and passerines.

Foraging by light geese created spatially heterogeneous landscapes composed of lightly and intensely foraged grazing lawns in the brood-rearing and molting region north of Karrak Lake, within the pre-existing mosaic created by variation in topography, moisture, and soil properties created by geomorphic processes. Although foraging light geese nearly depleted aboveground plant biomass in some areas in the Sanctuary, belowground biomass was largely intact and thus, plant communities have strong potential for aboveground regeneration. Nesting and foraging geese severely reduced aboveground plant biomass within the nesting colony at Karrak Lake. Colonizing plant species established on bare sediment or peat exposed by previous vegetation removal by geese, resulting in shifts in species composition of plant communities. High occupancy by nesting light geese resulted in transition of lowland communities dominated by grasses and sedges (collectively, 'graminoids'), *Sphagnum* spp., and willows (*Salix* spp.) to those comprised of exposed peat, birch (*Betula glandulosa*), non-*Sphagnum* mosses, marsh ragwort (*Tephroseris palustris*), and mare's tail (*Hippuris vulgaris*). Community changes were less apparent in upland regions that are naturally less vegetated even in the absence of geese, but fruticose lichens, crowberry *(Empetrum nigrum)* and white heather *(Cassiope tetragona)* dominated undisturbed plant communities whereas crustose lichens and bearberry (*Arctostaphylos* spp.) comprised disturbed communities.

Reduction of plant biomass and community shifts from graminoid dominance to those with high proportions of exposed peat and birch had negative effects on abundance of brown lemmings and occupancy by graminoid-specialist shorebirds; however, some open-nesting and generalist cover-nesting avian species showed neutral or positive responses to establishment of birch in altered habitats. Intact graminoid communities are important to ecosystem structure and function and population health of many resident and migratory arctic vertebrates. However, light geese often nest in localized, dense aggregations, and thus negative impacts on sympatric species may be spatially limited and confined to large nesting colonies and severely altered brood-rearing and molting regions. Moreover, altered upland and lowland habitats remained largely vegetated in the Sanctuary, contrasting sharply with altered coastal marshes in subarctic regions.

ACKNOWLEGEMENTS

In June 2015 on a helicopter flight from Cambridge Bay to Karrak Lake, I had nearly dissuaded myself from pursuing PhD research. Upon my arrival, Jim Leafloor greeted me with “let’s talk about your PhD”, and continued with statements such as “we need to support good people”. Evidently Jim viewed me in such company, as he assured me “that graduate work would not be an issue [for me]” (there were some issues), and to “let him know what I need”. Like Ray, Jim is hard to disappoint, and armed with his confidence and that of others, I sought approval from our management team to pursue graduate work concurrently with employment responsibilities. Thus, I am indebted to the support and encouragement of Kevin Cash, Roxanne Comeau, Elsie Krebs, Janine Murray, and Patrice Simon, and many others within the Wildlife Research Division of Environment and Climate Change Canada, and at the Prairie and Northern Wildlife Research Centre.

I owe most of my professional success from long association with, and encouragement and mentorship by Ray Alisauskas. Ray is a coauthor on all my publications to date, except one. Under his guidance as a graduate student and technician, I have learned analytical techniques and improved writing skills, as well as gained decades of practical and leadership experience with co-management of a remote research site. The greatest encouragement to pursue a PhD came from Ray, who simply repeated on a number of occasions “you’re going to do it [write the papers] anyway”. Like many of his former students, Ray, Penny, and their family have become my extended family. My earliest memories of the Alisauskas clan include their youngest child Andrea, a toddler in the mid-1990s, hanging off the underside of Drake, a black Labrador retriever. More recently, Ray and Penny are blessed grandparents, marking the passage of time. I am thankful to have been watched over by them all of these years.

I thank Erica Nol for agreeing to serve as my external examiner. An engaged advisory committee comprised of Douglas Clark, Jill Johnstone, Philip McLoughlin, and Christy Morrissey has guided me; I thank them for their insights, questions, and suggestions, and look forward to an equally engaging final defense. I certainly wish this could occur in person, and I look forward to the future meeting of Erica beyond the confines of our computers.

Research presented in this dissertation drew from data collected in all years that the Karrak Lake Research Station (established 1991) has been in existence, and historical data from

John Ryder, Bob McLandress, Richard Kerbes, and others. Arctic Goose Joint Venture, Central and Mississippi Flyway Councils, Environment and Climate Change Canada, Natural Sciences and Engineering Research Council of Canada, Polar Continental Shelf Project, and University of Saskatchewan have most recently supported Alisauskas-led research within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary. Historical supporting agencies have included California Waterfowl Association, Delta Waterfowl Foundation, Institute for Wetlands and Waterfowl Research, Sea Duck Joint Venture, Northern Ecosystems Initiative, Northern Scientific Training Program, and Nunavut Wildlife Management Board. The majority of this extensive data collection from 1991-present occurred at Karrak Lake, with efforts provided by over 200 field assistants to date (Appendix A). In the early days, I am thankful for the training and guidance of Stuart Slattery, Garry Gentle, and Edith MacHattie. In later years, the list is too long to pen for fear of missing someone (see Appendix A), but a special nod to those that toiled on the lemming project (minimal fun), guided by leadership of Brian Malloure and Nick Sanchez. I have been privileged to interact with nearly all those folks listed in Appendix A, and many have become long-term friends and collaborators, as have others in the arctic goose clan, with Cody Deane, Chris Nicolai, and many others among the latter.

Kiel Drake continues to be a close friend and ally, and a supportive, flexible, and collaborative partner in parenting. Our children Reese and Brie are now ages 16 and 13, and some might question the decision to pursue such an undertaking while parenting two teenage girls (yet Kiel completed his PhD while parenting a toddler). Yet, their strong sense of self, awareness of others, and independence created no additional burden, and they are among my favourite adventure and travel partners. The acroyoga community in Saskatoon (and beyond) provided a reprieve from the ~seriousness of science and an opportunity for playful creativity and expression in movement. I appreciate all those with which I have been privileged to play, explore, teach, train, (snowshoe, paddle), and perform, with notable mention to individual partnerships in Sarah Hunter, Philippe Lepage, and Jeremy Dahlgrin, as well to Scott O'Byrne for all he does for our local community. Jeremy has been an enthusiastic partner throughout the entirety of this research; I didn't always want to ski in the dark at -20ºC or close down Grip It, Freedom, or Taiso on a weeknight, but at the end of each outing I was (almost always) glad we did.

Much has and will continue to be written about the psychological impacts of COVID-19 on human societies. Gatherings of the Maple Street Gang and evening meals with LeeAnn Latremouille, Kiel, and the girls on a daily basis during the past year provided comfort and perspective in an era of societal uncertainty and strangeness. COVID came with loss and change for most, and I am extremely grateful for my employment and financial and personal stability, as well as for uninterrupted time to complete this dissertation. Yet, I cherish memories of currently-absent experiences – conference hospitality rooms (particularly at NAAG), the companionship and debauchery of remote field camps (to include Nasaruvaalik Island – thanks Mark Mallory for a different perspective on arctic ecology), and partnered acrobatics in a swirling, mingling menagerie filled with laughter.

My parents Jim and Janie Kellett remain ever supportive and celebratory, and often provided more accolades than are deserved. Uncle Norman, who served as my earliest notion of the duties of a scientist, signed his dissertation (Gentner 1967) to his parents with “this is as much yours as mine”, a statement that also applies to Jim and Janie. I do wish you had been able to explore an arctic landscape, Dad. Know that Karrak Lake resembles your childhood tent camps along the Petaigan River: celebration of, immersion in, and communion with natural spaces, curious exploration of ecosystems, companionship with like-minded people, and a humble reminder of one’s place in the Universe.

Finally, and importantly: this research occurred on Inuit Nunangat. Wandering this landscape scattered with tent rings and other signs of humanity brings with it admiration for a resilient and resourceful people.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Herbivore-plant relationships

Trophic relationships among species is a central tenet of ecology. Under this paradigm, plants are consumed by herbivores, which in turn are consumed by predators (Hobbs 1996). However, herbivores regulate and change plant communities through complexities of both direct and indirect processes, thereby modulating entire ecosystems. Herbivore-mediated mechanisms of alteration of nutrient cycles, influences on net primary production, and modification of fire regimes act at various spatiotemporal scales to modulate plant community structure and succession, transition between alternative states, and creation and maintenance of spatial heterogeneity (McNaughton 1976, 1979, 1983, 1984; Cargill and Jefferies 1984b, Hik and Jefferies 1990, Hobbs 1996, Jeltsch et al. 1997, Person et al. 1998, 2003; Slattery 2000, Fuller 2001, Handa et al. 2002, McLaren and Jefferies 2004, Olofsson et al. 2004a, van der Graaf et al. 2005, O et al. 2006, van der Wal 2006, Johnson et al. 2011, Martin et al. 2011, Beard et al. 2019, Uher-Koch et al. 2019).

The resultant pattern of plant community structure (i.e., quantity of biomass and plant architecture) and species composition in response to herbivores depends on many factors, including intensity of herbivory, selectivity among plant species and patches, and historical (e.g., soil development, plant-herbivore coevolution) and proximate contexts (e.g., climate, moisture availability; Huntly 1991, Hobbs 1996). In ecosystems with environmental conditions supportive of plant growth (e.g., adequate moisture) and history of plant-herbivore coevolution, optimal levels of grazing (McNaughton 1979) often results in a vegetation community of low-growing, highly productive species with elevated nutrient content: a ‘grazing lawn’ (McNaughton 1976, 1979, 1984; Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; Slattery 2000, van der Graaf et al. 2005, O et al. 2006, Johnson et al. 2011, Beard et al. 2019, Uher-Koch et al. 2019). The degree to which plants can exhibit compensatory growth following defoliation depends on nutrient and water availability, but also on evolutionary history (‘opportunity’ and ‘capacity’, respectively, sensu Hobbs 1996); for grazing lawn species, rapid regrowth is an alternative to investment in metabolically expensive chemical deterrents (McNaughton 1979, 1984, 1986; Cargill and Jefferies 1984b; Hik and Jefferies 1990, Hobbs 1996). As well, herbivores accelerate nutrient recycling (*i*) indirectly through modification of quantity and quality of plant litter available for decomposition, and (*ii*) directly by nutrient inputs through excretions; herbivore excreta provides an accelerated alternative to litter decomposition as a pathway for nitrogen turnover and provides plants with nutrients in an accessible form (Hobbs 1996, Augustine and McNaughton 1998). Yet, complex soil-microbial interactions govern processes of litter decomposition and availability of nutrients to plants (Hobbs 1996), and typically plant species with an evolutionary history of grazing show enhanced responses to fecal and urine nutrient inputs (Cargill and Jefferies 1984a, Bazely and Jefferies 1986, Hik and Jefferies 1990, Ruess et al. 1997).

Thus, coevolved plant-herbivore systems such as grazing lawns depend on nitrogen cycling by herbivores, consisting of plant species adapted to grazing through compensatory growth. In fact, grazing in these systems often elevates nutrient content and productivity of vegetation above that of ungrazed landscapes (references given above). Thus, grazing herbivores are able to elevate their own carrying capacity of ecosystems that they inhabit (e.g., van der Graaf et al. 2005).

1.2 Agricultural subsidy of herbivore nutrition

Humans have long exploited the response of primary productivity to nutrient addition (reviewed by Gruner et al. 2008) to improve food production. Early agricultural civilizations increased plant production through application of vegetative composts and livestock manures, both rich in nitrogen and other elements, as well as cultivation of legumes with nitrogen-fixing bacteria (Wilkinson 1982, Hager 2008). The development of the Haber–Bosch process early in the twentieth century enabled the production of ammonia from atmospheric nitrogen, and released human reliance on naturally-occurring nitrogen sources (Hager 2008). Application of inorganic fertilizers, recently estimated at 140 kg per hectare of arable land, facilitates the annual production of nearly three billion metric tons of cereal crops alone (World Bank 2016). As well, development of higher-yielding crop strains, use of agrichemicals for weed and pest control, irrigation, and increase in extent of cultivated land have contributed to substantial increase in global food production (Tilman 1999). To feed a burgeoning human population, more than a third of global ice-free land is now devoted to agriculture (World Bank 2016) and has facilitated a rise in global human population to over 7.8 billion individuals (United Nations 2019). However, intensified agriculture, defined as ‘making as great a proportion of primary production as possible available for human consumption' (Krebs et al. 1999), often has negative consequences for natural ecosystems.

Agriculture is the largest contributor to declining global biodiversity, driven by loss of habitat by conversion of forested and grassland ecosystems to farms and pastures, lethal and sublethal effects of agrochemicals, and release of pollutants (Dudley and Alexander 2017). Production of cereal crops of rice, maize, and wheat – historically-rare grasses that now occupy 40% of global cropland (Tilman 1999, Chaudhary et al. 2016) – contribute disproportionately to declining global biodiversity in regions with many endemic species (Chaudhary et al. 2016). In less-biodiverse regions such as temperate northern latitudes, cultivation of cereal crops, even at large geographic scales, has resulted in fewer species extinctions (Chaudhary et al. 2016). Regardless, intensification of agriculture in temperate regions has resulted in declining population trajectories and reduced geographic ranges of many species associated with such landscapes (Sampson and Knopf 1994, Chamberlain et al. 2001, Donald et al. 2001, Benton et al. 2003, Mineau and Whiteside 2013, Fox and Abraham 2017, Stanton et al. 2018, Rosenberg et al. 2019), contributing to global defaunation (Urban et al. 2015) with effects on ecosystem structure and function (Rosenberg et al. 2019).

Negative anthropogenic effects on Earth's climate and biota are not to be understated; in fact, humans are the main driver of global change (Oro et al. 2013, Dirzo et al. 2014). Agriculture has had enduring and unprecedented effects on species distributions and abundances since the appearance of agricultural societies in the Holocene, long before its intensification (Boivin et al. 2016). From the standpoint of individual species, however, not all impacts are negative. Although a major driver of biodiversity loss, agriculture has concurrently facilitated range expansion and increase in abundance of some vertebrates, invertebrates, plants, and pathogens (Stenseth et al. 2003, Côté et al. 2004, Oro et al. 2013, Dawe et al. 2014, Boivin et al. 2016, Fox et al. 2017), along with domesticated plants and livestock (Diamond 2002, Boivin et al. 2016). Species that benefit from agriculture often include those that favor open or early-successional landscapes (for example, white-tailed deer (Côté et al. 2004)), herbivores that consume agricultural products (e.g., rodents (Stenseth et al. 2003)), or predators that prey on such species (e.g., bats (Cleveland et al. 2006)). In particular, monoculture crops and managed grasslands such as pastures provide herbivores with highly abundant and concentrated food that is often more nutritious and more easily accessible than naturally-available forage (Alisauskas

1998, Oro et al. 2013, Fox and Abraham 2017). Species exhibiting positive numerical responses to such abundant and reliable food sources have thus been deemed as pests by ancient and contemporary agriculturalists (Panagiotakopulu 2001, Stenseth et al. 2003, Gordon 2009, Oro et al. 2013, Linz et al. 2015, Fox and Madsen 2017). Despite unprecedented net loss of avifauna in North America, many waterfowl species and populations have increased, owing in part to successful harvest management and wetland conservation and restoration (Rosenberg et al. 2019). Moreover, many waterfowl species, and geese in particular, benefit from nutritious and abundant agricultural crops and pasturelands, and are often designated as contemporary agricultural 'pests' throughout the Holarctic, drawing the interest, involvement, and occasionally the ire of a diversity of human interest groups (Buij et al. 2017, Fox and Madsen 2017, Fox and Leafloor 2018).

1.3 Agriculture's role in population increase of Holarctic geese

Thirty extant species of geese in nine genera are recognized globally, and 16 species of the genera *Anser* and *Branta* inhabit Holarctic regions (Winkler et al. 2020). Owing to overexploitation and habitat loss, many Holarctic geese persisted at low abundance, with some populations on the verge of extirpation as recently as the early part of the last century (Abraham and Jefferies 1997, Fox and Madsen 2017). Conservation efforts including implementation of harvest regulations and establishment of wetland refuges facilitated population increases throughout the twentieth century, but the expansion of agriculture has been particularly responsible for unprecedented increases of many Holarctic goose populations (Abraham and Jefferies 1997, Abraham et al. 2005a, Abraham et al. 2012, Fox and Madsen 2017).

Prior to widespread intensified agriculture, many Holarctic geese wintered in coastal and inland wetlands. Morphological adaptations for efficient foraging of wetland vegetation, ranging from grazing of short grass swards to excavation of roots and tubers, were also suited to exploitation of a variety of agricultural crops, including spilled and uncollected grain, newly emerged growth, tuberous crops, and managed grasslands such as pastures and parks (Alisauskas et al. 1988, Alisauskas and Ankney 1992, Abraham and Jefferies 1997, Abraham et al. 2005a, Abraham et al. 2012, Buij et al. 2017). Northward shifts of wintering distributions and stopovers in agricultural landscapes created shortened migration distances and a stepping-stone for migratory movement to and from breeding regions, allowing for energy savings associated with migration (Abraham et al. 2012, Fox and Abraham 2017). As well, high quality and easily accessible agricultural foods meant that birds arrived at breeding areas in better condition than historically, with larger endogenous reserves that supported investments in reproduction, in addition to fueling migration (Prop et al. 1998, Fox et al. 2005, Abraham et al. 2012, Fox and Abraham 2017). Prior to widespread agriculture, young geese that fledged in arctic and subarctic regions were required to achieve sufficient condition to successfully endure long migrations to coastal wintering areas, but migratory stopovers within agricultural landscapes allowed for enhanced survival of juvenile, as well as adult birds. As a result, populations foraging in agricultural landscapes demonstrated enhanced fitness and survival and subsequent increases in population abundance disproportionate to those species that did not exploit such opportunities (Batt et al. 1997, Kelly et al. 2001, Abraham et al. 2005a, Fox et al. 2005, Madsen et al. 2014, Fox and Abraham 2017, Fox and Madsen 2017, Lefebvre et al. 2017).

Most Holarctic geese that currently show population declines are those wintering on natural wetlands under the threat of habitat loss, mainly in central and eastern Asia, whereas populations exploiting anthropogenic agricultural subsidies in North America and Europe are generally considered to be stable or increasing (Fox et al. 2005, Fox and Madsen 2017, Fox and Leafloor 2018, Doyle et al. 2020). Of these, the most successful at achieving high population abundance, and currently the only Holarctic goose population exceeding ten million adults, is the North American midcontinent population of lesser snow geese (*Anser caerulescens caerulescens*, Fox and Leafloor 2018).

1.4 Light geese: a success story

Snow geese (*Anser caerulescens*) encompasses two subspecies: lesser and greater (*A. c. atlantica*). Morphologically similar and closely related genetically to Ross's geese (*Anser rossii*, Avise et al. 1992), these two subspecies together with Ross's geese are collectively referred to as 'light geese' (Leafloor et al. 2012, Calvert 2015; but see Fox and Leafloor (2018): 'white geese' consist of six populations of snow, Ross's and emperor geese (*A. canagicus*)). North American in distribution, light geese share the genus *Anser* with nine other species distributed throughout the Nearctic and Palearctic.

Lesser and greater snow geese and Ross's geese, like many Holarctic geese, have expanded and shifted winter ranges and altered migratory behavior in response to nutritional subsidies provided by widespread and intensified agriculture. Historical and current distributions are described below, summarized from Lefebvre et al. (2017), Fink et al. (2020), Jónsson et al. (2020), Mowbray et al. (2020), and references therein.

Lesser snow geese historically wintered in natural wetlands in coastal regions along the Gulf of Mexico. Increased reliance on agricultural foods and landscapes resulted in initial expansion of winter ranges to include irrigated rice fields of Texas and Louisiana, and later further inland to other agricultural production regions substantially north of former winter ranges, presently to about 40ºN. Lesser snow geese occupy the three western flyways in North America – Pacific, Central, and Mississippi – and western and midcontinent birds comprise distinct populations. The western population in the Pacific Flyway winters in coastal and inland regions along the Pacific Coast, from southern British Columbia to Mexico, and breeds on Alaska's Arctic Coastal Plain eastward to Canada's MacKenzie and Anderson River Deltas, as well as on Banks and Wrangel Islands (Wrangel Island is considered a separate population by Fox and Leafloor 2018). The midcontinent population of lesser snow geese occupying the Central and Mississippi Flyways now winter in the highlands of Mexico, along the Gulf Coast and Mississippi River Valley, and in mid-latitude states of these flyways. Midcontinent lesser snow geese breed throughout the central and eastern subarctic and arctic regions of Canada, primarily along the south and west coasts of Hudson Bay, James Bay, Baffin and Southampton Islands, eastern Victoria Island, and on mainland regions south of Queen Maud Gulf (Ahiak).

Greater snow geese occupy the Atlantic Flyway, wintering along the Atlantic coast from Massachusetts to South Carolina. Increased exploitation of agricultural foods resulted in short-stopping along migration routes and a northward shift in winter distribution, and increased staging in Quebec's agricultural landscapes, away from historical staging areas in the marshes of the St. Lawrence River. Greater snow geese breed in the northern and eastern Canadian Arctic Archipelago, and northwest Greenland.

Historically confined to California, the majority of the winter population of Ross's geese occurred in the Sacramento and San Joaquin Valleys. Presently, in addition to California's central valleys, Ross's geese winter throughout the highlands of Mexico, along the Gulf Coast and Mississippi River Valley, and in mid-latitude states of the Central and Mississippi Flyways as far north as about 40ºN. Migrating throughout the Pacific, Central, and Mississippi Flyways but considered as one continental population, Ross's geese often occur sympatrically with lesser snow geese on wintering and staging areas, and along migration corridors. As the last of the light goose species for which breeding areas were discovered, nearly all Ross's geese historically nested in the region south of Queen Maud Gulf in the central Canadian arctic, now designated as the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (established in 1961 (Kerbes 1994)). Presently, a large portion of Ross's geese continue to breed in the Sanctuary, but the species also nests along the west and south coasts of Hudson Bay, on Southampton and Baffin Islands, and less commonly along the mainland coast of the western arctic and Banks Island.

Light goose populations in North America have exhibited increasing population trajectories in recent decades, largely in response to widespread availability of agricultural food subsidies. The greater snow goose population, estimated at 3000 individuals in the early 1900s, has stabilized at about 876,000 individuals (Lefebrve et al. 2017, Fox and Leafloor 2018). North American Ross's geese, considered to be rare in the early 1900s (Bent 1925), have also demonstrated an increasing trajectory, with population size most recently estimated at about 2.3 million birds (Fox and Leafloor 2018). The western population of lesser snow geese (including Wrangel Island), most recently estimated at 1.1 million adult individuals, numbers substantially fewer than the midcontinent lesser snow goose population, at over 12 million adults (Fox and Leafloor 2018). Moreover, long-term population trajectories of midcontinent lesser snow geese and sympatric Ross's geese are among the highest of Holarctic geese, at increases of 6.3% and 11.7% per annum, respectively (Fox and Leafloor 2018). High population abundances and rapidly increasing trajectories have caused concern for integrity of northern ecosystems inhabited by light geese, and particularly those affected by midcontinent lesser snow geese (hereafter, snow geese) and continental Ross's geese. Hereafter, I refer to these two populations collectively as 'midcontinent light geese' (Leafloor et al. 2012).

1.5 Concern for the integrity of northern ecosystems

Exploitation of agricultural landscapes by light geese during winter and migration has not eliminated their need to feed in arctic and subarctic wetlands during pre-breeding staging and nesting (Abraham et al. 2005a). Despite evidence for increased primary productivity resulting from global climate change (Madsen et al. 2011; Gauthier et al. 2013, Campbell et al. 2020), productivity of northern wetlands dominated by grasses and sedges, primary foraging habitats of light geese (Slattery and Alisauskas 2007), has not kept pace with directly anthropogenic-driven increases in southern agricultural landscapes. In fact, subarctic and arctic ecosystems exhibit low primary productivity due to nutrient limitations and short growing seasons (Porsild 1964, Shaver et al. 1997), and are sensitive to intense grazing beyond moderate levels required for effective maintenance of grazing lawns. Moreover, foraging methods used by light geese in northern regions are not limited to grazing. As occurs in southern coastal marshes and agricultural lands during winter and migration (Alisauskas et al. 1988, Alisauskas and Ankney 1992), geese exploit belowground and basal portions of vegetation through shoot-pulling and grubbing in early spring prior to annual regeneration of aboveground growth (Abraham et al. 2005b, 2012). Further, geese uproot forage and non-forage species for incorporation into nests (McCracken et al. 1997, Alisauskas et al. 2006, Abraham et al. 2012). Removal of vegetation through grazing, grubbing, shoot-pulling, and nest construction by large numbers of snow and Ross's geese can alter northern plant communities. Migratory animals such as light geese connect seasonal habitats in widely separated ecosystems (Webster et al. 2002), although there may be vast differences in carrying capacity in such different ecosystems. Thus, the high energy and nutrient density of foods provided by anthropogenic subsidies of geographically-vast southern agricultural landscapes may exceed that available in less resilient and spatially smaller northern ecosystems. Anthropogenic agricultural inputs may continually support large numbers of light geese during migration and winter, but such high abundance likely exceeds the carrying capacity of arctic and subarctic ecosystems. If so, plant communities may not withstand foraging and nesting pressure by these hyperabundant herbivores, leading to shifts in plant community structure, with knock-on effects to sympatric resident and migrant species cohabiting these ecosystems.

Although alteration of vegetation communities was reported as early as the late 1960s on the McConnell River Delta (Lieff 1973, in Kerbes et al. 2014), it was decades later that earliest authors sounded concern for potential integrity of northern ecosystems (Ankney 1996, Batt et al. 1997), citing evidence for severe and widespread alteration of plant communities in subarctic regions along the southern and western coasts of Hudson Bay and James Bay. Nesting and transient light geese, the latter enroute to more northerly arctic breeding areas, have effectively altered subarctic coastal salt and freshwater ecosystems, resulting in removal of vegetation, erosion, hypersalinity, loss of the soil seed bank, desertification, and creation of an alternate stable state of bare sediment (Kerbes et al. 1990, Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996, Abraham and Jefferies 1997, Kotanen and Jefferies 1997, Chang et al. 2001, Handa et al. 2002, Jefferies and Rockwell 2002, Walker et al. 2003, McLaren and Jefferies 2004, Abraham et al. 2005a, b; O et al. 2005, Jefferies et al. 2006, Abraham et al. 2012, Peterson et al. 2013). These observations, together with high population abundance and increasing trajectories of midcontinent light geese, prompted their designation as 'overabundant' under the Migratory Birds Regulations for snow and Ross's geese in 1999 and 2014, respectively (CWS 2013, 2014). Here, 'overabundant' was explicitly defined as when "the rate of population growth has resulted in, or will result in, a population whose abundance directly threatens the conservation of migratory birds (themselves or others) or their habitats, or is injurious to or threatens agricultural, environmental or other similar interests" (CWS 2013). Using harvest by hunters as a primary management tool, a goal of reducing abundance of light geese through liberalized harvest regulations was implemented through a Conservation Order amendment to the International Migratory Bird Treaty in 1999, allowing hunting of midcontinent geese throughout their range during the entire annual cycle in the United States and Canada.

However, these high populations were unresponsive to harvest and populations continued to grow (Alisauskas et al. 2011, Alisauskas et al. 2012a, Dufour et al. 2012, Johnson et al. 2012, Koons et al. 2014, 2019; Calvert et al. 2017). As such, interest in population status of Holarctic geese remains, and of midcontinent light geese in particular, and "perhaps most relevant in the present context, by nature of their recent abundance, geese have been proven to cause trophic cascades in delicate arctic ecosystems caused by the effects of their foraging. For this reason, geese have become ecosystem engineers in a fashion not always conducive to maintaining arctic biodiversity given the destructive nature of their localized impacts which have knock-on effects for the flora and fauna of sites affected" (Fox and Leafloor 2018). In fact, the Arctic Goose Joint Venture suggested that future research should include investigations of the extent of habitat alteration, potential for recovery, and impacts to other species in northern ecosystems (Leafloor et al. 2012).

Changes to plant communities and, to a lesser extent, impacts to other species in subarctic ecosystems have been well documented, particularly in brackish coastal wetlands used by light geese during spring migration. However, most midcontinent light geese breed in arctic regions (Alisauskas et al. 2011, Kerbes et al. 2014), where they rely on inland freshwater wetlands, such as south of Queen Maud Gulf (Slattery and Alisauskas 2007). Comparatively less is known about effects on terrestrial and freshwater arctic ecosystems that differ from coastal brackish marshes in subarctic regions in terms of climate, soil chemistry, and vegetation communities. Remote sensing and limited ground-based investigations revealed removal of vegetation, expanded areas of exposed peat, establishment of moss carpets, and increase in colonizing species (Alisauskas et al. 2006, Fontaine and Mallory 2011, Conkin and Alisauskas 2017, Flemming et al. 2019b), with even fewer investigations of knock-on effects to sympatric species such as birds (Flemming et al. 2019a, 2019b, 2019c) and rodents (Samelius and Alisauskas 2009). This paucity of information about impacts by high densities of midcontinent light geese on their main foraging habitats motivated the following research.

1.6 Dissertation structure and research objectives

In addition to this introductory chapter, I have organized this dissertation into four data chapters, a concluding synthesis, and two appendixes. I have structured the data chapters as independent manuscripts intended for eventual publication. To avoid redundancy, I have included a description of the study area in the final section of this chapter and omitted this information from the data chapters, and compiled all cited literature in a separate chapter.

The overarching objectives of this research were to investigate (*i*) potential changes to plant communities in response to high abundance of nesting and foraging light geese; specifically evaluating reduction in plant biomass (Chapter 2) and changes to community species composition (Chapter 3), and (*ii*) population responses of rodents (Chapter 4) and sympatrically-breeding birds (Chapter 5) to ornithogenic alteration of plant communities.

In Chapter 2, I used a replicated experimental design with herbivore exclosures to quantify reduction of aboveground and belowground plant biomass in treatment (enclosed) versus control (open to grazing) plots. My primary objective was to estimate reduction of plant biomass by foraging and nesting geese, and secondarily to investigate spatial heterogeneity in biomass removal. Although this work focused on changes to graminoid vegetation, the preferred forage of geese, I was also interested in reduction in non-forage vegetation.

Chapter 3 describes changes in species composition of plant communities in relation to intensity and duration of occupancy by nesting and foraging light geese. Although primarily focused on habitats varying in edaphic state (i.e., upland and lowland plant communities) within a large nesting colony, I also investigated changes to less-intensely occupied lowland communities within molting and brood-rearing regions.

In Chapters 4 and 5, I evaluated the effect of alteration of vegetation communities by light geese on arvicoline rodents and passerine and shorebird species. In Chapter 4, I estimated the effect of vegetation alteration on density of lemmings, and in Chapter 5, I estimated this effect on species-specific probability of occupancy on sympatrically-breeding birds. Independent of habitat alteration, I also evaluated the direct effect of light goose presence on occupancy of avian species.

1.7 Study area

1.7.1 Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary

I conducted this research in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (hereafter, QMGMBS, or the Sanctuary) located on the Arctic Coastal Plain of the mainland of Nunavut, Canada. The QMGMBS region is a generally flat plain of post-glacial emergence, stretching 300 km along the south coast of Queen Maud Gulf (Ahiak) and extending 135 km inland, covering over 62,900 km^2 of contiguous terrestrial (56,375 km^2) and marine (6,553 km^2) habitat (Fig. 1.1, ECCC 2020). Habitat important to many mammalian and avian species in the Sanctuary consists of meadows and marshes, streams and shallow lakes, and uplands containing boulder fields and rock outcrops (Didiuk and Ferguson 2005), ranging from low elevation to about 600 m above sea level (ECCC 2020). The QMGMBS is the largest Migratory Bird Sanctuary in Canada, the second largest designated Ramsar Site in the world, and identified by Inuit as a place of cultural significance with numerous archaeological features (ECCC 2020).

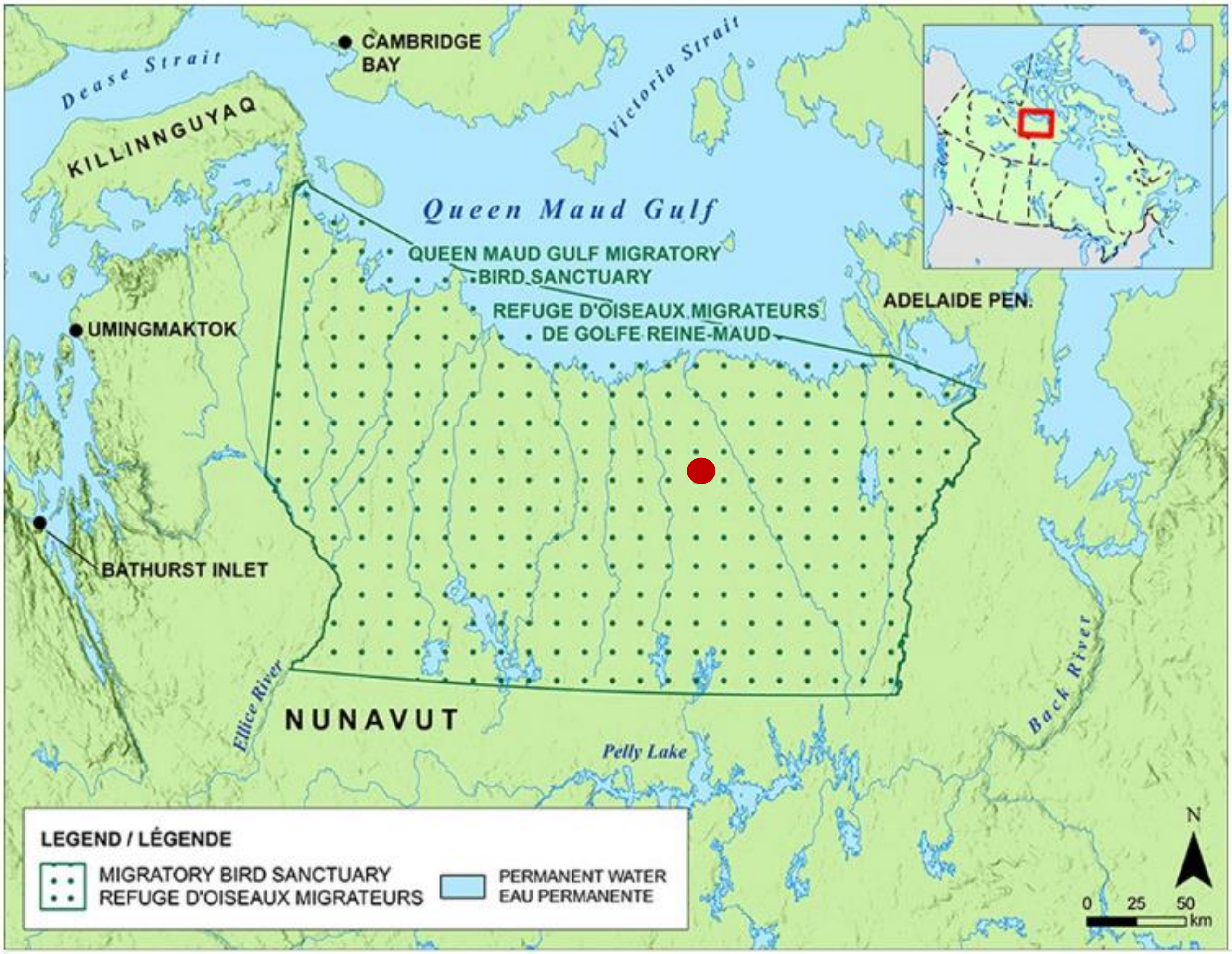

Figure 1.1. Map showing the location of the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut in relation to Cambridge Bay, Queen Maud Gulf (Ahiak) and nearby topological features. The map shows the boundaries of the Sanctuary, which includes a part of Queen Maud Gulf. The location of the Karrak Lake snow and Ross's goose nesting colony is indicated by the red circle. The inset map shows the location of the Sanctuary in Canada. Adapted from Environment and Climate Change Canada (2020) https://www.canada.ca/en/environment-climate-change/services/migratory-bird-sanctuaries/locations/queen-maud-gulf-ahiak.html; accessed 28 December 2020.

Established in 1961 primarily to protect the nesting grounds of what was at that time a reduced continental population of Ross's geese (Kerbes 1994), the Sanctuary is occupied by continental Ross's geese and midcontinent lesser snow geese that nest together in spatially discrete colonies. Nest densities within QMGMBS are typically higher than at other arctic breeding regions such as Baffin and Southampton Islands (Kerbes et al. 2014). At the time of the last aerial photographic survey (2006), light geese occupied 63 of 110 known locations of nesting colonies in the Sanctuary (Kerbes et al. 2014). Of these, one of the largest known colonies is located at Karrak Lake (Kerbes et al. 2014).

1.7.2 Karrak Lake nesting colony

The nesting colony at Karrak Lake (67° 14' N, 100° 15' W) is the second largest colony within the Sanctuary (Kerbes et al. 2014), and was first documented by John Ryder during aerial reconnaissance surveys in 1965 (Ryder 1969). Nesting studies of light geese, and of Ross's geese in particular, were conducted at Karrak Lake during 1966-1968 (Ryder 1970, 1971, 1972) and 1976 (McLandress 1983). Ray Alisauskas established the Karrak Lake Research Station in 1991 (Kellett and Alisauskas 2020) and ground-based demographic research of light geese has occurred annually since that time. As well, abundance of the nesting colony was estimated periodically by aerial photographic surveys in 1988, 1998, and 2006 (Kerbes 1994, Kerbes et al. 2006, 2014).

In the mid-1960s, light geese nested on about a third of the islands of Karrak Lake, with an estimated population size of 17,000 geese (Ryder 1969). By 1991, the nesting colony had expanded to mainland regions surrounding the lake. The nesting colony reached its maximum spatial extent (to date) in 2011, occupying over 270 km^2 of terrestrial habitat, and its maximum abundance in 2012, at nearly 1.3 million individuals (R. Alisauskas unpubl. data; see also Alisauskas et al. 2012b).

Light geese use all terrestrial habitat types for nesting, described in detail by Ryder (1972) and updated by Alisauskas et al. (2006), and these differ slightly from Landsat categorizations (see Conkin and Alisauskas 2017). Briefly, terrestrial habitats in QMGMBS are delineated primarily on edaphic state, ranging from low-lying saturated habitats heavily vegetated (at least historically) by grass and sedge species (collectively referred to as graminoids) to sparsely vegetated upland habitats dominated by lichens and a variety of vascular plants. Vegetation in all habitats is typically short, ranging from <1 cm to ~45 cm.

1.7.3 Molting and brood-rearing region north of Karrak Lake

Following hatching of eggs, adult geese disperse from Karrak Lake with their goslings in a dominantly northward direction (Slattery 1994, 2000; Slattery and Alisauskas 2007) to raise their young and undergo remigial molt. Breeding adults and their young, together with failed and nonbreeding individuals, occupy preferred habitats of riparian zones, wet sedge meadows, and hummock graminoid tundra (Slattery and Alisauskas 2007). In the mid-1990s, birds were uniformly distributed after hatch within this brood-rearing region, with some evidence of higher densities of geese near the coast of Queen Maud Gulf, 70 km north of Karrak Lake (Slattery 2000, Slattery and Alisauskas 2007). In recent years, however, most birds disperse to coastal areas to raise young and molt (R. Alisauskas unpubl. data).

CHAPTER 2: HETEROGENEITY OF VEGETATION BIOMASS RESULTING FROM FORAGING AND NESTING LIGHT GEESE

2.1 Introduction

Under optimal levels of grazing, herbivores can significantly reduce aboveground vegetative biomass, creating and maintaining “grazing lawns” of altered growth form characterized by short, prostrate, and dense vegetation of high nutritional content (McNaughton 1976, 1979, 1984; Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; Slattery 2000, van der Graaf et al. 2005, O et al. 2006, Johnson et al. 2011, Uher-Koch et al. 2019; see also Chapter 1). McNaughton (1976, 1979, 1984) conducted foundational research describing grazing lawns maintained by ungulates in tropical grassland ecosystems, and similar vegetation responses to grazing have been described in aquatic (Hart et al. 1985, Carpenter 1986, Carpenter et al. 1987, Power 1990) and other terrestrial ecosystems (references above).

Creation and maintenance of productive vegetation swards, which optimize herbivore foraging efficiency by increasing energy and nutrient intake by modifying productivity, quality and availability of forage plants, is often achieved by foraging by many individuals (McNaughton 1984, Person et al. 2003, Uher-Koch et al. 2019). In addition to reduced predation facilitated by group-living, creation and maintenance of grazing lawns may be a major force guiding natural selection leading to the evolution of gregarious behavior among herbivores (McNaughton 1984). Under optimal grazing pressure, geese that nest, molt, and rear young in large flocks in subarctic and arctic regions regularly create and maintain grazing lawns (Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; van der Graaf et al. 2005, O et al. 2006, Uher-Koch et al. 2019). Year after year, geese often consume much of the aboveground primary production available annually (Cargill and Jefferies 1984b, Gauthier et al. 1995, Person et al. 1998, Slattery 2000, Madsen et al. 2011), demonstrating the resilience of such plant communities that have coevolved with their consumers. However, extremely intense herbivory of aboveground vegetation due to high herbivore abundance can reduce belowground plant biomass (McNaughton 1979, Beaulieu et al. 1996), inhibiting plant production and survival, and thus, potential for regeneration.

Northern habitats occupied by geese, and by highly gregarious Ross’s (*Anser rossii*) and lesser snow geese (*Anser caerulescens caerulescens*, hereafter, snow geese, and collectively, light geese) in particular, are subjected to both grazing of aboveground plant biomass and exploitation of belowground biomass. In early spring before and during snowmelt prior to regeneration of aboveground primary production, birds consume belowground portions of graminoid vegetation (grass and sedge species) acquired through shoot-pulling and grubbing for roots and rhizomes (Abraham and Jefferies 1997, Kotanen and Jefferies 1997, Kerbes et al. 1990, Henry and Jefferies 2008, Jefferies and Rockwell 2002, Abraham et al. 2012). Both Ross's and snow geese can effectively grub for belowground vegetation (Mowbray et al. 2020, Jónsson et al. 2020), but the large robust bills of snow geese are particularly adapted for such excavation (Alisauskas 1998). In addition to foraging, geese uproot a diversity of plant species for nest construction (McCracken et al. 1997, Alisauskas et al. 2006). Nesting colonies can extend over large contiguous areas (e.g., maximum terrestrial area covered by the Karrak Lake colony was 277 km^2 in 2010, R. Alisauskas unpubl. data). Increasing density and abundance of light geese in arctic regions has amplified their ability to alter tundra plant communities on a landscape scale (Fontaine and Mallory 2011, Conkin and Alisauskas 2017, Abraham et al. 2020). Such alteration has raised concern for the ability of northern ecosystems to withstand cumulative impacts of long-term nesting and foraging by these herbivores (Ankney 1996, Batt et al. 1997, Jefferies et al. 2003), despite recognition that moderate to intense grazing may maintain ecosystems in an alternative stable state of grazing lawns (van der Wal 2006).

Exponential growth of light geese and decades-long history of nesting and intense herbivory has resulted in extensive effects on arctic plant communities over a wide area within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (hereafter, the Sanctuary). Analysis of 1988 Landsat imagery revealed the existence of 269 km^2 of exposed peat associated with light goose nesting colonies in the eastern region of the Sanctuary (Didiuk and Ferguson 2005). Exposed peat results from removal of overlying vascular plant cover, revealing underlying moss species (primarily *Sphagnum* spp.) that may then desiccate and erode. By 2011, the extent of exposed peat within this same region had increased to 1373 km^2 (a fivefold increase) and was prevalent in molting and brood-rearing areas, in addition to nesting colonies (Conkin and Alisauskas 2017). Sampling of aboveground vegetation in the mid-1990s revealed substantial removal of aboveground graminoid biomass north of Karrak Lake (Slattery 2000). Slattery (2000) estimated the loss of 50% of aboveground biomass from a 5000 km^2 region by this time, and described a biodeteriation zone radiating from the Karrak Lake colony due to cumulative annual grazing pressure. Alisauskas et al. (2006) inferred biomass loss through species composition data and detection of bare substrate, and hypothesized that cumulative effects of vegetation removal may persist for decades, as has been suggested for some subarctic regions (Iacobelli and Jefferies 1991, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies et al. 2003, 2004; Abraham et al. 2005b, Jefferies et al. 2006, Peterson et al. 2013).

Building on earlier efforts, I investigated the extent to which foraging and nesting by light geese has affected above- and belowground vegetation biomass in a mesic and hydric terrestrial ecosystem in the Karrak Lake region. Foraging geese during pre-breeding, nesting, molting, and brood-rearing stages of their annual cycle select lowland plant communities (Slattery 2000, Slattery and Alisauskas 2007), and at moderate densities, maintain grazing lawns of palatable grass and sedge species. I used a replicated experimental design of herbivore exclosures with enclosed treatment and open control plots in these preferred habitats to estimate differences between above- and belowground biomass of vegetation (graminoids, forbs, mosses) exposed and not exposed to grazing by large herbivores, predominantly light geese. I predicted that grazing by geese was sufficiently intense such that graminoid vegetation subjected to grazing would exhibit lower biomass of both live and dead components relative to treatment plots with grazing excluded, in accordance with documented characteristics of grazing lawns. Due to trampling or less selective foraging by high population density of light geese, I predicted lower biomass of non-forage species on plots subjected to grazing. I also tested the hypothesis that intense grazing of aboveground vegetation in absence of grubbing or shoot-pulling resulted in depletion of belowground vegetation.

Light geese occupy all available unsaturated habitats varying in edaphic state (i.e., upland and lowland regions) during nesting; earlier-nesting snow geese tend to occupy upland areas with earlier disappearance of snow cover (Mowbray et al. 2020), and later-nesting Ross’s geese tend to occupy lowland areas (Jónsson et al. 2020), although there is considerable overlap in nesting habitat between species. Within the nesting colony at Karrak Lake, I quantified differences in biomass of graminoids and foliose and fruticose lichens, as representatives of forage and non-forage vegetation, respectively. As preferred forage species, I predicted that graminoid biomass should decline with increasing duration and intensity of nesting. Similarly, I predicted less severe but negative impacts of nesting on lichen biomass, due to loss by trampling and nest construction. I tested the hypothesis that reduction in nesting pressure in areas in which the colony has recently receded would result in regeneration of graminoid and lichen communities. For convenience, I use the terms ‘plant’ and ‘vegetation’ to include lichen species (Kingdom Fungi) as well as vascular and non-vascular plant species (Kingdom Plantae), although I acknowledge this distinction.

2.2 Methods

2.2.1 Field methods

2.2.1.1 Herbivore exclosures

In 1994, Ray Alisauskas, Stuart Slattery, and colleagues established 5 pairs of enclosed and open plots at each of six sites in the brood-rearing region north of Karrak Lake: two sites within the oldest part of the nesting colony at Karrak Lake (earliest documented nesting: 1982), and four sites at distances of 15, 30, 45, and 60 km north of the colony. At each site, they constructed 1 by 1 m enclosed plots with chicken wire or hardware cloth (1 by 1 inch mesh) supported by 1 m metal poles. The top of each exclosure was open and adjacent control plots measuring 1 by 1 m were delineated with metal poles (Fig. 2.1). I assumed that due to the small dimensions and mesh size of exclosures that grazing of vegetation inside exclosures by large herbivores (caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*)), as well as by geese, would be negligible or nil, but that grazing by invertebrates and arvicoline rodents (collared and brown lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*, respectively) and red-backed voles (*Myotes rutilus*)) could occur. Field staff photographed exclosure sites annually to track visually the difference in vegetation height between treatment (enclosed) and control (open) plots. We also repaired exclosures as required during visits to maintain their structural integrity.

Figure 2.1. An example of an herbivore exclosure established near the coast of Queen Maud Gulf, Nunavut, in 1994 (left photo) and the same exclosure at the time of sampling for biomass in 2017 (right photo).

I investigated whether differences in vegetation biomass resulted from differential grazing inside and outside exclosures and not to effects of the exclosures themselves (e.g., snow catchment). I recorded vegetation data from outside of five exclosures within the nesting colony in mid-July 2018. In each of the four cardinal directions, I recorded height of graminoids (±1 cm) at 9 points spaced at 10 cm along transects at distances of 10, 20, 50, 100, and 200 cm from exclosures. I hypothesized that if exclosure material affected plant growth, graminoid height should vary with distance from exclosures.

In mid-July 2017, I sampled pairs of treatment and open plots by collecting vegetation and soil cores (surface area of 78.5 cm^2, one from each plot). I sampled plots only if fencing that enclosed treatment plots was intact, and so I was unable to obtain samples from all exclosure sites. I refrigerated samples until processing in the laboratory.

In the laboratory, I separated above- and belowground biomass by clipping plant material at the soil-moss interface. This interface is not completely distinct in ecosystems such as in this region where plants grow in organic soil formed by mosses. Belowground, I truncated the soil portion of each core sample just beyond the depth at which visible roots ended (about 6.5 cm, resulting in soil cores of 510.3 cm^3), and separated visible roots from soil. I dried plant material to constant mass at 60 degrees Celsius and weighed components (±0.01 g), defined as follows. I separated aboveground biomass into live and dead graminoids (grasses and sedges, all species combined), live and dead forbs and shrubs combined (herbaceous and woody dicotyledons, but for simplicity refer to these hereafter as forbs), and moss (all species combined). After drying, it was difficult to discern live and dead moss, so I did not separate moss into live and dead components. I report biomass data as $g \cdot m^{-2}$.

2.2.1.2 Nesting colony sample plots

I conducted vegetation surveys on sample plots in mid-July 2017. I determined locations of systematically-spaced sample plots using the Universal Transverse Mercator (UTM) grid system (Alisauskas et al. 2012b). The primary purpose of these circular sample plots, of radius 20 m (1991-1995) or 30 m (1996-present) spaced at 500 or 1000 m intervals, was to facilitate ongoing annual estimation of nest density, species composition, nest initiation date, clutch size, and nest success of snow and Ross's geese (Alisauskas et al. 2012b). The sampling frame for geese was determined each year by mapping the colony boundary from a helicopter (Alisauskas et al. 2012b). For vegetation surveys, I added plots to the sample region to include locations outside the colony boundary. As well, the spatial extent of this nesting colony has shifted over time to the north and west, and retracted from formerly-occupied southern regions. As such, some sample plots outside the colony in 2017 had been inside in the past, while others had never been exposed to nesting by colonial geese in the previous 4-5 decades, to the best of my knowledge, based on information provided by Kerbes et al. (2014).

At each sample plot, I conducted point-intersect surveys similar to earlier vegetation surveys in this region (Alisauskas et al. 2006), at 0.5 m intervals along a 30 m transect extending northward from the plot center, resulting in 60 observations per plot. If observed species were either foliose or fruticose lichens or graminoid species, I measured their height (±0.5 cm).

2.2.2 Statistical analyses

I performed all statistical analyses using the R Statistical Computing Environment (R Core Team 2018). I used linear mixed models (package *lmerTest*, Kuznetsova et al. 2017) to investigate the potential effect of fencing material on graminoid height, using cardinal direction (north (N), east (E), south (S), west (W)) and distance from exclosure (10, 20, 50, 100, 200 cm) as fixed effects and exclosure unit as a random effect. I included interaction between distance and cardinal direction in the most-parameterized model. I tested residuals of this model for normality and log-transformed the dependent variable (graminoid height) if required. I then reduced this model by sequentially removing the non-significant interaction and fixed main effects ($p>0.05$) to obtain the most parsimonious model, but retained the random effect of site.

I used linear mixed models (package *lmerTest*, Kuznetsova et al. 2017) to investigate differences in plant biomass (aboveground total, belowground total, moss, graminoid total, graminoid live, graminoid dead, forb total, forb live, and forb dead) between enclosed and open plots. I modelled treatment (enclosed or open) and distance from the nesting colony (0, 15, 30, 60 km) as fixed effects and exclosure site as a random effect. I included interaction between distance and treatment in the most parameterized models. I tested residuals of the most parameterized model for each vegetation component for normality and log transformed dependent variables (biomass) as required. I modeled each vegetation component separately. I reduced models by sequentially removing non-significant interactions and fixed effects ($p>0.05$) to obtain the most parsimonious model for each vegetation component, but retained the random effect of site in all models.

I used linear models to investigate variation in vegetation height (species groups (graminoids (GramHt) and lichens (LichHt)), modeled separately) on sample plots. I used mean number of goose nests (Nests), number of years in the colony (YrsIn), number of years since retraction of the colony (YrsRet), and elevation (Elev) as potential covariates. I considered mean height as a reasonable index of biomass (Tilly et al. 2015), and for plots without graminoids or lichens, I set mean height to zero. I examined Pearson's product-moment correlations among explanatory variables, and the candidate set of models did not include highly correlated variables in the same model (YrsIn and Nests, see Results). I tested residuals of the most-parameterized models {GramHt or LichHt=YrsIn+YrsRet+Elev} and {GramHt or LichHt=Nests+YrsRet+Elev} for normality and log-transformed dependent variables as required. I used Moran's I to measure the degree of spatial autocorrelation both in raw data and the residuals of the most-parameterized models, and employed spatial models if required. I only report results for normality of residuals and spatial autocorrelation of most-parameterized models from model {GramHt or LichHt=YrsIn+YrsRet+Elev} for simplicity, as results from the other most-parameterized model of {GramHt or LichHt=Nests+YrsRet+Elev} were equivocal. I used Akaike's Information Criterion for small sample size (AIC_c) to examine the relative fit of each candidate model, and incorporated model selection uncertainty by using a 90% confidence set of models (Akaike 1973, Burnham and Anderson 2002) from which I model-averaged slope values (and associated variance) of covariates.

I derived goose covariates (mean number of nests (Nests), number of years in the colony (YrsIn), and number of years since retraction of the colony (YrsRet)) for each plot from long-term data (1966-2017; Ryder 1970, 1971, 1972; McLandress 1983, Kerbes 1994, Kerbes et al. 2006, 2014; Alisauskas et al. 2012b, R. Alisauskas unpubl. data; described in Chapter 1). I calculated mean number of nests for 1991-2017 (1966-1990 data were not available); for plots observed to be outside the colony in all years, mean number of nests was zero. For plots recorded as in the colony for one or more years but calculated mean nest density was zero (as was the case for plots on the colony perimeter where nest density was extremely low), I set mean number of nests to 0.1. I calculated number of years within the colony and number of years since retraction of the colony perimeter for each sample plot from colony boundaries. The extent of the colony was monitored only periodically during 1966-1991, and so I interpolated the colony boundary over time during this interval. However, the spatial extent of the colony during this interval was small and largely confined to the islands of Karrak Lake, requiring interpolated values for very few plots. The extent of the nesting colony was unknown before 1966, and so the maximum value for number of years that a plot was within the colony was 52 years.

I extracted elevation data (m above sea level (asl)) for each plot from the Federal Geospatial Platform of Canada (https://maps.canada.ca/), and thus, these analyses contain information licensed under the Open Government Licence – Canada (https://open.canada.ca/en/open-government-licence-canada). I interpolated plot elevation (±0.1 m) from the four nearest cells of this raster data with spatial resolution of 20 m.

2.3 Results

2.3.1 Effect of fencing material on graminoid height

Transformation of GramHt measured outside of exclosures improved normality of residuals in the most-parameterized model (W=0.995, p=0.180 versus W=0.949, p<0.001 for transformed versus untransformed data, respectively), so I analyzed transformed values. Although I predicted that snow catchment by exclosure fencing would result in taller graminoid vegetation immediately adjacent to exclosures, graminoid height outside of five exclosures within the colony was higher at greater distances north of exclosures (interaction between distance and north cardinal direction: *p*=0.014), and suggested a slight influence of fencing material on plant growth in a direction contrary to prediction (Fig. 2.2). However, all other interactions between distance and cardinal direction were not significant, nor were both main effects of distance and direction. A significant random effect of exclosure (*p*<0.001) suggested that graminoid height was not greatest at further distances north of exclosures in all cases. Examination of raw data revealed that this significant interaction appeared to result from greater graminoid height outside of only one exclosure. When I repeated the analysis ignoring the exclosure and cardinal direction combination in question, all interactions and main effects were insignificant. Thus, I conclude that the interaction effect at one exclosure was spurious.

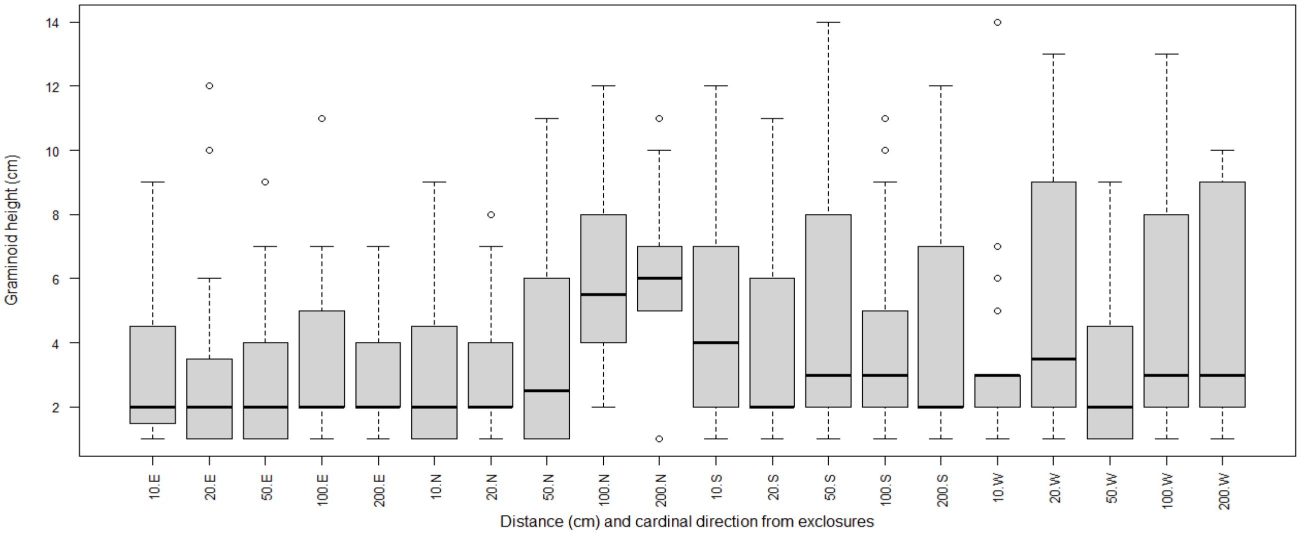

Figure 2.2. Height of graminoid vegetation outside five exclosures within the Karrak Lake nesting colony measured in July 2018, in four cardinal directions at distances of 10, 20, 50, 100, and 200 cm from exclosures. Boxplots are compiled from raw data. Thick lines represent median values, boxes enclose 25th and 75th percentiles, whiskers enclose 5th and 95th percentiles, and open circles represent data outside 95th percentiles. Notes: N=north, E=east, S=south, W=west.

2.3.2 Experimental effects of herbivore exclosures on plant biomass

I collected vegetation and soil cores from 14 herbivore exclosures, each with paired enclosed treatment and open control plots: 5 within the nesting colony, and 3 each from sites at distances of 15, 30, and 60 km from the colony. Due to travel constraints, I did not collect biomass samples from the site at 45 km from the colony.

Transformation of biomass data improved normality of residuals in the most-parameterized model for graminoid total (W=0.969, *p*=0.550 versus W=0.912, *p*=0.023), graminoid live (W=0.941, *p*=0.119 versus W=0.938, *p*=0.101), graminoid dead (W=0.980, *p*=0.846 versus W=0.937, *p*=0.090), forb live (W=0.941, *p*=0.119 versus W=0.938, *p*=0.101), and forb dead (W=0.959, *p*=0.325 versus W=0.816, *p*<0.001), so I used transformed values for analysis of these components. Untransformed biomass values performed better for aboveground total (W=0.959, *p*=0.324 versus W=0.920, *p*=0.035), belowground total (W=0.967, *p*=0.492 versus W=0.950, *p*=0.193), moss (W=0.929, *p*=0.058 versus W=0.898, *p*=0.010), and forb total (W=0.954, *p*=0.248 versus W=0.939, *p*=0.101), so I analyzed untransformed values for these biomass components.

For all vegetation components, biomass was greater in enclosed treatment plots of herbivore exclosures than control plots open to grazing; grazing reduced aboveground biomass by 61% and belowground biomass by 29% (Table 2.1). The most parsimonious model for aboveground total, moss, forb live, and forb dead included only the fixed effect of treatment, whereas a significant interaction between treatment and distance from colony was evident for belowground total, graminoid total, graminoid live, and graminoid dead (Table 2.1, Fig. 2.3). For forb total, the most parsimonious model included only distance, but I report results from the model with additive effects of treatment and distance, as I was most interested in the treatment effect (Table 2.1, Fig. 2.3).

Table 2.1. Model point estimates and associated variance of dry biomass (g m^{-2}) of vegetation components collected from experimental herbivore exclosures (*n*=14 paired open control and enclosed treatment plots) located 0, 15, 30, and 60 km from the light goose nesting colony at Karrak Lake, Nunavut. Results from most parsimonious models are shown for each vegetation component, with associated *p* values for fixed effects of treatment (Treat) and distance (Dist), interaction of fixed effects (Inter), and random effect of site (Site). Model estimates were derived using only fixed effect of treatment and do not incorporate interaction between distance and treatment, and are therefore less relevant for belowground total, graminoid total, graminoid live, and graminoid dead.

Plant Component	Model	Treatment	Biomass			% Reduction by Grazing	*p* Treat	*p* Dist	*p* Inter	*p* Site
			Estimate	SE	L95, U95					
aboveground	treat+site	open	374.3	109.8	146.1, 602.4	61.1	0.000	NA	NA	0.069
total		enclosed	961.5	109.8	733.3, 1189.7					
moss	treat+site	open	260.5	90.8	70.8, 450.0	52.1	0.005	NA	NA	0.030
		enclosed	543.5	90.8	353.8, 733.0					
belowground	(treat*dist)+site	open	365.7	67.6	224.0, 507.0	29.1	0.729	0.549	0.039	0.005
total		enclosed	515.8	67.6	375.0, 657.0					
graminoid	(treat*dist)+site	open	42.8	1.3	24.8, 74.0	87.0	0.054	0.556	0.008	0.426
total		enclosed	329.3	1.3	190.8, 569.1					
graminoid	(treat*dist)+site	open	15.5	1.2	9.8, 24.5	82.9	0.075	0.000	0.006	1.000
live		enclosed	91.0	1.2	57.4, 144.0					
graminoid	(treat*dist)+site	open	24.5	1.4	12.7, 47.5	89.1	0.040	0.019	0.013	0.200
dead		enclosed	224.8	1.4	115.6, 437.0					
forbs	treat+distance+site	open	14.4	7.5	-1.1, 29.9	53.5	0.070	0.049	NA	0.173
total		enclosed	30.9	7.5	15.4, 46.4					
forbs	treat+site	open	0.7	2.1	0.2, 3.4	76.0	0.126	NA	NA	0.200
live		enclosed	3.0	2.1	0.6. 14.0					
forbs	treat+site	open	0.4	1.8	0.1, 1.4	82.3	0.029	NA	NA	0.200
dead		enclosed	2.3	1.8	0.6, 8.2					

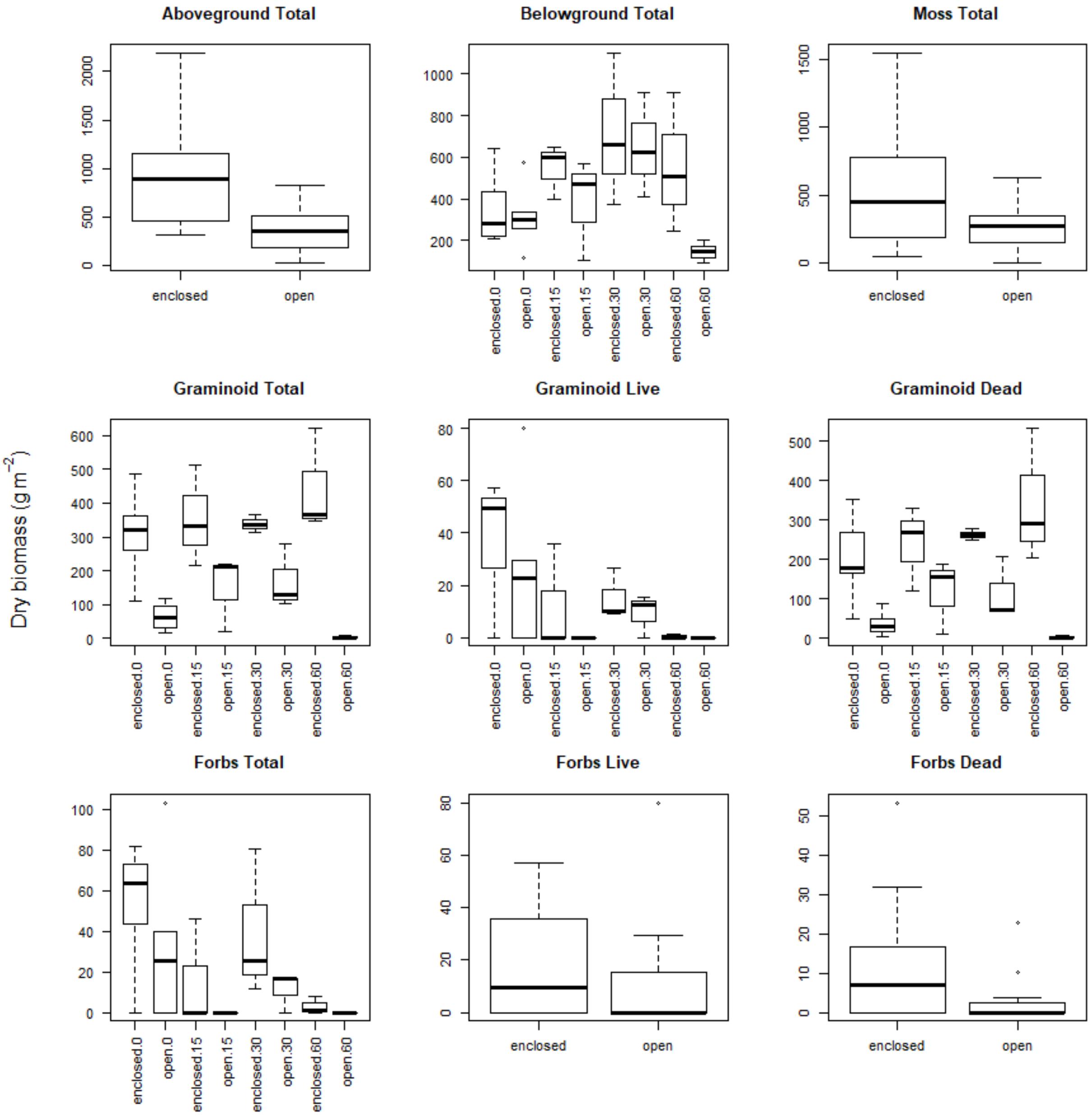

Figure 2.3. Dry biomass (g m^{-2}) of aboveground total, belowground total, moss, graminoid total, graminoid live, graminoid dead, forbs total, forbs live, and forbs dead from enclosed treatment and open control plots at distances of 0, 15, 30, and 60 km from the nesting colony at Karrak Lake, Nunavut. Shown are fixed effects for most parsimonious model for each vegetation component: treatment only for aboveground total, moss, forbs live, and forbs dead, and treatment by distance interaction for belowground total, graminoid total, graminoid live, graminoid dead, and forbs total. Boxplots are compiled from raw data. Thick lines represent median values, boxes enclose 25th and 75th percentiles, whiskers enclose 5th and 95th percentiles, and open circles represent data outside 95th percentiles.

2.3.3 Effects of nesting on spatial variation of graminoid and lichen height

I sampled 255 plots in 2017. GramHt and LichHt ranged between 0-18.5 cm and 0-3 cm, respectively. Number of nests (Nests) ranged between 0-31.7 nests, YrsIn ranged between 0-52 years, YrsRet ranged between 0-17 years, and Elev ranged between 50-97 m asl.

Nests and YrsIn were the most highly correlated variables with r=0.603 (p<0.001), so these effects were not included in the same model. All other correlations were r<0.3. Correlations of ~0.3 were often significant, due to large sample size. Thus, the resulting candidate set of models included 12 models, which included an intercept-only model and all possible combinations of my four covariates.

2.3.3.1 Graminoids

Transformation of GramHt only slightly improved normality of residuals in the most-parameterized model (W=0.946, p<0.001 versus W=0.928, p<0.001), so I used untransformed values for simplicity. Monte Carlo simulation of Moran's I for GramHt indicated spatial autocorrelation of both raw data (Moran's I=0.350, p<0.001) and residuals from the most-parameterized model (Moran's I=0.104, p=0.002). Monte Carlo simulation of Moran's I of both spatial error (Moran's I=-0.020, p=0.755) and spatial lag (Moran's I=-0.001, p=0.417) models indicated that spatial autocorrelation was successfully accounted for by spatial models. I confirmed this result by comparing AIC_c values of spatial error and spatial lag models (1361.9 and 1367.6, respectively), which were lower than the non-spatial model (1385.9). The spatial error model outperformed the spatial lag model by 5.7 AIC_c units, so I drew inference from the former.

There were two models in the 90% confidence set of models with effects of YrsIn, YrsRet, and Elev (Table 2.2, Fig. 2.4), and Elev and YrsIn had greatest influence on graminoid height. Graminoid height declined at higher Elev (-0.190 (95% CI: -0.281, -0.100), and with YrsIn (-0.180 (-0.266, -0.095)), and these effects were included in both models of the confidence set. Graminoid height increased with YrsRet (0.012 (-0.141, 0.167)), although confidence intervals included zero and this variable was included in only one model of the confidence set.

Table 2.2. Model selection results based on Akaike's Information Criterion corrected for small sample size (AIC_c) of mean graminoid height on 255 sample plots at Karrak Lake, Nunavut, 2017. All candidate models are shown. Model variables are plot-specific and included number of years in the goose nesting colony (YrsIn), number of years since retraction of the colony (YrsRet), mean number of nests (Nests, 1991-2017), and Elevation (Elev). All models incorporate spatial error structure. I present the number of parameters (K), AIC_c values, the difference in AIC_c values between each model and the model with the lowest AIC_c value (ΔAIC_c), and normalized Akaike weights (ω_i).

Model	K	AIC_c	ΔAIC_c	ω_i
Elev+YrsIn	5	1360.2	0.0	0.732
Elev+YrsIn+YrsRet	6	1362.3	2.1	0.260
Elev+Nests	5	1371.7	11.5	0.002
YrsIn	4	1371.8	11.6	0.002
Elev	4	1373.0	12.8	0.001
YrsIn+YrsRet	5	1373.0	12.8	0.001
Elev+YrsRet+Nests	6	1373.8	13.6	0.001
Elev+YrsRet	5	1375.1	14.9	0.000
Nests	4	1382.8	22.6	0.000
Intercept only	3	1383.5	23.3	0.000
Nests+YrsRet	5	1384.6	24.4	0.000
YrsRet	4	1385.3	25.1	0.000

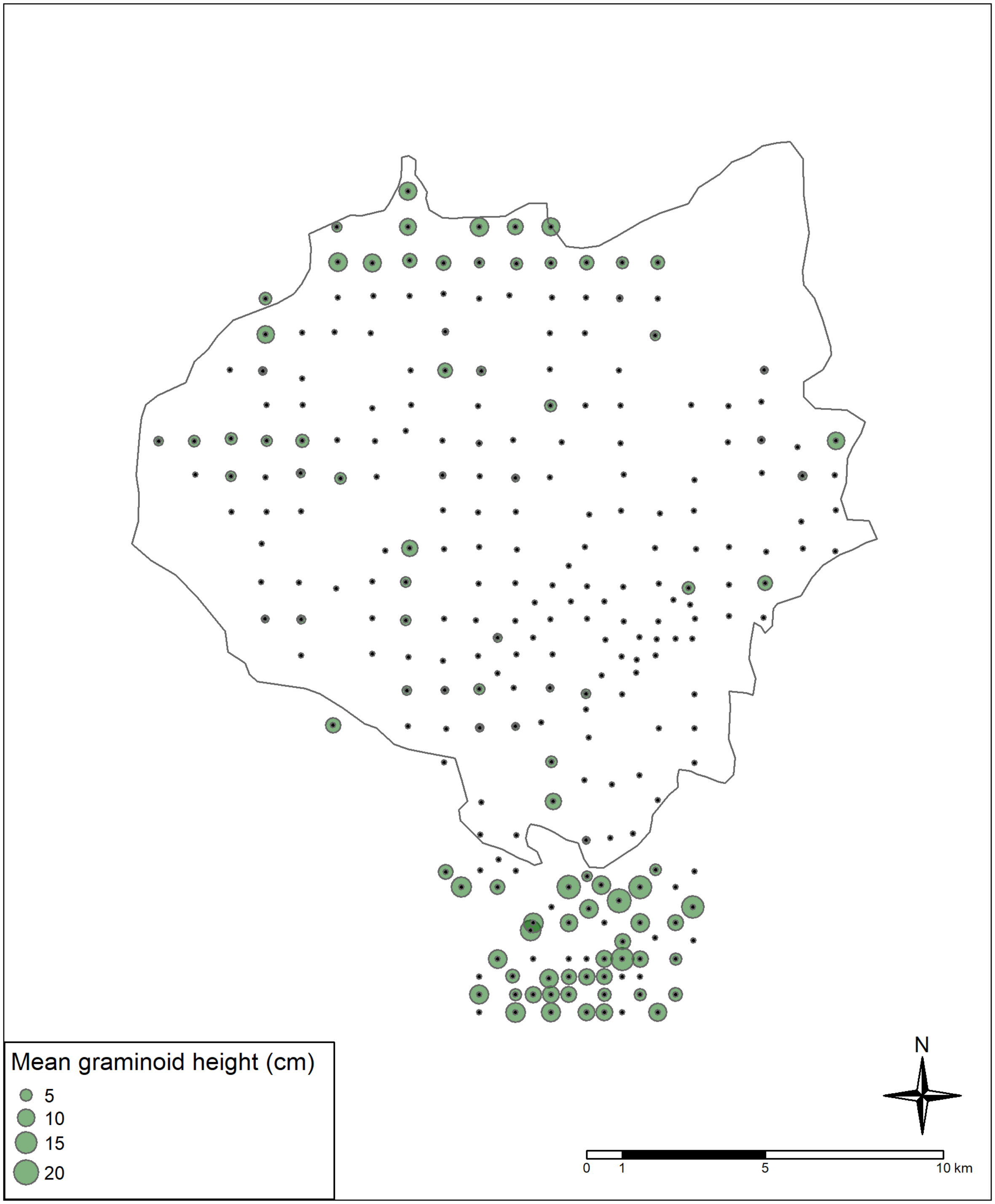

Figure 2.4. Spatial distribution of mean height of graminoid species (grass and sedge species combined) on 255 sample plots in and near the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, 2017. Black dots without filled circles indicate sample plots with mean graminoid height equal to zero. The black line depicts the 2017 colony boundary.

2.3.3.2 Lichens

Transformation of LichHt did not improve normality of residuals (W=0.764, $p<0.001$ versus 0.973, $p<0.001$), so I analyzed untransformed values. Monte Carlo simulation of Moran's I for LichHt indicated no spatial autocorrelation of raw data (Moran's I=-0.003, $p=0.397$) or residuals of the most-parameterized model (Moran's I=-0.033, $p=0.922$). I confirmed this result by comparing AIC_c values of spatial error and spatial lag models (484.4 and 486.1, respectively) to the non-spatial model (484.9), and found them to be equivocal. Therefore, I drew inference about variation in lichen height from non-spatial models.

There were four models in the 90% confidence set of models including all covariates considered (Table 2.3, Fig. 2.5), and Elev, YrsIn, and YrsRet had greatest influence on lichen height. Lichen height increased with Elev (0.014 (95% CI: 0.004, 0.023), a covariate in all models of the confidence set. Lichen height declined with YrsIn (-0.010 (-0.018, -0.002)) and YrsRet (-0.026 (-0.050, -0.002)), and these covariates were in two models of the confidence set. Lichen height also declined with Nests, although the confidence interval included zero (-0.013 (-0.029, 0.003)), and this effect was included in only one model of the confidence set.

Table 2.3. Model selection results based on Akaike's Information Criterion corrected for small sample size (AIC_c) of mean lichen height on 255 sample plots at Karrak Lake, Nunavut, 2017. All candidate models are shown. Model variables are plot-specific and included number of years in the goose nesting colony (YrsIn), number of years since retraction of the colony (YrsRet), mean number of nests (Nests, 1991-2017), and Elevation (Elev). I present the number of parameters (K), AIC_c values, the difference in AIC_c values between each model and the model with the lowest AIC_c value (ΔAIC_c), and normalized Akaike weights (ω_i).

Model	K	AIC_c	ΔAIC_c	ω_i
Elev+YrsIn+YrsRet	5	485.1	0.0	0.643
Elev+YrsIn	4	487.9	2.7	0.165
Elev+YrsRet+Nests	5	490.4	5.3	0.046
Elev	3	490.7	5.6	0.039
Elev+YrsRet	4	490.8	5.6	0.038
Elev+Nests	4	491.5	6.4	0.027
YrsIn+YrsRet	4	492.2	7.0	0.019
YrsIn	3	492.4	7.3	0.017
Nests	3	496.7	11.6	0.002
Intercept only	2	496.7	11.6	0.002
Nests+YrsRet	4	497.6	12.5	0.001
YrsRet	3	498.4	13.3	0.001

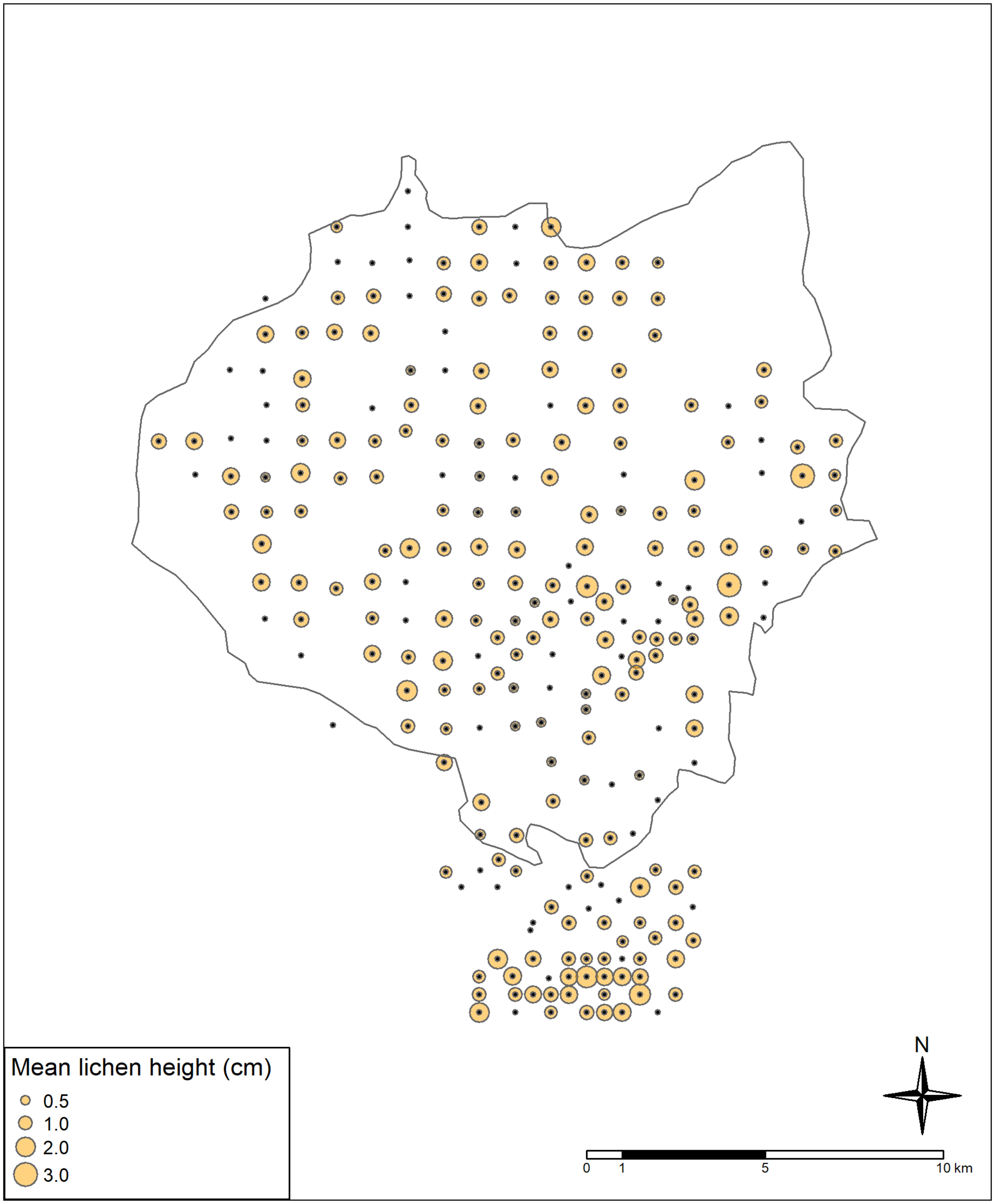

Figure 2.5. Spatial distribution of mean height of foliose and fruticose lichen species on 255 sample plots in and near the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, 2017. Black dots without filled circles indicate sample plots with mean lichen height equal to zero. The black line depicts the 2017 colony boundary.

2.4 Discussion

2.4.1 Grazing lawns in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary

As Ross's and snow geese are dominant herbivores in the Karrak Lake region (light geese: Alisauskas et al. 2012b; compared to caribou: Campbell et al. 2012; cackling and greater white-fronted geese: Conn and Alisauskas 2018; arvicoline rodents: Samelius et al. 2017, Chapter 4), they are largely responsible for reduction of aboveground biomass within the nesting colony at Karrak Lake and their molting and brood-rearing areas north of the colony. Aboveground biomass in ungrazed treatment plots was greater than on grazed control plots by 61%, largely driven by differences in graminoid vegetation (Table 2.1, Fig. 2.3), the dominant vegetation type at exclosure sites. Reduction of aboveground biomass by foraging geese substantiates earlier work conducted in brood-rearing areas used by geese that nested in the Karrak Lake colony (Slattery 2000, Didiuk and Ferguson 2005, Alisauskas et al. 2006, Conkin and Alisauskas 2017), and reflects that reported for other ecosystems in which geese are dominant herbivores (e.g., Cargill and Jefferies 1984a, Sedinger and Raveling 1986, Gauthier et al. 1995, Abraham et al. 2020).

Grazing lawns exhibit a short and prostrate growth form, yet contain plants with high nutritional content. This results from frequent grazing that maintains tissues at digestible, immature forms with high nitrogen and low structural carbohydrates (McNaughton 1976, 1979, 1984; Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; Slattery 2000, van der Graaf et al. 2005, O et al. 2006, Johnson et al. 2011, Uher-Koch et al. 2019). I did not investigate potential differences in nitrogen content, an index of nutrition, of grazed versus ungrazed swards, but this has been confirmed for goose-maintained grazing lawns in many northern regions (Cargill and Jefferies 1984b, Bazely and Jefferies 1986, Sedinger and Raveling 1986, Gauthier et al. 1995, Beaulieu et al. 1996, Person et al. 1998, Ruess et al. 1997, Beard et al. 2019), including this ecosystem (Slattery 2000). Nor did I assess nutritional content indexed by carbon to nitrogen ratios (e.g. Person et al. 1998). Intuitively, however, carbon is lower in grazed patches through reduction of dead or senescing tissues (Bazely and Jefferies 1986, Gauthier et al. 2004, van der Graaf et al. 2005, Johnson et al. 2011, Nishizawa et al. 2020, this study (Table 2.1, Fig. 2.3)), increasing proportion of nitrogen in aboveground vegetation subjected to grazing. Broadly speaking, I conclude that vegetation in lowland habitats north of the large nesting colony at Karrak Lake resembles a functional grazing lawn maintained by light geese.

Differences in combined live and dead biomass of graminoids between grazed control and ungrazed treatment plots in this study was largely due to differences in quantity of dead graminoid biomass (Table 2.1, Fig. 2.3). At all exclosure sites except one within the nesting colony, grazed and ungrazed plots differed little in live graminoid biomass. Removal of dead or senescing biomass by grazing likely facilitates growth by mechanisms such as removal of less functional tissues and increased light to more active tissues (McNaughton 1979, Bazely and Jefferies 1986, reviewed by Augustine and McNaughton 1998), which may in part explain the relative scarcity of live graminoids within ungrazed treatment plots containing ample dead biomass. In addition, creation and maintenance of grazing lawns in nutrient-limited arctic plant communities (Cargill and Jefferies 1984a, Shaver and Chapin 1995, Nishizawa et al. 2020) benefits from nutrient inputs by herbivore fecal nitrogen recycling (Cargill and Jefferies 1984b, Hik and Jefferies 1990, Ruess et al. 1997, 2019; van der Wal and Brooker 2004, van der Wal et al. 2004, Abraham et al. 2012, but see Beaulieu et al. 1996, Nishizawa et al. 2020). Plant growth dependent on nutrient cycling via herbivore dung and urine is an integral part of coevolved herbivore-plant ecosystems, such that, “this is so well known as to warrant little comment” (McNaughton 1979, reviewed by Huntly 1991, Hobbs 1996, Augustine and McNaughton 1998). Thus, large quantities of dead and senescing plant tissue without herbivore fecal nutrient inputs likely explains the paucity of live graminoids in our long-term (established 1994) herbivore exclosures.

2.4.2 Habitat spatial heterogeneity

Heterogeneity in vegetation community biomass and species composition results from abiotic gradients, such as topography, moisture, and soil properties (McNaughton 1983, Gough et al. 2000, Handa et al. 2002, Jones and Henry 2003, Suvanto et al. 2014, Steward et al. 2016, this study). Additionally, herbivory, which is generally highly variable both spatially and temporally, further increases heterogeneity in plant community structure (McNaughton 1976, 1983; Jeltsch et al. 1997, Person et al. 1998, Slattery 2000, Handa et al. 2002, McLaren and Jefferies 2004, Olofsson et al. 2004a, O et al. 2006, Uher-Koch et al. 2019). I detected spatial heterogeneity of aboveground biomass due to abiotic and grazing effects both within and north of the colony. Within the nesting colony, intensity of nesting by light geese contributed to variation of graminoid and lichen height (Table 2.2, 2.3; Fig. 2.4, 2.5). Outside of the colony, best-supported models that explained variation in components of aboveground biomass often included both distance from the colony as a fixed effect and a significant random effect of site (Table 2.1, Fig. 2.3), both indicative of spatial heterogeneity. Thus, in addition to abiotic factors, I conclude that spatial variation in aboveground biomass can be also be attributed to foraging and nest construction by geese. Likewise, Slattery (2000) reported a gradient in vegetation structure due to foraging by light geese within the landscape mosaic (caused by abiotic physiographic factors) of this same region. However, I detected greatest removal of aboveground biomass within the colony as well as near the coast of Queen Maud Gulf, where river deltas support vast tracts of graminoid vegetation, with less reduction at the 30 km site and the unsampled 45 km site (Table 2.1, Fig., 2.3, 2.4, 2.5; D. Kellett pers. obs.). This contrasted with findings by Slattery (2000), who detected a linear gradient in standing crop and protein composition of graminoid vegetation between Karrak Lake and the coast of Queen Maud Gulf. I suspect that change in spatial distribution of flightless geese (Slattery and Alisauskas 2007) since Slattery's (2000) study likely explains deviation from spatial patterns in vegetation reported here.

2.4.3 Evidence for degradation or an alternate stable state?

At intense levels of herbivory, productivity will decline if loss of plant biomass is uncompensated by regrowth (e.g., Manseau et al. 1996). I suggest that, at some sites within the nesting colony and molting and brood-rearing areas, severe reduction of live aboveground biomass represents evidence that herbivore optimization has been exceeded and perhaps existence of an alternative stable state resembling that associated with light geese in other regions (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b, 2020; O et al. 2005, Henry and Jefferies 2008). Grazing lawns have largely disappeared from the nesting colony at Karrak Lake, as indicated by extremely low mean graminoid height in intensively used areas of the colony (Fig. 2.4) and existence of moss carpets and devegetated peat barrens (Alisauskas et al. 2006, Chapter 3). Likewise, Alisauskas et al. (2006) reported low graminoid cover in the colony as early as 1999. Both Didiuk and Ferguson (2005) and Conkin and Alisauskas (2017) demonstrated existence of exposed peat in the colony, which results when the overlying cover of graminoid vegetation has been removed. In addition to reduction of graminoids, I detected reduction of lichens with increasing nesting intensity (Fig. 2.5; see also Abraham et al. 2020). Likewise, Alisauskas et al. (2006) reported declines of lichens, which are sensitive to tramping (Manseau et al. 1996, Cooper et al. 2001), as well as declines of ericaceous species in oldest regions of the colony, and increases in exposed peat and mineral substrate. Whereas graminoids represent preferred forage for geese, forbs, lichens, and mosses also are consumed occasionally after local depletion of graminoids (Gloutney et al. 2001), but are most often used for nesting material (McCracken et al. 1997, Alisauskas et al. 2006, D. Kellett pers. obs.).

On molting and brood-rearing areas north of Karrak Lake, I detected extremely depleted aboveground biomass in lowland habitats at the 60 km site: grazed plots contained less than 1% of biomass than ungrazed plots (Table 2.1, Fig. 2.3). Concomitant reduction of belowground biomass at this site suggests that nearly complete elimination of aboveground biomass by grazing (there was no visual evidence of grubbing or shoot-pulling at exclosure sites) negatively influenced belowground biomass (Beaulieu et al. 1996). On the other hand, high shoot to root ratios may be an adaptation to grazing (Cargill and Jefferies 1984b). I estimated root (belowground biomass total) to shoot (aboveground live graminoid) ratios on grazed plots as ranging between 7:1 to 30:1 at sites within 30 km of the Karrak Lake colony, in agreement with that reported by Cargill and Jefferies (1984b). At the 60 km site, however, this ratio averaged 116:1, due to extremely low aboveground live graminoid biomass. At this site, I also observed extensive colonization by marsh ragwort (*Tephroseris palustris*), a non-forage species common at disturbed sites (formerly *Senecio congestus*, Kerbes et al. 1990, Handa et al. 2002), suggesting that herbivore foraging has exceeded optimization within some lowland habitats utilized by flightless light geese.

Slattery (2000) described a biodeterioration zone of “negative ecological impacts of herbivory attenuating with distance” (e.g. Jeltsch et al. 1997), and reported reduced standing crop, protein density, and apparent net aboveground primary productivity closer to the nesting colony at Karrak Lake. At the time of Slattery’s (2000) study in the mid-1990s, groups of flightless light geese were uniformly distributed between the colony and the coast of Queen Maud Gulf, with some larger aggregations near the coast. However, most geese investigated in recent capture-mark-recapture analyses in the Sanctuary (e.g., Wilson et al. 2016, Weegman et al. 2020) were captured near the coast (R. Alisauskas, unpubl. data), suggesting a change in spatial distribution of light geese since the mid-1990s (Slattery 2000, Slattery and Alisauskas 2007). It is likely that grazing pressure is now concentrated near the coast, leading to a severe reduction in aboveground biomass and discernable negative effects on belowground biomass (Table 2.1, Fig. 2.3) in such intensively foraged regions.

Despite moderate to severe reductions in aboveground biomass in some areas such as near the coast, other areas appear only lightly grazed. Importantly, removal of aboveground biomass was rarely complete at any sampled site in the nesting colony (Table 2.1, Fig. 2.3, see also Chapter 3) and brood-rearing and molting regions, and I conclude that vegetation within our study area, as well as throughout the Sanctuary (R. Alisauskas, unpubl. data), is not as severely impacted as at several subarctic nesting regions (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008).

2.4.4 Regeneration potential

Graminoid communities regenerate annually from belowground plant stores (Shaver and Chapin 1995, Handa et al. 2002, Abraham et al. 2012, Nerlekar and Veldman 2020). Despite some reduction of belowground biomass at intensively grazed areas, belowground biomass remained on grazed control plots associated with experimental exclosures. Arctic graminoid communities highly adapted to grazing and low nutrient availability inherently exhibit high root to shoot ratios (Cargill and Jefferies 1984b, this study). Grubbing of belowground vegetation and shoot-pulling has obvious negative consequences for plant production and regeneration, and these activities occur throughout the Sanctuary. I did not quantify the extent of alteration directly resulting from grubbing and shoot-pulling, but they are likely in part responsible, together with grazing, for extensive exposed peat throughout the Sanctuary (Conkin and Alisauskas 2017). In most regions, persistence of aboveground organic matter (including exposed peat) contrasts with extensive bare substrate in subarctic regions along the western coast of Hudson Bay (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008). In subarctic coastal regions, an alternative stable state of bare sediment is created by positive feedback from removal of organic matter, evaporation resulting in hypersalinity, and impeded plant growth and survival. In the Sanctuary, exposed mineral soil is largely limited to oldest regions of large nesting colonies (Alisauskas et al. 2006) and along drainages and coastal regions, the majority of the latter due to drawdown, tidal influences, solifluction and erosion by water (Slattery 2000, Conkin and Alisauskas 2017, D. Kellett pers. obs.) and not subjected to the same positive feedback impeding plant establishment and growth. In inland freshwater communities, elimination of occupancy by nesting geese (colony retraction) resulted in regeneration of graminoids, indicated by increased height, similar to that reported by O et al. (2006). Further, revegetation of bare substrate in heavily-impacted regions despite changes to soil properties appears probable (K. Schnaars-Uvino, pers. comm.).

The significant negative effect of colony retraction on lichen height (Table 2.3) was contrary to expectation. Lichens regenerate slowly from fragments of thalli (Cooper et al. 2001), and so I expected that insufficient time had elapsed to garner a positive effect of colony retraction on lichen regeneration.

2.4.5 What about climate change?

Together with fire, herbivory facilitates creation and maintenance of heterogenous temperate and tropical grassland communities through disturbance (Huntly 1991, Díaz et al. 2007, Nerlekar and Veldman 2020). Fire and herbivory often interact to arrest ecosystems in grassland states (McNaughton 1983, Hobbs 1996, Augustine and McNaughton 1998) and impede succession towards shrub- or forest-dominated ecosystems (Nerlekar and Veldman 2020). In graminoid-dominated tundra ecosystems, in which transition to shrubby or forested ecosystems is impeded by permafrost with limited opportunity for burning (but see Jones et al. 2009), herbivory alone can function to maintain ecosystems in grassland states (van der Wal 2006). As climate warms and graminoid-dominated tundra communities, at least at lower latitudes, are subject to encroachment by woody vegetation (Olofsson et al. 2009, Elmendorf et al. 2012, Carlson et al. 2018), herbivory may slow this transition (Olofsson et al. 2009, Leffler et al. 2019; but see Carlson et al. 2018). Whereas climate change has potential to alter quantity, quality, or timing (Elmendorf et al. 2012, Gauthier et al. 2013, Bêty et al. 2014, Doiron et al.

2014, Beard et al. 2019, Leffler et al. 2019) of forage available to arctic herbivores, it remains to be seen whether herbivores can mitigate impacts of climate change on their own food sources.

2.5 Summary and Transition to Chapter 3

Foraging and nesting by light geese at the intensity observed in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary near Karrak Lake created spatial heterogeneity of lightly and intensely-foraged grazing lawns in lowland areas within the landscape mosaic created by variation in topography, moisture, and soil properties. Whereas some areas experienced nearly complete depletion in aboveground biomass, belowground plant stores are overall intact (grazing reduced belowground biomass by only 29%), with strong potential for regeneration.

Selectivity of forage species may be relatively low in situations of high herbivory (Augustine and McNaughton 1998, McLoughlin et al. 2016). I found evidence for severe reduction of both preferred forage (graminoids) and lichens by light geese, particularly in areas with long-term occupancy by nesting geese. Under conditions of intense herbivory that lead to depletion of preferred forage, however, less palatable species may be consumed (Gloutney et al. 2001). High densities of herbivores can as well severely impact vegetation through non-foraging activities such as trampling or nest construction (McNaughton 1979, Huntly 1991, Augustine and McNaughton 1998). Nest construction by geese is likely largely responsible for removal of non-forage species within the nesting colony at Karrak Lake. Non-foraging impacts typically occur at relatively small spatial scales and temporally isolated events (e.g. Serengeti ungulates, McNaughton 1979), but repeated annual nest construction and occupancy by light geese of surrounding nesting territories (Alisauskas et al. 2012b) in which birds uproot vegetation for nest construction results in cumulative, landscape-level impacts (Conkin and Alisauskas 2017).

In addition to changes in aboveground biomass, shifts between alternative stable states also involve changes to species composition of plant communities. Grazing intensity that exceed optimal levels for maintenance of nutritious grazing lawns can result in shifts from graminoid-dominated communities to those dominated by colonizing species, such as marsh ragwort (Kerbes et al. 1990, Abraham and Jefferies 1997, Abraham et al. 2005b, Alisauskas et al. 2006, Abraham et al. 2012, Kotanen and Abraham 2013). Within the nesting colony at Karrak Lake, graminoids have been largely eliminated from intensively-used areas where they previously existed (Alisauskas et al. 2006, Samelius and Alisauskas 2009, this study) and replaced by other species. Herbivory and nesting activity by two sympatric avian herbivores is an example of large-scale alteration of tundra plant communities that has implications for shifts in other aspects of ecosystem structure. Alteration of species composition of plant communities under intense grazing and nesting pressure is the subject of Chapter 3.

CHAPTER 3: PLANT COMMUNITY SHIFTS RESULTING FROM FORAGING AND NESTING LIGHT GEESE

3.1 Introduction

Many grassland ecosystems evolved in response to disturbance by fire and herbivory with convergent adaptations to these disturbances as well as to low water availability: plants with basal meristems, small stature, high densities of shoots, and ample belowground nutrient reserves (Huntly 1991, Augustine and McNaughton 1998, Díaz et al. 2007, Nerlekar and Veldman 2020). Vegetation of graminoid-dominated subarctic and arctic ecosystems, only rarely subjected to fire (e.g. Jones et al. 2009, but see Beamish et al. 2020), are also shaped by herbivory (Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; van der Graaf et al. 2005, O et al. 2006, van der Wal 2006, Uher-Koch et al. 2019), with plant species sharing many of the same traits as those of temperate and tropical grasslands. Northern grazing lawns, created and maintained under optimal levels of herbivory, maintain a steady state of high nutrient composition and consist of plant species adapted to grazing by exhibiting prostrate and rapid growth and positive response to nutrient inputs from herbivore fecal and urine deposits (Cargill and Jefferies 1984b, Hik and Jefferies 1990, Person et al. 1998, 2003; van der Graaf et al. 2005, O et al. 2006, van der Wal 2006, Uher-Koch et al. 2019). Despite short growing seasons with limited soil nutrient availability (Porsild 1964, Shaver and Chapin 1995), grazing lawns in northern regions demonstrate a remarkable resilience to high levels of grazing by regenerating from belowground biomass, often after extensive removal of annual aboveground production (Cargill and Jefferies 1984b, Gauthier et al. 1995, Person et al. 1998, Slattery 2000, Madsen et al. 2011).

Whereas most vertebrate herbivores such as caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), and rodents primarily forage on aboveground plant production in northern regions (Batzli et al. 1983, Thomas and Hervieux 1986, Larter and Nagy 1997, Soininen et al. 2015, Fauteux et al. 2017), some species of geese are particularly adapted for extracting nutrient-rich belowground portions of plants. Lesser and greater snow geese (*Anser caerulescens caerulescens* and *Anser caerulescens atlantica*) have robust, chisel-like bills (Alisauskas 1998) adapted for excavating belowground plant biomass (roots and tubers) and pulling plant shoots from the ground in which the basal portion is consumed (Mowbray et al. 2020). The diminutive bill of Ross's geese (*Anser rossii*; with snow geese, collectively referred to as light geese) is adapted for grazing (Jónsson et al. 2020) but this species also forages by grubbing for belowground biomass, particularly in association with lesser snow geese (hereafter, snow geese) in which foraging by the larger species facilitates exploitation of previously-disturbed sediments (Didiuk et al. 2001, Alisauskas et al. 2006, Jónsson et al. 2020). Changes to winter range distribution of snow geese from coastal saltmarshes to inland agricultural regions (Mowbray et al. 2020) has released coastal vegetation from intense foraging by currently high populations. On northern staging and breeding areas, however, widespread disturbance to belowground biomass by high populations of light geese continues by grubbing and shoot-pulling (Abraham and Jefferies 1997, Kotanen and Jefferies 1997, Kerbes et al. 1990, Henry and Jefferies 2008, Jefferies and Rockwell 2002, Abraham et al. 2012), often with negative consequences for grazing lawns (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008, Fontaine and Mallory 2011, Conkin and Alisauskas 2017). As well, light geese exhibit fidelity to nesting colony locations where spatially dense nesting and uprooting of vegetation for nest construction (McCracken et al. 1997, Alisauskas et al. 2006, Abraham et al. 2020) can lead to devegetation of plant communities (Alisauskas et al. 2006, Samelius and Alisauskas 2009, Abraham et al. 2020). Combined and cumulative effects of foraging of above- and belowground biomass and disturbance to vegetation by nesting activities can result in changes to plant communities on a landscape scale. Along the west coast of Hudson Bay, exposure of marine sediments following removal of vegetation by geese resulted in changes to plant community species composition (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008). In this region, optimal levels of herbivory slows succession governed by isostatic uplift from a community dominated by *Puccinellia phryganoides* and *Carex subspathacea* to that dominated by grasses such as *Festuca rubra* and *Calamagrostis deschampsioides* and various dicotyledons (Jefferies et al. 1979). Intense grubbing of graminoid-dominated communities results in removal of plant biomass and exposure of underlying marine sediments. Increased evaporation from sediments concentrates marine salts and results in hypersalinity, impeding graminoid regeneration and produces an alternative stable state of bare sediment, which may be eventually colonized by halophytic species (references given above).

Although subarctic habitats are used extensively for staging and nesting, arctic regions support most nesting, brood-rearing, and molting light geese (Kerbes et al. 2014, Alisauskas et al. 2011, Alisauskas et al. *in review*). In arctic coastal and inland regions, light geese forage on graminoids in lowland plant communities (Slattery and Alisauskas 2007, Abraham et al. 2020), and nesting occurs in a variety of upland and lowland habitats. Compared to subarctic regions, less is known about changes in species composition of arctic plant communities in response to disturbance by high population abundance and densities of light geese. Remote sensing investigations (Didiuk and Ferguson 2005, Fontaine and Mallory 2011, Conkin and Alisauskas 2017) have reported dramatic increases in exposed peat coinciding with increased abundance of geese. Ground-based investigations have also reported increases in exposed peat and bare substrate, loss of biomass, changes in cover of individual plant taxa, and encroachment of colonizing species (Chapter 2, Alisauskas et al. 2006, Samelius and Alisauskas 2009, Fontaine and Mallory 2011, Abraham et al. 2020). However, there have been few multispecies assessments (e.g., Abraham et al. 2020) of arctic plant community response to disturbance by light geese across a range of edaphic states (e.g., upland versus lowland habitats) and variation in intensity of disturbance (e.g., within and among habitats used for nesting and foraging).

I investigated potential shifts in species composition of plant communities in relation to intensity of vegetation disturbance by nesting and foraging light geese in an arctic breeding area in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (hereafter, the Sanctuary). Alternative stables states in tundra plant communities are "relatively resistant to change, but, if forced, can exhibit rapid shifts to another state" (van der Wal 2006). Bare mineral sediments in northern regions have been described as an alternative stable state that results when grazing by caribou (van der Wal 2006) and geese (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008) has exceeded optimal levels. Bare mineral sediment in arctic regions is common along rivers from solifluction, but is less common when vegetation is removed by herbivores (Slattery 2000, Conkin and Alisauskas 2017, but see Abraham et al. 2020), at least in lowland regions. Instead, intense foraging and nesting by light geese in lowland habitats primarily resulted in conversion of graminoid-dominated communities to those with extensive proportions of exposed peat, and may represent an alternative stable state (Alisauskas et al. 2006, Conkin and Alisauskas 2017, Abraham et al. 2020). In upland habitats, exposed mineral soil resulting from vegetation removal is more common (Alisauskas et al. 2006), and may constitute an alternative stable state, as found in subarctic regions exposed to intense foraging by geese (references given above). Here, I describe plant communities that constitute altered states, and the empirical relationship of their occurrence following decades of intense foraging and nesting by light geese. In lowland habitats, I predicted that exposed peat would be more prevalent in intensively-used nesting and foraging areas, and that colonizing species such as marsh ragwort (*Tephroseris palustris*) and marsh cinquefoil (*Potentilla palustris*) may thrive here, as occurs in subarctic regions (Kerbes et al. 1990). In upland habitats, I predicted bare substrate to be more prevalent in areas subjected to intense nesting, but had no predictions about which species may colonize bare substrate, although species resistant to uprooting should persist. As well, within the nesting colony, I monitored response of altered lowland and upland plant communities upon release from nesting by light geese. In addition to description of plant communities comprising altered states, I investigated the competing hypotheses that (1) exposed peat and bare substrate in lowland and upland habitats, respectively, are alternative stable states, or (2) given that belowground biomass remained in altered habitats (Chapter 2) and if sufficient time had elapsed since colony retraction, that these habitats revert to former communities when grazing and nesting pressure subsides.

3.2 Methods

3.2.1 Field methods

I conducted vegetation surveys on sample plots within and near the light goose nesting colony at Karrak Lake during growth phases for all species in mid-July in 1998, 1999, 2010, 2014, and 2017. I determined locations of systematically-spaced plots using the Universal Transverse Mercator (UTM) grid system (Alisauskas et al. 2012b). The primary purpose of these circular sample plots, of radius 20 m (1991-1995) or 30 m (1996-present) spaced at 0.5 or 1.0 km intervals, was to facilitate ongoing annual estimation of nest density, species composition, nest initiation date, clutch size, and nest success of snow and Ross’s geese (Alisauskas et al. 2012b). The sampling frame for geese was determined each year by mapping the colony boundary from a helicopter (Alisauskas et al. 2012b). For vegetation surveys, I added plots to the sample region to include locations outside the colony boundary in 1999 and 2017. Due to recent retraction of the colony perimeter, some of these plots outside the colony in 2017 had been inside in the past, while others had never been exposed to nesting by colonial geese, to the best of my knowledge based on historical data (Kerbes et al. 2014).

At each sample plot, I conducted point-intersect surveys described by Alisauskas et al. (2006). I recorded substrate or plant or lichen species or species groups at 0.5 or 1.0 m intervals along 30 m transects extending from the plot center. I recorded observations only north of the plot center in 2017 (0.5 m intervals, 60 observations per plot). For all other years, I recorded observations in the four cardinal directions (at 1.0 m intervals, 120 observations per plot). I did not identify grasses, sedges, lichens, and mosses to species, most often because of identification difficulties due to grazing effects, and instead refer to these categories as species groups (Table 3.1).

I also conducted point-intersect surveys at 49 sites within the Sanctuary in early August of 2014. I randomly selected sites from lowland habitat identified by Didiuk and Ferguson (2005) located north of 67 10’ N, as such habitat is favoured by light geese for brood-rearing after exodus from nesting colonies following hatch (Slattery and Alisauskas 2007). I recorded substrate or plant or lichen species or species groups at 1.0 m intervals along 50 m transects, resulting in 50 observations per plot. Forty-three sites were in brood-rearing areas outside of nesting colonies, and six sites were located within nesting colonies.

Plant nomenclature follows Aiken et al. (2007).

3.2.2 Statistical analyses

3.2.2.1 Vegetation communities near the Karrak Lake nesting colony

I performed all statistical analyses using the R Statistical Computing Environment (R Core Team 2018) except for assessment of habitat state change (see below). Data from the nesting colony (1998, 1999, 2010, 2014, 2017) and Sanctuary (2014) were used to construct year-specific ordinations (nesting colony data for 1998, 2010, and 2014 presented in Appendix B), and data from 1998 and 2014 were used to investigate habitat change.

I used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distance (package *vegan*, Oksanen et al. 2019) to characterize vegetation communities on sample plots within and near the nesting colony of light geese at Karrak Lake, constructing ordinations for each year separately. NMDS is an unconstrained multivariate ordination technique based on ranked distances which improves ability to extract information from nonlinear relationships between species occurrences (McCune and Grace 2002, Oksanen 2015), and is thus often used to explore patterns in community ecology (e.g. Elliott and Vose 2016). A metric of goodness-of-fit, stress (S; low S indicates improved fit), is a function of observed dissimilarities in original data and resulting ordination distances (Oksanen 2015). I compiled input data by summing point-intersect observations of each species or species group per plot. I included only those species or species groups in analyses in which occurrence across all plots in a given year was greater than 1% to reduce the influence of rare species (Rettie et al. 1997, Elliott and Vose 2016), with a few exceptions. I included species correlated with high nesting density and intense foraging by colonial geese (Kerbes et al. 1990, Alisauskas et al. 2006). Therefore, I included marsh ragwort (*Tephroseris palustris*) in all ordinations even when occurrence was <1%, as this species occurs in disturbed habitats such as those heavily used by geese (Kerbes et al. 1990, Alisauskas et al. 2006). I included crowberry (*Empetrum nigrum*) in all ordinations for consistency, because in most years occurrence was about 1%. In 2010, 2014, and 2017, I also included marsh cinquefoil (*Comarum palustre*) and mare's tail (*Hippuris vulgaris*) when occurrence was <1%, as I hypothesized these species to occur more frequently in areas heavily used by geese, based on anecdotal observations. Prior to 2010, occurrence of both marsh cinquefoil and mare's tail was negligible, and so I did not include these species in construction of ordinations in these years. Exploratory analyses revealed that inclusion of species that occurred at low frequencies did not appreciably influence structure of resulting ordinations. Not all species groups were recorded consistently across years due to evolving research protocol; this was the case with moss species (SPHA, MOCA, MOOT, and MOSS; Table 3.1). In 2017, I discerned lichen species by growth form (crustose, foliose, fruticose; Table 3.1).

Table 3.1. Percent occurrence (%) of species and species groups and resulting axis loadings from nonmetric multidimensional scaling (NMDS) ordination of vegetation community data collected on 30 m radius sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 1999 (*n*=167) and 2017 (*n*=256). Twelve and 17 species and species groups accounted for 98.2 and 98.4% of point-intersect observations in 1999 and 2017, respectively.

Code	**Species or Species group**	**1999**				**2017**			
		%	**NMDS1**	**NMDS2**	**NMDS3**	**%**	**NMDS1**	**NMDS2**	**NMDS3**
LICH	all lichen species	15.5	0.4557	0.2433	-0.2682				
LICRUST	lichen species (crustose form)					2.7	-0.2785	0.1204	0.3498
LIFRUT	lichen species (fruticose form)					15.7	-0.6899	-0.4326	0.2705
PEAT	dead moss species	9.7	-0.1894	-0.2341	-0.2263	8.2	0.4729	0.2131	0.2114
SPHA	*Sphagnum* spp.					1.8	0.9624	-0.6977	0.1871
MOOT	moss species, not *Sphagnum* spp.					15.0	0.5338	0.0537	0.2217
MOSS	all moss species	25.2	-0.3187	-0.1583	-0.0847				
GRAM	graminoids (grass and sedge spp.)	11.6	-0.7727	0.3935	0.1346	8.1	0.9403	-0.7632	-0.5035
BIRC	birch *(Betula glandulosa)*	5.9	-0.1988	-0.1914	0.0751	14.3	0.4246	0.5751	-0.4504
WILL	willows *(Salix* spp.)	3.2	-0.7150	0.2733	0.1263	3.3	0.9508	-0.4419	-0.3474
CRAN	cranberry *(Vaccinium vitis-idaea)*	8.1	0.1721	-0.1833	0.2530	11.4	-0.2491	0.3482	0.0863
CROW	crowberry *(Empetrum nigrum)*	0.6	0.5317	0.5407	0.6446	0.7	-0.8331	0.1247	0.0151
BEAR	bearberry (*Arctous* spp.)	0.9	0.6209	-0.2160	0.8098	0.9	-0.6924	0.9169	0.4338
LABT	Labrador tea *(Ledum palustre)*	13.1	0.3429	-0.0797	-0.0631	11.0	-0.4436	0.0856	-0.0883
HEAT	white heather *(Cassiope tetragona)*	4.0	0.4020	0.1808	-0.3053	3.4	-0.5432	-0.2405	-0.4718
BLUE	blueberry *(Vaccinium uliginosum)*					0.7	0.2765	-0.1918	-0.8147
RAGW	marsh ragwort *(Tephroseris palustris)*	0.4	-0.3729	-1.3970	-0.3280	0.5	1.1096	0.3745	0.8455
MACI	marsh cinquefoil *(Comarum palustre)*					0.4	1.4850	-0.4497	0.7432
MATA	mare's tail *(Hippuris vulgaris)*					0.3	0.7734	0.3653	1.2165

For each year, I first constructed ordinations with 1-9 axes, with a maximum of 500 iterations for each configuration. I determined the appropriate number of axes for each data set by seeking low stress values (for ecological community data, $S<0.20$ are acceptable) and beyond which additional axes resulted in low reductions of stress (McCune and Grace 2002). I then constructed multiple (>10) ordinations with the chosen number of axes, and visually examined them to ensure reproducibility.

I then investigated how patterns of vegetation species composition reflected in NMDS ordinations were related to environmental and biological covariates of plot elevation (Elev), mean number of goose nests (Nests), number of years within the colony (YrsIn), and number of years since retraction of the colony (YrsRet, 2017 only) by vector overlays on the NMDS ordination using the function *envfit*. I used Pearson correlation coefficients between environmental and biological variables and NMDS scores to define the strength of correlations with ordination axes, with significance determined using 999 permutations. I derived goose covariates (Nests, YrsIn, YrsRet)) for each plot from long-term data described in Chapters 1 and 2. I extracted elevation data for each plot from the Federal Geospatial Platform of Canada (https://maps.canada.ca/), and thus, my analyses contain information licensed under the Open Government Licence – Canada (https://open.canada.ca/en/open-government-licence-canada). This raster data provided spatial resolution of 20 m. I used the *bilinear* function to interpolate elevation from the four nearest cells for each plot (±0.1 m).

In this chapter, I focus on vegetation communities in 1999 and 2017. Many plots were sampled in both years and so these are not independent assessments, but represent snapshots of plant communities temporally separated by nearly two decades. As well, I sampled areas outside the colony in these years, allowing for comparisons of vegetation communities inside the colony with areas outside the colony not occupied by nesting geese or had experienced recent retraction of the colony boundary. I refer readers to Appendix B for results for 1998, 2010, and 2014 (Fig. B.1, B.2, and B.3, respectively).

3.2.2.2 Lowland vegetation communities across the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary

I used NMDS with Bray Curtis distance (package *vegan*, Oksanen et al. 2019) to characterize vegetation communities in a combined sample of (*i*) 49 randomly-selected plots across the Sanctuary (Sanctuary subsample, Fig. 3.1) sampled in 2014, and (*ii*) systematically-spaced lowland plots in and near the nesting colony at Karrak Lake (Karrak Lake subsample) sampled in 2014. I included only lowland plots from the Karrak Lake subsample based on a combination of elevation and examining ordinations described above for sample plots as follows. Elevation of lowland plots from the Sanctuary subsample followed an elevation gradient from highest in the south-west and lowest near the coast, so I could not simply use that range of elevation (0-106 m above sea level (asl)) to identify lowland plots to include in the Karrak Lake subsample. Elevation of two lowland plots in the Sanctuary subsample that also were located in the Karrak Lake region had a mean elevation of 66 m. Examination of ordinations using all plots from the Karrak Lake subsample confirmed that species typical of lowland habitats (D. Kellett, pers. obs.) were found at elevations <74 m asl. Thus, I included only 87 plots in the Karrak Lake subsample with elevations of <74 m asl and examined effects of elevation on vegetation communities in analyses with vector overlay.

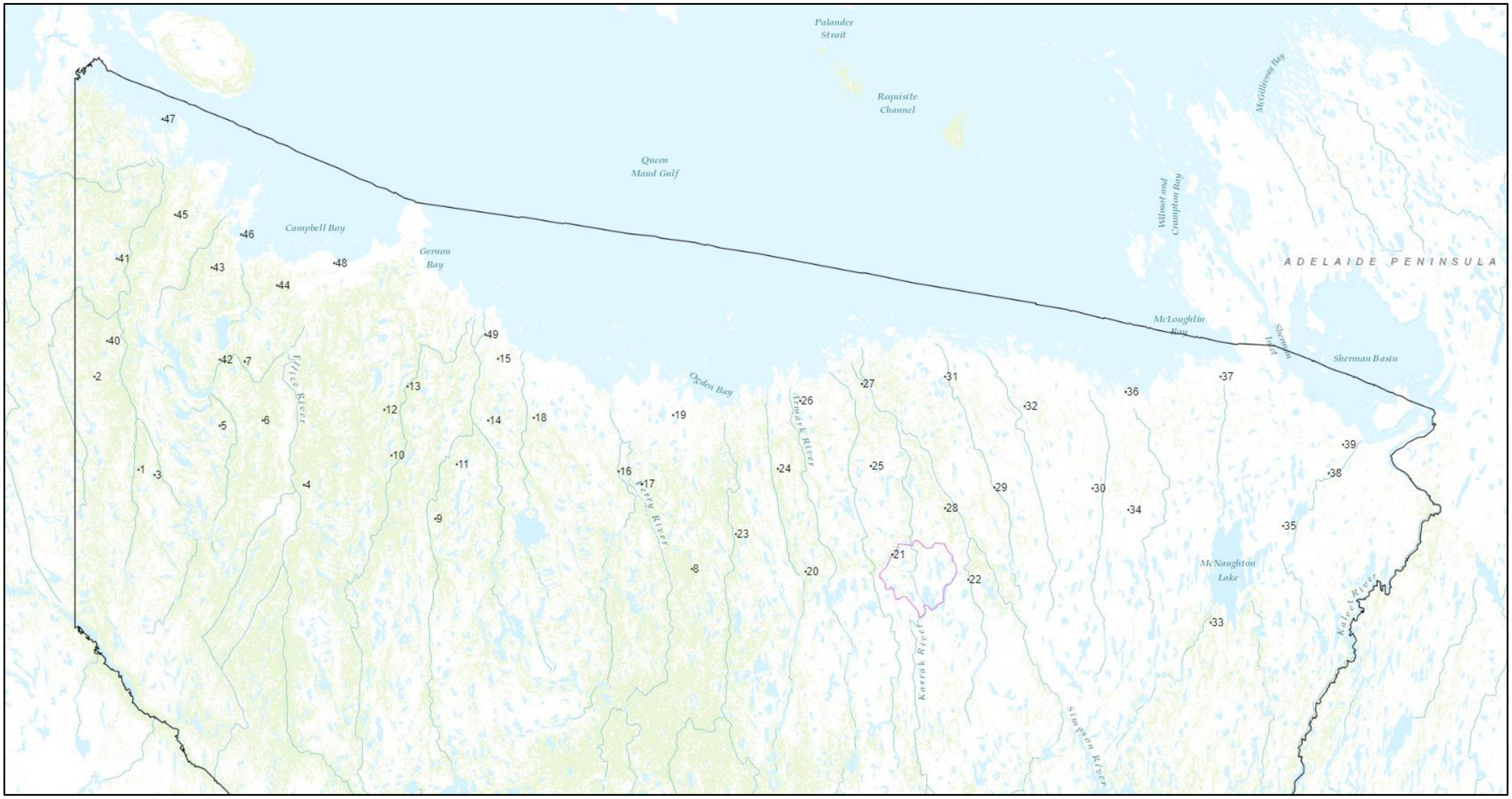

Figure 3.1. Map showing location of lowland plots (*n*=49) within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary sampled in 2014. The black line depicts the boundary of the Sanctuary (southern boundary not shown) and the purple polygon indicates the extent of the nesting colony of snow and Ross’s geese in 2014.

I compiled input data by first converting each species or species group to proportions so the Sanctuary and Karrak Lake subsamples could be directly comparable. I included only those species or species group in analyses in which occurrence across all plots was greater than 1%, with the exception of marsh ragwort, for reasons given above (Table 3.2). Using the same criteria as above to determine the appropriate number of axes, I chose among ordinations with 1-9 axes, with a maximum of 500 iterations for each configuration. I then constructed multiple (<10) ordinations with the chosen number of axes and visually examined them to ensure reproducibility.

Table 3.2. Percent occurrence (%) of species and species groups and resulting axis loadings from nonmetric multidimensional scaling (NMDS) ordination of vegetation community data collected on 136 sample plots in lowland habitat within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut. Twelve species and species groups accounted for 97.1% of point-intersect observations.

Code	**Species or Species group**	**%**	**NMDS1**	**NMDS2**	**NMDS3**
LICH	all lichen species	3.6	-0.9706	-0.4732	-0.0637
PEAT	dead moss species	11.2	0.4726	-0.2273	-0.1710
SPHA	*Sphagnum* spp.	3.5	0.1124	0.4490	0.8769
MOSS	all moss species	7.8	0.2136	0.3573	-0.2537
GRAM	graminoids (grass and sedge spp.)	25.3	0.7887	-0.3189	0.0359
BIRC	birch *(Betula glandulosa)*	12.9	-0.2285	0.2649	0.0675
WILL	willows *(Salix* spp.)	6.2	0.6282	0.1994	-0.1050
CRAN	cranberry *(Vaccinium vitis-idaea)*	10.3	-0.6277	0.0576	0.0434
LABT	Labrador tea *(Ledum palustre)*	11.3	-0.7358	-0.1608	0.0067
HEAT	white heather *(Cassiope tetragona)*	3.5	-0.9197	-0.3388	-0.1368
RAGW	marsh ragwort *(Tephroseris palustris)*	0.4	-0.5122	0.7266	-0.5632
MACI	marsh cinquefoil *(Comarum palustre)*	1.1	0.6951	0.4385	0.7658

As above, I investigated how patterns of vegetation species composition were related to environmental and biological covariates of plot elevation (Elev) and location of plots relative to a light goose nesting colony (Colony (in or out)) by vector and ellipse overlays on the ordination, respectively. For ellipse overlays, I used function *ordiellipse* to draw ellipses for each group with 95%CI of standard deviations of point scores. I considered distances of <5 km to be associated with a nesting colony (Colony=in), as I reasoned that vegetation within ~5 km was likely impacted primarily by nesting geese as opposed to brood-rearing geese. Conkin and Alisauskas (2017) demonstrated that increase in exposed peat was minimal at ~15 km from large nesting colonies, but impact outside of nesting colonies may have been due to brood-rearing geese. As before, I extracted elevation data for each plot from the Federal Geospatial Platform of Canada (https://maps.canada.ca/).

I repeated this NMDS analysis *a posteriori* using only the sample of 49 randomly-selected lowland plots in the Sanctuary. I was motivated to do so by concerns of bias in the initial analysis due to oversampling in the Karrak Lake region. I included nine species and species groups in construction of the ordination based on the 1% occurrence guideline: those included in the initial analysis with exclusion of lichen, white heather, and marsh ragwort. As before, I investigated how vegetation patterns related to environmental and biological covariates using vector and ellipse overlays for continuous and categorical covariates, respectively. I included plot elevation (Elev) and location of plots relative to a light goose nesting colony (Colony), as before. As only six plots in this sample were inside nesting colonies (Colony=in), I included distance to the perimeter of the nearest colony (Dist) as an additional continuous covariate. I also included density of goose droppings (Droppings) measured along a 25 m transect as an index of goose presence on plots; I did not include the Droppings covariate in the initial analysis because these data were not available for the Karrak Lake subsample.

3.2.2.3 Vegetation community species richness near the Karrak Lake nesting colony

I used linear models to investigate variation in vegetation species richness (SppRich, number of species or species groups detected) on sample plots in and near the nesting colony at Karrak Lake in 2017. I note that because I assigned some species to species groups (i.e., a species group contains multiple species) that this is an index of species richness, but one that is comparable across sites in my study. I used mean number of goose nests (Nests), number of years in the colony (YrsIn), number of years since retraction of the colony (YrsRet), and elevation (Elev) as potential covariates explaining variation in SppRich. I examined Pearson's product-moment correlations among explanatory variables, and my candidate set of models did not include highly correlated variables in the same model. I tested residuals of the most-parameterized models {SppRich=YrsIn+YrsRet+Elev} and {SppRich=Nests+YrsRet+Elev} for normality and square root-transformed dependent variables as required. I used Moran's I to measure the degree of spatial autocorrelation both in raw data and the residuals of the most-parameterized models, and employed spatial models if required. I report results of normality of residuals and spatial autocorrelation of most-parameterized models from model {SppRich=YrsIn+YrsRet+Elev} for simplicity; results from model {SppRich=Nests+YrsRet+Elev} were equivocal. I used Akaike's Information Criterion for small sample sizes (AIC_c) to examine the relative fit of each candidate model, and incorporated model selection uncertainty by using a 90% confidence set of models (Akaike 1973, Burnham and Anderson 2002) from which I model-averaged slope values (and associated variance) of covariates.

I derived goose covariates (Nests, YrsIn, YrsRet) for each plot from long-term data described in Chapters 1 and 2. I extracted elevation data for each plot from the Federal Geospatial Platform of Canada (https://maps.canada.ca/).

3.2.2.4 State change in vegetation communities near the Karrak Lake nesting colony between 1998 and 2014

I classified vegetation communities on sample plots with hierarchical cluster analysis employing Bray-Curtis distance (package *vegan*, Oksanen et al. 2019) with combined data for 1998 and 2014, assigning each plot in each year to a class (i.e., state). I compiled input data by summing point-intersect observations of each taxon per plot. I included 14 taxa with either >1% representation across all plots in a given year, or those thought to be indicative of habitat change.

I fit multistate models implemented in Program MARK (White and Burnham 1999) to model habitat change (transition between habitat classes assigned by hierarchical clustering, described above) on sample plots between 1998 and 2014. Multistate models allow estimation of probabilities of survival (S) and recapture or detection (p) probabilities, and transition among states (ψ). My sample consisted of plots for which vegetation surveys were conducted in both

1998 and 2014, thus, both *S* and *p* were absolute so I fixed these values to 1. I predicted that transition between habitat states would be influenced by extent of use by nesting geese (Nests) and the number of years plots were exposed to nesting geese (YrsIn), and may be differentially influenced by number of years since retraction of the colony boundary (YrsRet); these covariates were derived from long-term data, to 2014, as described above. I reasoned that these variables were likely to influence transition between habitat states differently and so only included interactive models involving these covariates in the candidate set.

My most general model was $\{S(=1)\ p(=1)\ \psi((h*\text{Nests})+(h*\text{YrsIn})+(h*\text{YrsRet}))\}$, where both *S* and *p* were fixed at 1, and ψ varied interactively in response to habitat type, h, and Nests, YrsIn, and YrsRet. Goodness-of-fit (GOF) test can only be tested on models without covariates so I conducted bootstrap GOF testing on model $\{S(=1)\ p(=1)\ \psi(h)\}$. The estimate of c-hat was 1, so I used Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002) to examine the relative fit of nine *a priori* candidate models to data. My candidate set of models included all possible combinations for parameterizations of ψ. To aid in numerical convergence, particularly of more complicated models, I used initial parameter estimates (provided by model $\{S(=1)\ p(=1)\ \psi(h)\}$) to ensure that I arrived at global (and not local) maxima. In the final candidate set of models, I retained the model of a given parameterization based on the best estimation (estimable standard errors, correct number of parameters estimated). I used multinomial logit link function for ψ estimation so that transitions from a given habitat summed to one. I based inference on model-averaged parameter and slope estimates (β) from a 90% confidence set of models.

3.3 Results

3.3.1 Vegetation communities near the Karrak Lake nesting colony

3.3.1.1 NMDS 1999

I sampled 167 plots within and near the goose colony at Karrak Lake in 1999. Ordination of 12 species or species groups accounting for 98.2% of point-intersect observations resulted in a three-dimensional solution capturing 29.4% of variation in the ranked distance matrix (Table 3.1, Fig. 3.2). I used three axes for the final configuration because convergence was achieved easily (20-50 iterations over multiple attempts), reproducible (plots were very similar) and stress was minimal (0.131) and only slightly greater than an ordination using four axes (0.098). In comparison, an ordination using only two axes had stress of 0.180.

The second axis of the 3-axis ordination represented the biological covariates of number of years in colony (YrsIn) and mean number of goose nests (Nests). Number of years in colony was strongly correlated only with the second axis (-0.997) and not with the first or third axes (0.077 and 0.024, respectively, r^2=0.374, p<0.001, Fig. 3.1). Likewise, Nests was most strongly correlated with the second axis (-0.938) compared with the first and third axes (0.136 and 0.318, respectively, r^2=0.495, p<0.001, Fig. 3.2). Thus, positive axis 2 (NMDS2) values represented communities composed of species typically associated with habitats less disturbed by geese (Table 3.1, Fig. 3.2). Elevation (Elev) was not strongly associated with any single axis but most correlated with the third axis (-0.646) than with the first or second axes (0.504 and -0.573, respectively, r^2=0.191, p<0.001, Fig 3.2).

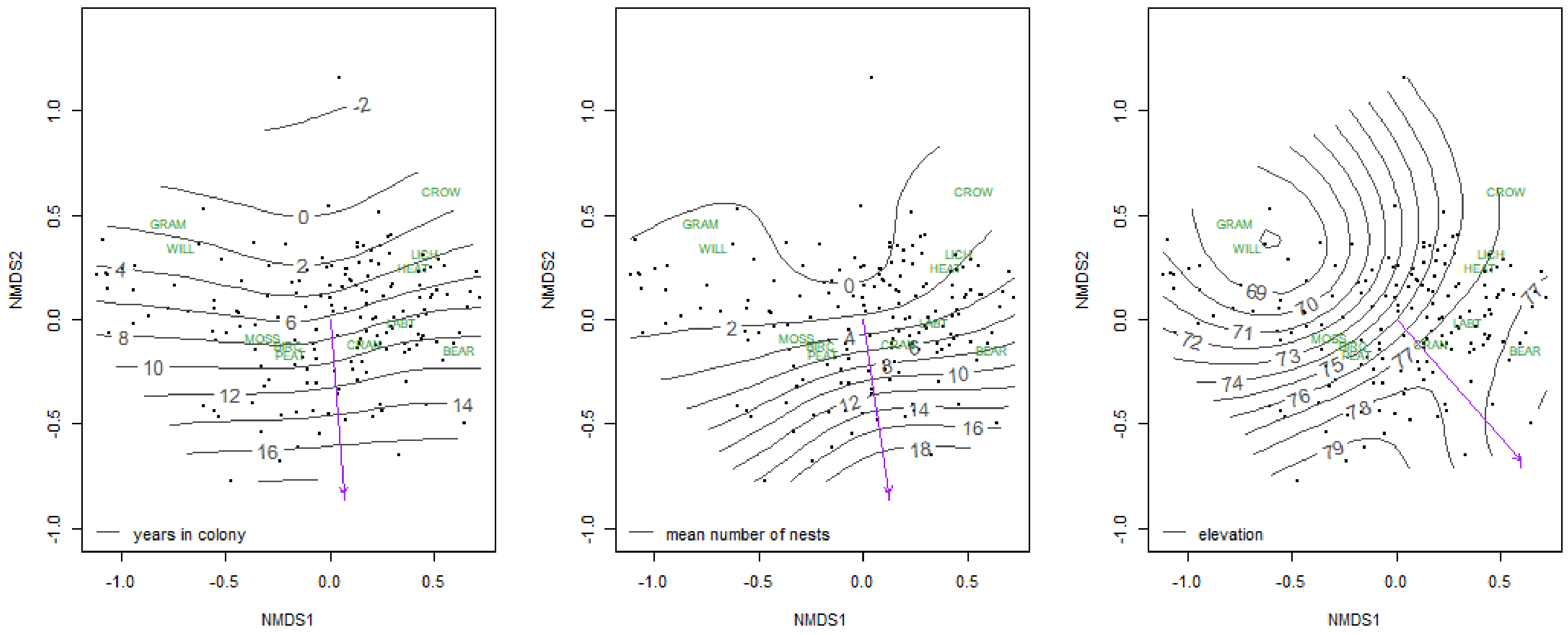

Figure 3.2. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 12 vegetation taxa on 167 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 1999. The three axes (third axis not shown) captured 29.4% of variation in the ranked matrix, with axes 1-3 capturing 16.3, 7.4, and 5.7% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel (left: years in colony (YrsIn), middle: mean number of nests (Nests), right: elevation (Elev)), with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are also shown for each covariate. Species and species groups: LICH, all lichen species; PEAT, dead moss species; MOSS, all moss species; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows (*Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; CROW, crowberry *(Empetrum nigrum)*; BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris)*.

3.3.1.2 NMDS 2017

I sampled 256 plots within and near the goose colony at Karrak Lake in 2017. Ordination of 17 species or species groups, accounting for 98.4% of point-intersect observations, resulted in a three-dimensional solution capturing 24.1% of variation in the ranked distance matrix (Table 3.1, Fig. 3.3). I used three axes for the final configuration because convergence was achieved easily (68-323 iterations over multiple attempts), reproducible (plots were very similar) and stress was minimal (0.147) and only slightly greater than an ordination using four axes (0.117). In comparison, an ordination using only two axes did not achieve convergence after 1000 iterations and estimated (but unreliable) stress was 0.195.

Similar to vegetation data from 1999, the second axis of the ordination for the 2017 data represented the biological covariates of YrsIn, Nests, and time since retraction of the colony boundary (YrsRet). Number of years in colony was strongly correlated with the second axis (-0.944) and not with the first and third axes (0.071 and -0.322, respectively, r^2=0.324, p<0.001, Fig. 3.3). Likewise, Nests was strongly correlated with the second axis (-0.978) and not with the first or third axes (0.094 and -0.182, respectively, r^2=0.356, p<0.001, Fig. 3.3). Despite small sample size limiting inference (only 37 of 256 plots experienced cessation of nesting geese), years since retraction was also correlated with the second axis (0.945) and not the first or third axes (-0.062 and 0.320, respectively, r^2=0.080, p<0.001), but in the opposite direction to YrsIn and Nests (Fig. 3.2). Thus, as for 1999 data, positive axis 2 values characterized communities composed of species typically associated with habitats less disturbed by geese (Table 3.1, Fig. 3.3). Elev was not associated with any one axis, but was more strongly correlated with the first axis (-0.789) than with the second or third axes (0.614 and -0.041, respectively, r^2=0.117, p<0.001, Fig 3.3).

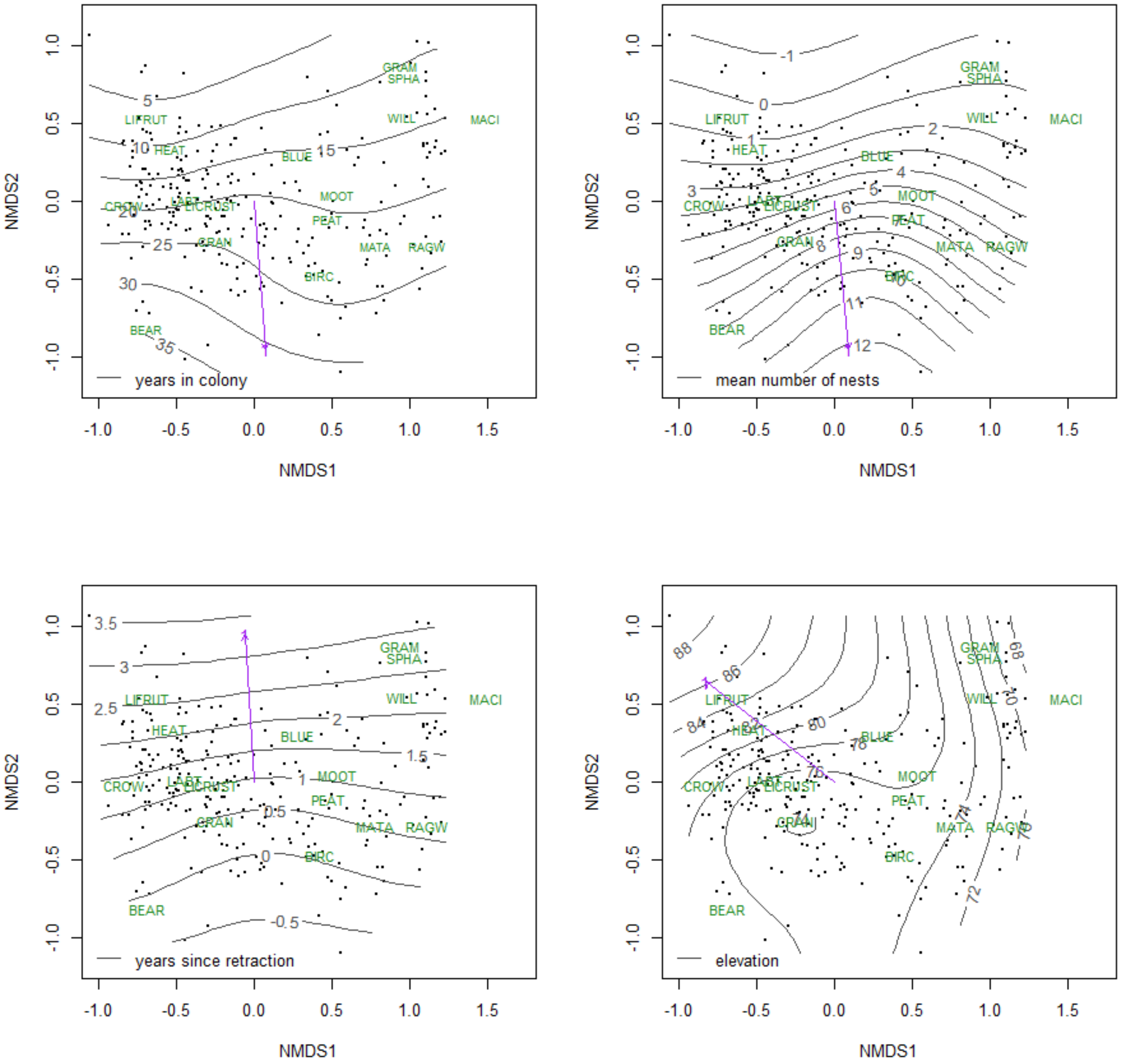

Figure 3.3. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 17 vegetation taxa on 256 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2017. The three axes (third axis not shown) captured 24.1% of variation in the ranked matrix, with axes 1-3 capturing 14.2, 6.0, and 3.9% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel (top left: years in colony (YrsIn), top right: mean number of nests (Nests), bottom left: years since colony retraction (YrsRet, bottom right: elevation (Elev)), with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are also

shown for each covariate. Species and species groups: LICRUST, lichen species with crustose growth form; LIFRUT, lichen species with fruticose growth form; PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOOT, moss species other than *Sphagnum* spp.; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; CROW, crowberry *(Empetrum nigrum)*; BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; BLUE, blueberry (*Vaccinium uliginosum*); RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*).

3.3.2 Lowland vegetation communities across the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary.

I included 136 plots in the Sanctuary ordination; 49 from the randomly-selected lowland plots throughout the Sanctuary (Sanctuary subsample), and 87 lowland plots in the Karrak Lake region (Karrak Lake subsample). Ordination of 12 species or species groups, accounting for 97.1% of point-intersect observations, resulted in a three-dimensional solution capturing 35.1% of variation in the ranked distance matrix (Table 3.2). I used three axes for the final configuration because convergence was achieved easily (29-55 iterations over multiple attempts), reproducible (plots were very similar) and stress was minimal (0.102) and only slightly greater than an ordination using four axes (0.080). In comparison, an ordination using only two axes did not achieve convergence after 1000 iterations and imprecisely estimated stress (0.141). The first axis represented disturbance by geese. Ellipses for plots inside (in) and outside (out; variable Colony) of nesting colonies were separated on the ordination plot along the first axis, as indicated by the centroids of each ellipse (In (axis1: -0.285, axis2: 0.041, axis3: 0.013, n=93), Out (axis1: 0.617, axis2: -0.090, axis3: -0.029, n=43), r^2=0.327, p<0.001, Fig. 3.4). Elev was similarly correlated with the first and second axes (-0.709 and 0.583, respectively), and less with the third axis (0.397, r^2=0.477, p<0.001, Fig 3.4).

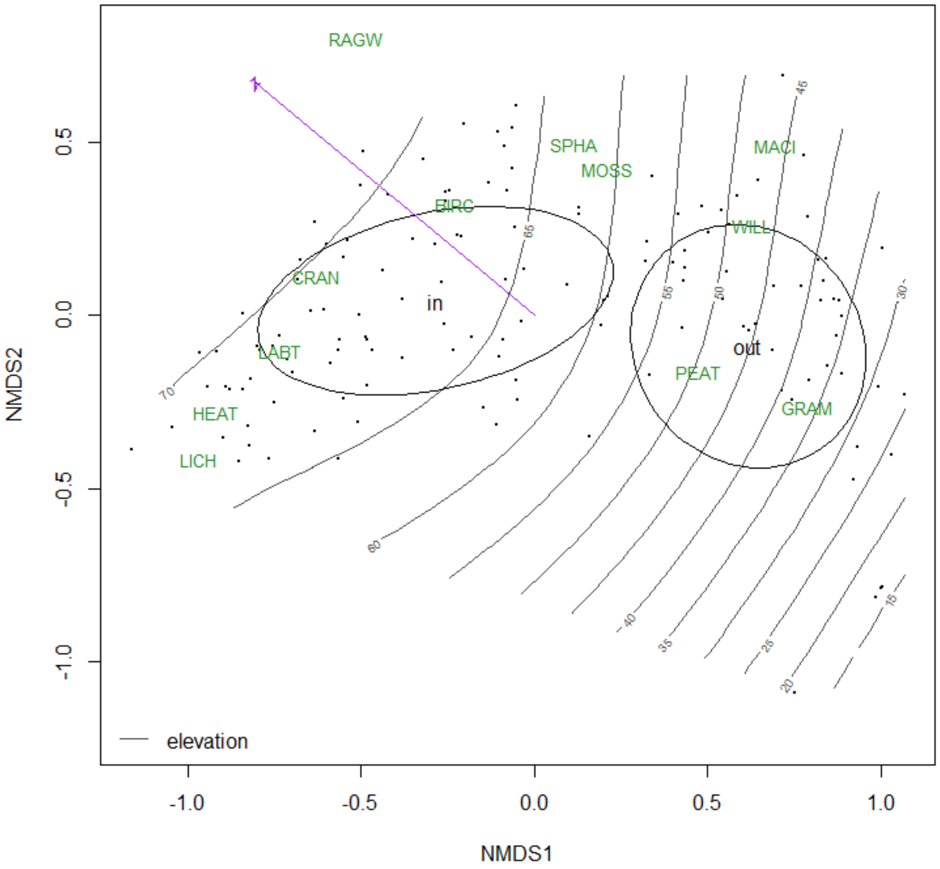

Figure 3.4. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 12 vegetation taxa on 136 sample plots in lowland habitat within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut, in 2014. Included in this sample are randomly selected plots within the Sanctuary (*n*=49) and plots in and near the nesting colony at Karrak Lake (*n*=87). The three axes (third axis not shown) captured 35.1% of variation in the ranked matrix, with axes 1-3 capturing 22.0, 15.1, and 10.2% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlay representing of elevation is depicted by the purple arrow, with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for elevation. Ellipses represent centroids (position of label) and standard deviations of points (perimeter defining ellipse) for plots inside (in) and outside (out) of snow and Ross's goose nesting colonies. Species and species groups: LICH, all lichen species; PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOSS, all moss species; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*).

Motivated by concern of possible bias in the initial analysis due to relative oversampling in the Karrak Lake region, I repeated the above analysis using only the Sanctuary subsample (*n*=49 plots), as a check. Excluding rare species contributing <1% of point intersect observations, ordination of 9 species or species groups, accounting for 98.8% of observations, resulted in a three-dimensional solution capturing 44.4% of variation in the ranked distance matrix. I used three axes for the final configuration because convergence was achieved easily (20 iterations over all attempts), reproducible (plots were very similar) and stress was minimal (0.116) and only slightly greater than an ordination using four axes (0.078). In comparison, stress for an ordination with two axes was 0.177. As before, all covariates were most strongly correlated with the first axis, so this axis appears to represent both an elevational gradient and use by geese, but these could not be separated. Elev was strongly correlated with the first axis (-0.981) and not with the second or third axes (-0.091 and -0.170, respectively, r^2=0.303, p<0.001, Fig 3.5). Density of goose droppings (Droppings) was also strongly correlated with the first axis (0.937) and less so with the second or third axes (0.274 and 0.217, respectively) but not significantly (r^2=0.130, p=0.101, Fig 3.5). Distance to nearest nesting colony (Dist) was most strongly correlated with the first axis (-0.843) and less so with the second or third axes (0.518 and -0.144, respectively, r^2=0.288, p<0.001, Fig 3.5), and as expected, in the opposite direction as Droppings. The ellipses defining inside and outside of nesting colonies were not significantly different but separated most along the first axis (in (axis1: 0.351, axis2: -0.179, axis3: -0.002, *n*=6) versus out (axis1: -0.049, axis2: 0.025, axis3: -0.002, *n*=43), r^2=0.042, p=0.101, Fig. 3.5). Thus, these results were similar to the initial analysis, but less conclusive.

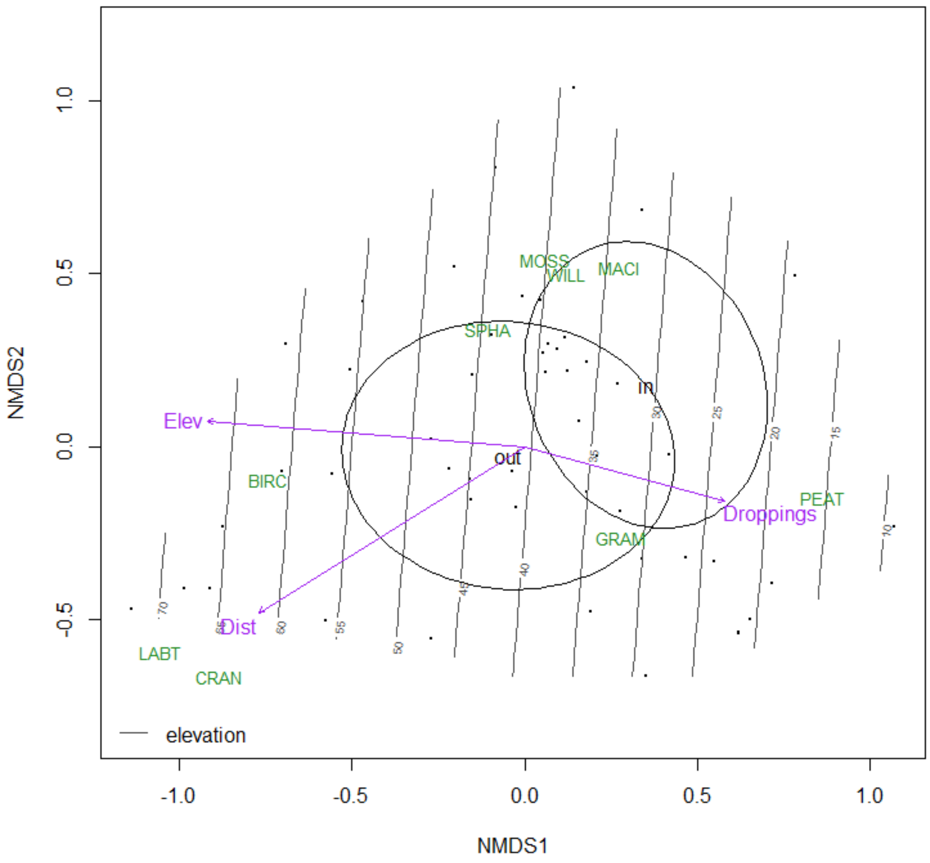

Figure 3.5. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 9 vegetation taxa on 49 sample plots in lowland habitat within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut, in 2014. The three axes (third axis not shown) captured 44.4% of variation in the ranked matrix, with axes 1-3 capturing 19.1, 15.1, and 10.2% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays representing of distance to nearest nesting colony of snow and Ross's geese (Dist), density of goose droppings (Droppings), and elevation (Elev) are depicted by purple arrows labelled with respective covariates, with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for elevation. Ellipses represent centroids (position of label) and standard deviations of points (perimeter defining ellipse) for plots inside (in) and outside (out) of snow and Ross's goose nesting colonies. Species and species groups: PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOSS, all moss species; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*).

3.3.3 Richness of vegetation communities near the Karrak Lake nesting colony.

Species richness (SppRich) on 256 sampled plots in 2017 ranged between 1-14 taxa (species and species groups). I reported numerical range and correlation of covariates in Chapter 2; because Nests and YrsIn were the most highly correlated, these effects were not included in the same model. Thus, the resulting candidate set had 12 models, including an intercept-only model and all possible combinations of single effects.

Transformation of SppRich did not improve normality of residuals in the most-parameterized model (W=0.893, $p<0.001$ versus W=0.985, $p=0.009$), so I analyzed untransformed values. Monte Carlo simulation of Moran's I for SppRich indicated no spatial autocorrelation of raw data (Moran's I=-0.035, $p=0.945$) or of residuals from the most-parameterized model (Moran's I=-0.040, $p=0.955$), so I did not employ spatial models in this analysis.

The 90% confidence set was composed of nine models that included effects of Nests, YrsIn, YrsRet, and Elev (Table 3.3). Species richness was higher for those areas with longer times since colony retraction, as the confidence interval barely bounded zero (0.073 (95% CI: -0.004, 0.149) and was included in most of the top models of the confidence set. This was somewhat surprising, given small sample size limiting inference (only 37 of 256 plots experienced cessation of nesting geese) and relatively short time periods (1-17 years since retraction). Model-averaged estimates of slopes for all other covariates included zero (Elev: -0.001 (-0.032, 0.030); YrsIn: -0.009 (-0.035, 0.018); Nests: 0.002 (-0.053, 0.056)).

Table 3.3. Model selection results based on Akaike's Information Criterion adjusted for sample size (AIC_c) of species richness (number of species and species groups) on 256 sample plots at Karrak Lake, Nunavut, 2017. All candidate models are shown. Model variables are plot-specific and included number of years in the goose nesting colony (YrsIn), number of years since retraction of the colony (YrsRet), mean number of nests (Nests, 1991-2017), and Elevation (Elev). I present the number of parameters (K), AIC_c values, the difference in AIC_c values between each model and the model with the lowest AIC_c value (ΔAIC_c), and normalized Akaike weights (ω_i).

Model	K	AIC_c	ΔAIC_c	ω_i
YrsRet	3	1110.2	0.0	0.281
Intercept only	2	1111.9	1.7	0.118
YrsIn+YrsRet	4	1112.0	1.8	0.112
Nests+YrsRet	4	1112.2	2.0	0.102
Elev+YrsRet	4	1112.2	2.0	0.102
YrsIn	3	1112.8	2.7	0.075
Nests	3	1113.9	3.7	0.045
Elev	3	1113.9	3.7	0.045
Elev+YrsIn+YrsRet	5	1114.1	3.9	0.041
Elev+YrsRet+Nests	5	1114.3	4.1	0.037
Elev+YrsIn	4	1114.9	4.7	0.027
Elev+Nests	4	1115.8	5.7	0.017

3.3.4 State change in vegetation communities near the nesting colony at Karrak Lake between 1998 and 2014

I classified 476 plots (n_{1998}=188, n_{2014}=288) in hierarchical cluster analysis. I cut the resulting dendrogram to seven habitat states and then visually inspected taxa means for each state (similar to Table 3.4) to determine potential similarities among them. I combined some states to reduce complexity in the number of possible transition probabilities for estimation in multistate modeling, as follows. Of the seven states identified by cluster analysis, I considered four (each with *n*=231, 7, 1, and 2 plots) as upland (*UP;* habitat states given in italicized capitals to distinguish from species codes) habitat; these classes were characterized by highest occurrence of LICH and xeric species such as BEAR and CROW, as well as high occurrence of LABT, CRAN, and HEAT typical of both mesic and xeric habitats (Table 3.4). I considered two of seven states (each with *n*=43 and 46 plots) as lowland graminoid (*GRAM*) habitat; these classes exhibited highest occurrence of GRAM, MOSS (mainly *Sphagnum* spp.), and WILL, all typically occurring in hydric to mesic habitats (Table 3.4). I classified the remaining 146 plots as a state represented by birch (*BIRCH*) habitat, as these plots were characterized by highest incidence of BIRC with presence of PEAT, CRAN, and LABT (Table 3.4). I then used these resulting habitat classes of *UP*, *GRAM*, and *BIRCH* as states in multistate modeling.

Table 3.4. Mean (±1SD) number of point-intersections (of possible 120) for each species or species group in upland (*UP*, *n*=241 plots), birch (*BIRCH*, *n*=146 plots), and graminoid (*GRAM*, *n*=89 plots) habitats within and immediately outside of the snow and Ross's goose colony at Karrak Lake, Nunavut. I determined habitat states by hierarchical cluster analysis of 476 plots sampled in 1998 and 2014. Species and species groups: GRAM, graminoids (grass and sedge spp.); MOSS, all moss species; LICH, all lichen species; BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); LABT, Labrador tea *(Ledum palustre);* CRAN, cranberry *(Vaccinium vitis-idaea)*; CROW, crowberry *(Empetrum nigrum)*; BEAR, bearberry (*Arctous* spp.); HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*); PEAT, dead moss species.

	Habitat class		
Species or species group	*UP*	*BIRCH*	*GRAM*
GRAM	2.6 (4.8)	4.9 (7.7)	31.1 (22.1)
MOSS	7.6 (8.2)	16.2 (10.9)	31.3 (22.1)
LICH	23.3 (16.5)	3.9 (5.2)	3.5 (5.5)
BIRC	4.3 (5.4)	22.3 (15.0)	7.7 (8.4)
WILL	1.0 (2.3)	3.9 (5.7)	9.3 (11.4)
LABT	22.3 (11.2)	13.0 (9.4)	6.5 (8.9)
CRAN	13.9 (10.7)	15.0 (9.8)	8.3 (7.6)
CROW	1.4 (2.1)	0.6 (1.8)	0.3 (1.7)
BEAR	2.4 (4.9)	0.4 (1.3)	0.6 (1.8)
HEAT	8.7 (6.9)	3.6 (5.2)	1.4 (3.6)
RAGW	0.1 (0.8)	1.5 (3.5)	0.5 (2.2)
MACI	<0.1 (0.3)	0.5 (2.3)	1.0 (3.9)
MATA	<0.1 (0.4)	0.7 (2.2)	<0.1 (0.3)
PEAT	2.9 (4.0)	20.8 (17.2)	9.2 (10.5)

Individual covariates associated with 156 paired plots (sampled in both 1998 and 2014) ranged from: Nests (0-34.5 nests), YrsIn (0-49 years), and YrsRet (0-14 years). The top two models (combined weight of 0.994) describing transition probability among habitat states contained covariates Nests and YrsIn (Table 3.5). Model-averaged slope estimates from these two models suggested that probability of state transition from *GRAM* to *UP* and from *GRAM* to *BIRCH* over this 16-year period was directly related to Nests ($\beta_{\mathrm{Nests}*GRAM\rightarrow UP}$: 0.740 (95%CI: 0.141, 1.340); $\beta_{\mathrm{Nests}*GRAM\rightarrow BIRCH}$: 0.904 (0.328, 1.481)); all other 95% CI of slope values for Nests included zero. All 95% CI of slope estimates for influence of YrsIn on transition probabilities among habitats included zero.

Table 3.5. Candidate model set for transition probabilities (ψ) among upland (*UP*), graminoid-dominated lowland (*GRAM*), and birch-dominated lowland (*BIRCH*) habitat states between 1998 and 2014 on 156 sample plots within and immediately outside of the snow and Ross's goose colony at Karrak Lake, Nunavut. Parameters estimated were transition between *UP*, *GRAM*, and *BIRCH* states, while survival (S) and detection probability (p) were fixed at 1. Shown for each model are the difference in sample-size-corrected Akaike Information Criterion (AIC_c) relative to the top model ($\Delta\mathrm{AIC}_c$; minimum value of the top model was 207.617), relative model weight (ω_i), number of parameters (K), and model deviance.

Model	**$\Delta\mathrm{AIC}_c$**	**ω_i**	**K**	**Deviance**
S(1) p(1) ψ((h*Nests))	0.0	0.581	12	181.435
S(1) p(1) ψ((h*Nests)+(h*YrsIn))	0.7	0.413	18	167.307
S(1) p(1) ψ((h*Nests)+(h*YrsRet))	11.9	0.001	18	178.562
S(1) p(1) ψ((h*YrsIn)+(h*YrsRet))	12.1	0.001	18	178.698
S(1) p(1) ψ((h*Nests)+(h*YrsIn)+(h*YrsRet))	12.2	0.001	24	162.672
S(1) p(1) ψ(h)	13.0	0.001	6	208.078
S(1) p(1) ψ((h*YrsRet))	13.5	0.001	12	194.894
S(1) p(1) ψ((h*YrsIn))	16.9	0.000	12	198.315
S(.) p(.) ψ(.)	96.4	0.000	2	299.932

Transition probabilities varied among habitats, and model-averaged estimates (including effects of covariates) were highest for *GRAM* habitat (Table 3.6); of 47 plots classified as *GRAM* in 1998, only 8 plots persisted as *GRAM* in 2014, and sum of transition probabilities to a different state ($\psi_{GRAM\rightarrow BIRCH}$=0.843, $\psi_{GRAM\rightarrow UP}$=0.139) was 0.982. Of 24 plots classified as *BIRCH* in 1998, 19 remained as *BIRCH* in 2014, with a sum of transition probabilities to a different state ($\psi_{BIRCH \rightarrow GRAM}$=0.045, $\psi_{BIRCH \rightarrow UP}$=0.109) of 0.154 (Table 3.6). Of 85 plots classified as *UP* in 1998, 65 remained as *UP* in 2014, with a sum of transition probabilities to a different state ($\psi_{UP \rightarrow BIRCH}$=0.197, $\psi_{UP \rightarrow GRAM}$=0.012) of 0.209 (Table 3.6).

Table 3.6. Model-averaged transition probabilities estimated with multistate models between upland (*UP*), graminoid-dominated lowland (*GRAM*), and birch-dominated lowland (*BIRCH*) habitats between 1998 and 2014 on 156 sample plots within and adjacent to the snow and Ross's goose colony at Karrak Lake, Nunavut.

ψ	**Estimate**	**SE**	**L95%CI**	**U95%CI**
UP → *GRAM*	0.012	0.016	0.001	0.152
UP → *BIRCH*	0.197	0.050	0.118	0.312
GRAM → *UP*	0.139	0.060	0.057	0.300
GRAM → *BIRCH*	0.843	0.063	0.679	0.931
BIRCH → *UP*	0.109	0.095	0.017	0.456
BIRCH → *GRAM*	0.045	0.055	0.004	0.362

3.4 Discussion

Exposed peat in arctic regions can result from hydrological fluctuations by drawdown in lowland areas and under abnormally dry conditions in upland areas (Didiuk and Ferguson 2005). However, remote sensing work by Conkin and Alisauskas (2017) concluded that substantial increase of exposed peat in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary was due to ornithogenic effects of foraging and nesting by high densities of light geese, and this study supports that contention. I also demonstrate previously unreported shifts in species composition of arctic plant communities in upland and lowland habitats within the large nesting colony at Karrak Lake due to these ornithogenic effects.

3.4.1 Lowland communities used by flightless geese

Within lowland communities frequented by molting and brood-rearing light geese after departure from the nesting colony, incidence of exposed peat observed during ground-based vegetation surveys increased with density of goose droppings and declined with distance from goose colonies (Fig. 3.5), corroborating remote-sensing investigations (Conkin and Alisauskas 2017). However, I did not detect a drastic shift in species composition within these vegetation communities with increasing goose density. Graminoid and *Sphagnum* species were less prevalent in areas with more geese, as indexed by density of droppings and association with nesting colonies, but I did not detect a strong presence of colonizing species (Kerbes et al. 1990, Alisauskas et al. 2006) within these altered communities. Although marsh ragwort was visible on a landscape scale (i.e., from an aerial vantage point, D. Kellett pers. obs.), this species was not included in ordination analyses due to its rarity during vegetation surveys. Marsh cinquefoil, however, was included in ordinations, but without strong association with altered habitat composed of exposed peat (Fig. 3.5).

3.4.2 Lowland and upland community change at the Karrak Lake nesting colony

3.4.2.1 Species composition

Plant communities vary along abiotic gradients such as topography, moisture, and soil properties (McNaughton 1983, Gough et al. 2000, Handa et al. 2002, Jones and Henry 2003, Suvanto et al. 2014, Steward et al. 2016). Within the variation of plant communities imposed by abiotic gradients (e.g., elevation), I detected pronounced shifts in species composition of plant communities within the nesting colony at Karrak Lake due to variation in intensity of use by light geese (Fig. 3.2, 3.3). Compared to lowland areas outside of colonies that receive only foraging pressure by mobile flocks, light geese occupy nesting colonies for longer durations: birds initiate nesting shortly after arrival to colonies and remain there for the approximately 30-day laying and incubation periods, leaving colonies shortly after hatch (Jónsson et al. 2020, Mowbray et al. 2020). Much of this occupancy occurs before growth of aboveground production, placing disproportionate foraging pressure on belowground plant biomass. Together with cumulative impacts to vegetation communities by incorporating vegetation into nests (McCracken et al. 1997, Alisauskas et al. 2006), foraging and nesting resulted in shifts in species composition of both upland and lowland communities.

In upland habitats, fruticose lichens, crowberry and white heather were generally more abundant at low levels of disturbance (Fig. 3.2, 3.3). Lichen species were particularly sensitive to trampling (Manseau et al. 1996, Cooper et al. 2001), and geese incorporated lichens into nests (McCracken et al. 1997, D. Kellett pers. obs.). At high levels of disturbance, crustose lichens and bearberry were more prevalent (Fig. 3.2, 3.3; see also Appendix B). I did not include exposed mineral soil in plant community ordinations, but crustose lichens can readily colonize bare substrate (Belnap et al. 2001) and their presence is likely an indicator of exposed mineral soil resulting from vegetation removal and perhaps erosion of exposed peat in upland habitats. Bearberry forms a dense, prostate mat (Aiken et al. 2007) and whole plants (but occasionally leaves) are rarely used in nest construction (McCracken et al. 1997, D. Kellett pers. obs.), suggesting it is less easily uprooted. Cranberry and Labrador tea are widespread throughout the colony and occur within a wide range of elevations, but may also thrive in disturbed habitats (Manseau et al. 1996). As well, Conkin and Alisauskas (2017) reported conversion of upland habitats to exposed peat within nesting colonies. My multivariate analyses placed exposed peat in an intermediate position on the NMDS axis most correlated with elevation (Fig. 3.1 and 3.2), supporting observations of occurrence of exposed peat in upland as well as lowland areas. As well, I estimated state transition probability of 0.197 from upland habitat to birch habitat. Birch habitat contained substantial exposed peat, suggesting that conversion of disturbed upland plant communities to those containing exposed peat also occurs.

Disturbance to graminoid-dominated grazing lawns in lowland habitats within the nesting colony by foraging and nesting light geese resulted in an obvious and consistent shift in plant community species composition (see also Appendix B). At low levels of disturbance, NMDS ordinations demonstrated that graminoid, *Sphagnum*, and willow species dominated lowland communities (Fig. 3.2, 3.3). In areas subjected to intense and long-term nesting, altered lowland plant communities contained high incidence of peat, birch, non-*Sphagnum* moss species, marsh ragwort, and mare's tail (Fig. 3.2, 3.3), supporting observations by earlier investigations (Kerbes et al. 1990, Alisauskas et al. 2006, Fontaine and Mallory 2011, Conkin and Alisauskas 2017, Abraham et al. 2020). Non-Sphagnum mosses ('moss carpets', sensu Kotanen and Jefferies 1997, Fontaine and Mallory 2011), marsh ragwort, and marsh cinquefoil were previously identified as colonizers of disturbed inland northern habitats (Kerbes et al. 1990, Kotanen and Jefferies 1997, Alisauskas et al. 2006, Fontaine and Mallory 2011). I did not clearly identify marsh cinquefoil as a colonizer of disturbed habitats; at Karrak Lake, this species existed in intermediary positions on the NMDS axis correlated with disturbance by light geese, and generally occurred in more hydric conditions. Foraging by geese may speed desiccation of low-lying areas by increasing the rate of evaporation following removal of vegetation (Conkin and Alisauskas 2017), and marsh ragwort appears to thrive in such conditions (D. Kellett pers. obs.). In deeper basins where standing water remains, mare's tail colonized disturbed lowland areas at

Karrak Lake presumably formerly inhabited by graminoid species (wet sedge meadows, D. Kellett pers. obs.).

Overwhelmingly, however, birch was the most abundant species in altered habitats at lower elevations. As well, I estimated high transition probability (0.843 in a 16-year period) of graminoid-dominated to birch-dominated communities within the nesting colony. Conversion of upland to birch-dominated habitats also occurred within this same period, but less frequently (transition probability of 0.197). Conversion of wet sedge meadow habitat to low shrub and shrub thicket (primarily birch and willow species) also occurred, albeit at lower levels, within the Sanctuary (Conkin and Alisauskas 2017). Expansion of shrubs resulting from climate warming (Tape et al. 2006, Post and Pedersen 2008, Olofsson et al. 2009, Fraser et al. 2011, Elmendorf et al. 2012, Carlson et al. 2018, Beamish et al. 2020) likely at least partially explains the increase in birch observed in this study, but paradoxically, herbivory generally mitigates increased dominance of shrubs facilitated by climate change (Post and Pedersen 2008, Olofsson et al. 2009, Leffler et al. 2019, but see Carlson et al. 2018, Post et al. 2020). However, geese do not consume birch or willows (Kerbes et al. 1990, Gloutney et al. 2001) nor are these woody plants easily uprooted for nest construction (D. Kellett pers. obs.). Birch was more prevalent in heavily-used areas such as nesting colonies (Fig. 3.2, 3.3), suggesting that intense and long-term disturbance by light geese may function additively with climate change to expedite encroachment by birch. Shrub encroachment facilitated by climate change is most pronounced in warmer subarctic regions without permafrost or with discontinuous permafrost (Sturm et al. 2005, Fraser et al. 2011, Elmendorf et al. 2012, Beamish et al. 2020), but intense grazing of graminoids results in soil warming (Olofsson et al. 2004b) and may hasten shrub encroachment in this cooler arctic region. As well, birch responds to nutrient inputs (Gough et al. 2012), allowing this species to increase in goose-fertilized disturbed areas without competition from graminoids for nutrients, moisture or space. Once established, growth of birch may benefit from positive feedback involving increased snow accumulation, which provides insulation, moisture, and microbial-sourced nutrients (Sturm et al. 2005) as well as reduced shearing of branches by winter winds, leading to further growth and establishment.

3.4.2.2 Species richness

Foraging and nesting light geese had little impact on species richness in both upland and lowland vegetation communities within the nesting colony (Table 3.3). Although species composition of vegetation communities shifted to altered states, particularly at lower elevations, long-term occupancy by nesting light geese did not result in dominance by a limited number of species, at least within the range of occupancy experienced to date at Karrak Lake (but see Alisauskas et al. 2006). This contrasts with conditions along the west coast of Hudson Bay, in which long-term and intense occupancy by transient and nesting geese has reduced plant species richness (Handa et al. 2002).

Despite limited sample size, I found weak evidence for increase in species richness in areas that experienced retraction of the nesting colony (Table 3.3), suggesting that cessation of grazing and nesting pressure results in rapid reestablishment by locally eradicated species, particularly graminoids (see also Chapter 2). I suggest that future research strive to determine species of graminoids, willows, lichens, and mosses during vegetation surveys to investigate how plant species richness and succession among and within plant taxa or functional groups (e.g., graminoids) responds to release from grazing and nesting pressure by light geese.

3.4.3 Are bare substrate, exposed peat, or birch-dominated communities alternative stable states?

Alternative stable states are relatively resistant to change, but can exhibit rapid shifts to another state if forced (van der Wal 2006). Expressed differently (Beisner et al. 2003), a plant community in an alternative stable state returns to the same configuration after a small perturbation (e.g., optimal grazing of aboveground plant biomass), but may shift to a different equilibrium after a large perturbation (e.g., cumulative effects of intense grazing, grubbing, shoot-pulling, and nest construction). An alternative stable state of bare sediment in subarctic coastal regions that initially resulted from intense grazing by light geese can be maintained by positive feedback between soil salinity and plant regeneration, with the result that re-establishment of plant communities can be delayed even after complete cessation of grazing pressure (Iacobelli and Jefferies 1991, Svivastava and Jefferies 1996, Abraham and Jefferies 1997, Handa et al. 2002, Jefferies and Rockwell 2002, Jefferies et al. 2003, 2004; McLaren and Jefferies 2004, Abraham et al. 2005a, 2005b; O et al. 2005, Henry and Jefferies 2008).

I provide evidence that altered plant communities have potential to revert to former states upon cessation of intense grazing and nesting pressure, and are likely not alternative stable states. However, I am not confident that all birch-dominated communities will readily revert to former graminoid-dominated or upland communities, and suggest that more research is needed to determine eventual outcomes. Depending on the extent to which birch dominates such communities, it may be an alternative stable state in arctic inland regions, due to potential positive feedback between birch growth and establishment and snow catchment, as well as its unpalatability to geese and potential ability to out-compete graminoids for space, water, and nutrients. That is, once birch is established, it may become self-sustaining and continue to persist when its dominance reaches a threshold and geese no longer forage there, due to extirpation of graminoids. In this manner, birch-dominated communities may represent an alternative stable state, until other ecological factors perhaps such as a series of winters with little snow cover and high wind lead to its decline (Beamish et al. 2020). I suggest that future research may require a multidecadal perspective to test the hypothesis that birch-dominated communities represent an alternative stable state, by monitoring these habitats after cessation of intense foraging and nesting by light geese, which likely facilitated the ability of birch to establish and is at least partly responsible for its creation (Beisner et al. 2003).

3.5 Summary and Transition to Chapters 4 and 5

I demonstrated changes to plant biomass (Chapter 2) and species composition (this Chapter) of vegetation communities in response to herbivory and nesting by light geese within an arctic landscape mosaic of terrestrial plant communities. These herbivory and nesting effects were not uniform across the landscape, and together with influence of abiotic gradients, created a heterogeneous mosaic of habitat patches within the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary. However, impacts of light geese on vegetation communities have potential consequences for cohabitating species at various trophic levels, ranging from subterranean invertebrates and soil microbes to migrant and resident vertebrates. High nutritional quality of graminoid vegetation of grazing lawns maintained on molting and brood-rearing areas may benefit other herbivores such as caribou, muskoxen, and greater white-fronted (*Anser albifrons*) and cackling geese (*Branta hutchinsii*). Yet, reduction of biomass and/or changes to plant community species composition, the latter of which occurs primarily at nesting colonies, may have negative impacts on species that rely on less-disturbed communities for food and breeding habitat, such as shorebirds, passerines, and rodents. Considered to be ‘ecosystem engineers’, light geese can dramatically alter ecosystem structure; in Chapters 4 and 5, I investigate the impacts of vegetation changes on avian and arvicoline rodent communities, respectively.

CHAPTER 4: IMPACT OF HABITAT ALTERATION BY LIGHT GEESE ON DENSITY OF BROWN LEMMINGS

4.1 Introduction

Within food webs, direct and indirect interactions occur among and within trophic levels. For example, herbivores interact directly with producer trophic levels of their food webs through consumption of vegetation, and with consumer trophic levels by serving as prey. Such direct interactions can have reverberating indirect effects on many ecosystem components, with particularly pronounced impacts when herbivores are abundant. Intense foraging and nesting by high densities of lesser snow (*Anser caerulescens caerulescens*, hereafter snow geese) and Ross's geese (*Anser rossii*, collectively with snow geese referred to as light geese) have had effects on plant biomass and species composition of many northern vegetation communities (Chapters 2 and 3 and references therein). Such alteration of vegetation communities can influence sympatric species that rely on shared habitats for food or protection (Flemming et al. 2016).

In ecosystems with low primary production such as in many northern regions, low herbivore abundance may be insufficient to support functional predator communities, and such food webs are hypothesized to be dominated by plant-herbivore interactions (Oksanen and Oksanen 2000). However, substantial allochthonous inputs to subarctic and arctic ecosystems provided by migratory geese may benefit predators (Wilson and Bromley 2001, Gauthier et al. 2011, Samelius et al. 2007, 2011; Giroux et al. 2012). Light geese can serve as a seasonally abundant and, due to fidelity to breeding regions (Wilson et al. 2016), a predictable prey source for predators. Thus, seasonally abundant and predictable prey such as light geese influence functional and numerical responses of predators (Samelius et al. 2007, 2011; Giroux et al. 2012, McKinnon et al. 2013, Lamarre et al. 2017, Flemming et al. 2019a), and support predator communities. These impacts can potentially alter predator-prey dynamics with consequential impacts to other prey species (Flemming et al. 2016), including rodents. Thus, abundant light geese breeding in northern ecosystems have potential to affect sympatric species such as arvicoline rodents, which are foundational components of arctic ecosystems, through both bottom-up and top-down processes through changes to plant and predator communities, respectively.

Despite predictions of the exploitative ecosystem hypothesis, most evidence suggests that top-down processes, governed by predator-prey interactions, regulates population dynamics of northern lemmings and voles (Reid et al. 1995, 1997; Gilg et al. 2003, Krebs et al. 2003, Ims et al. 2011, Legagneux et al. 2012, Therrien et al. 2014, Fauteux et al. 2015, 2016; but see Kausrud et al. 2008, Bilodeau et al. 2013a, Domine et al. 2018 for climatic effects). Although foraging by arvicoline rodents can impact vegetation communities (Olofsson et al. 2004a, 2012, 2014; Oksanen et al. 2013, Bilodeau et al. 2014), hypothesized bottom-up regulation mediated by plant-herbivore interactions have received comparatively little empirical support (Pitelka and Batzli 2007). However, in ecosystems heavily grazed by sympatric herbivores such as light geese, food or shelter limitation in altered habitats, and thus, bottom-up processes, has the potential to limit population abundance of lemmings and voles (Samelius and Alisauskas 2009).

Few studies have investigated indirect effects of habitat alteration by light geese on arctic arvicoline rodent populations. Lemmings were reported as scarce near the East Bay light goose colony on Southampton Island, although no causative effect of goose abundance or associated habitat alteration was established (P. Smith, unpubl. data *in* Calvert 2015). Samelius and Alisauskas (2009) demonstrated decline in lemming abundance correlated with loss of aboveground plant biomass in lowland, but not upland, habitats near the large light goose nesting colony at Karrak Lake, and concluded that impacts to abundance was due to habitat alteration and not changes to predator-prey dynamics. To date, this has been one of very few studies linking negative effects of habitat alteration by geese to abundance of arvicoline rodents. However, habitat assessment by Samelius and Alisauskas (2009) was limited and the authors were unable to determine if differences in rodent abundance inside and outside the nesting colony was due to habitat alteration or presence of nesting geese.

I investigated potential effects of habitat alteration by light geese, as well as presence of light geese, on abundance of arvicoline rodents within lowland habitat in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary. Three species of arvicoline rodents exist within this region: collared lemmings (*Dicrostonyx torquatus*), brown lemmings (*Lemmus sibiricus*), and northern red-backed voles (*Myodes rutilis*). Brown lemmings most commonly inhabit lowland habitats (Batzli and Jung 1980, Batzli et al. 1983, Rodgers and Lewis 1986a, Samelius and Alisauskas 2009), and so I expected that this species would compose the majority of the sampled population. Brown lemmings consume graminoid, willow (*Salix* spp.), and moss species (Batzli and Jung

1980, Batzli and Pitelka 1983, Batzli et al. 1983, Rodgers and Lewis 1986b, Negus and Berger 1998, Soininen et al. 2015, Fauteux et al. 2017) and likely rely on adequately vegetated habitats for protection from predators (Batzli et al. 1983). Thus, I predicted brown lemmings to be more abundant in habitats less altered by geese that contained their preferred forage species (Chapter 3) and relatively high plant biomass (Chapter 2). Due to the relatively limited spatial extent in which I investigated variation in lemming density (see Methods), I did not expect variation in predator numerical or functional responses due to the presence or absence of light geese (Samelius et al. 2007, 2011) to exist and therefore influence abundance of brown lemmings. Yet, sympatric species may be disturbed by nesting and foraging activities of light geese (including territorial interactions, e.g., Baldwin et al. 2011), and so I predicted a negative response of lemming abundance to increasing density of nesting geese.

4.2 Methods

4.2.1 Field methods

I established four live-trapping grids in lowland habitat with locations determined from 2011 Landsat satellite imagery (see Conkin and Alisauskas 2017) and known distribution of nesting geese at Karrak Lake (Alisauskas et al. 2012b, R. Alisauskas unpubl. data). I chose lowland habitat for locations of all trapping grids from which to estimate density of rodents. This was because differences in vegetation biomass inside versus outside the colony boundary was far less pronounced in upland vegetation; unlike the strong reduction in small mammal density in lowland habitats from reduced vegetation structure due to nesting and foraging activities by geese, there was no difference in vegetation or rodent density in upland habitats (Samelius and Alisauskas 2009). I positioned one grid in each of: (*i*) lightly-impacted habitat inside the light goose colony (Inside-Intact, II), (*ii*) lightly-impacted habitat outside the colony (Outside-Intact, OI), (*iii*) heavily-impacted habitat inside the colony (Inside-Disturbed, ID), and (*iv*) heavily-impacted habitat outside the colony (Outside-Disturbed, OD; Fig. 4.1). Specific locations of each grid were also chosen to minimize likelihood of travel by lemmings between grids (Batzli and Jung 1980, Fauteux et al. 2018b), and yet accommodating logistical constraints experienced by researchers to efficiently access trapping grids.

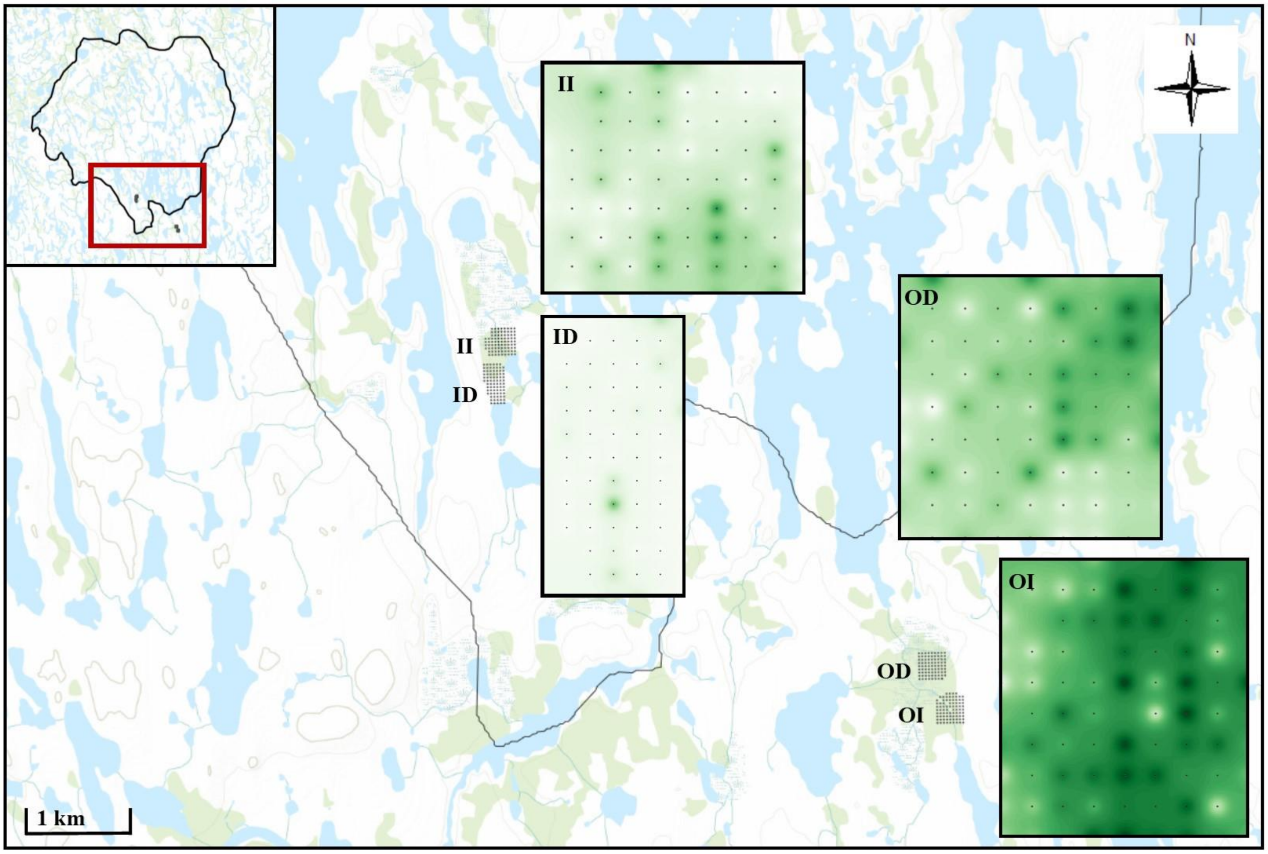

Figure 4.1. Map of study area showing locations of trapping grids inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut. The black line depicts the colony boundary in 2014. The red rectangle of the inset map depicts the extent of the enlarged area. Enlarged maps of live-capture grids show trap locations indicated by black dots and interpolated occurrence of graminoid (sedge and grass species) vegetation, with higher incidence of graminoids depicted in darker green. Live-capture grid notation: II, Inside-Intact; ID, Inside-Disturbed; OI, Outside-Intact; OD, Outside-Disturbed.

Each live-trapping grid consisted of 80-82 trap sites spaced at 30 m intervals in a square or rectangular grid, as the layout of terrestrial habitat allowed. I positioned one Longworth style 'Little Critter' trap (http://www.rogersmanufacturing.com/) at each trap site and baited traps with oats and apple, and provided cotton batting for warmth and bedding material.

I live-trapped arvicoline rodents on all four grids during June and July of 2014-2017 following Pollock's robust design (Williams et al. 2002). I aimed to space primary trapping sessions at 7-day intervals. Within each primary trapping session, I aimed to check traps every 4-6 hours, resulting in 8-14 secondary trapping sessions per primary period. Numbers of secondary sessions were consistent among grids for each primary session. I identified captured rodents to species, determined age and sex, and weighed each individual. I classified reproductive status of females, considering individuals as lactating when mammary glands were visible. I marked individuals with Passive Integrated Transponder (PIT, AVID_; Avid Identification Systems, Inc., Norco, California) tags inserted subcutaneously and dorsally at the base of the neck. I identified recaptures by scanning individuals with a scanner designed to detect PIT tags.

I conducted vegetation surveys at each trap location in July 2014, using point-intersect surveys following Alisauskas et al. (2006). I recorded substrate or plant or lichen species along 15 m transects extending in each of the four cardinal directions from trap locations. I did not identify lichens or mosses (Bryophyta) to species, but refer to each of these categories as species groups.

4.2.2 Statistical analyses

I performed all statistical analyses using the R Statistical Computing Environment (R Core Team 2018). I used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distance to characterize vegetation communities on trapping grids (package *vegan*, Oksanen et al. 2019). I used spatial capture-recapture (SCR) models to estimate components of population dynamics using the packages *openCR* (Efford 2019) and *secr* (Efford 2020) for open and closed models, respectively. Closed models allow estimation of population density for each sampling period (primary session composed of multiple secondary capture sessions, see below), whereas open models allow estimation of parameters such as survival and recruitment between primary sessions, in addition to estimation of density.

4.2.2.1 Environmental covariates

I initially intended to test for differences in lemming density among trapping grids according to a two-factor study design: inside versus outside of the nesting colony of light geese as determined by known extent of nesting geese, and heavily-impacted versus lightly-impacted as determined by Landsat imagery (Didiuk and Ferguson 2005, Conkin and Alisauskas 2017). However, anecdotal observations in the field suggested that habitat on both grids outside of the nesting colony were less altered (higher incidence of graminoid species with greater aboveground biomass) than either grid inside the colony, and this was confirmed by vegetation surveys (Fig. 4.1). Thus, instead of a factorial design, I used NMDS to ordinate vegetation communities on trapping grids with point-intersect vegetation data, as in Chapter 3.

I compiled input data by summing observations of each vegetation species or species group per trap site, and included only those species or species group in analyses in which occurrence across all traps sites was greater than 1%, as recommended to reduce influence of rare species (Rettie et al. 1997, Elliott and Vose 2016). I first constructed ordinations with 1-9 axes, with a maximum of 500 iterations for each configuration. I determined the appropriate number of axes by seeking low stress values (for ecological community data, stress values <0.20 are acceptable) and beyond which additional axes resulted in only small reductions of stress (McCune and Grace 2002). I then constructed multiple (>10) ordinations with the chosen number of axes, and visually examined them to ensure reproducibility. I extracted elevation data for each trap site from ArcticDEM (https://www.pgc.umn.edu/data/arcticdem/, Porter et al. 2018), which provided spatial resolution of 2 m, and used the *bilinear* function to interpolate elevation from the four nearest cells for each trap site (±0.1 m). I investigated how patterns of vegetation species composition related to elevation by vector overlay on the NMDS ordination with the function *envfit*. I used Pearson correlation coefficients between elevation and NMDS scores to define the strength of correlation with ordination axes, with significance determined using 999 permutations. There was no trap-specific information detailing use by geese, so I could not fit covariates of goose activity to the ordination. Instead, I visually inspected the ordination, relying on insight gained from previous analyses to infer correlation of habitat use by geese with NMDS axes (Chapter 3). I then used trap-specific NMDS axis scores as habitat covariates in SCR analyses. Habitat covariates did not account for the contemporaneous presence or absence of geese on trapping grids (only their resulting cumulative impacts on vegetation communities), so I also used a categorical binary covariate (Colony) to indicate whether trapping grids were inside or outside the light goose nesting colony. I used Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002) to evaluate relative support among estimable models.

4.2.2.2 Spatial capture-recapture (SCR)

SCR models specify a spatially explicit link between a summary of each individual's location or activity centre (s_i), and locations where they may be detected, as determined by trap locations (Kendall et al. 2019). This approach used the spatial structure of trapping grids and location of each captured individual to estimate density with a maximum likelihood approach (Efford and Fewster 2013). In SCR models, the state space, *S*, is a region or set of points that encompasses possible values of s_i (Royle et al. 2014) and should be sufficiently large that an individual with an activity centre on the periphery of *S* has negligible probability of capture.

I first modeled capture data with open SCR models (package *openCR*) for each year separately, following model notation of Efford (2019). My primary goal was estimation and modeling of density, so I used Jolly-Seber-Schwarz-Arnason model that incorporated Pollock's robust design (model *JSSAsecrD*) to model and estimate detection functions of intercept (λ_0), the scale of the detection parameter (σ), in m), the length of the detection 'tail' (*z*; Fig. 4.2), and survival (ϕ), and density (*D*). Using intercept-only models for survival, density, and all detection parameters, I first determined the optimal shape of decay with distance from among half-normal (HN), negative exponential (EX), and hazard-rate (HR) detection functions, guided by AIC_c scores and inspection of model output. I used the function *RPSV* to estimate σ *a priori* from capture histories for each primary session in order to establish an appropriate buffer width around the live-trapping grid to ensure that the state space, *S*, was sufficiently large. I applied a buffer width of ~4 times the maximum estimate of σ for each year to define habitat masks, and thus, habitat masks incorporated the area of trapping grids plus a surrounding buffer width of four times σ to generate an appropriate state space.

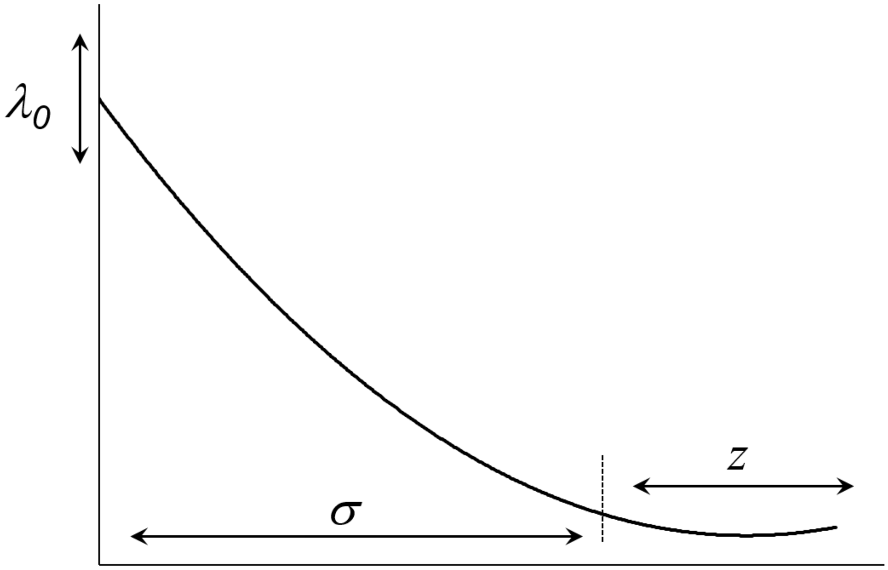

Figure 4.2. Schematic showing detection parameters of intercept (λ_0), the scale of the detection parameter (σ, in m), and the length of the detection 'tail' (z), used in spatial capture-recapture (SCR) modeling.

I determined model(s) of best fit with a multi-step process planned *a priori*. First, I determined the best parameterization of the detection parameters λ_0 and σ, retaining an intercept-only parameterization of z. I tested different parameterizations of λ_0 and σ by allowing (*i*) full temporal session-specificity (session) versus a linear temporal trend (Session), (*ii*) three behavioral parameterizations of a learned response (*b*), a detector-specific transient response (*B*), or a detector-specific learned response (*bk*), and biological covariates of (*iii*) habitat using NMDS axis scores (NMDS1, NMDS2, NMDS3) and (*iv*) the presence of nesting light geese (Colony (inside, outside)). I fit behavioral models to detection parameters because prior occupancy of a trap may leave olfactory cues that could change the likelihood of subsequent trap occupancy. If a behavioural response was evident, I considered additional models in which behavioural response varied with session (e.g., *bk*session). I first parameterized λ_0 with these effects, retained the best parameterization of λ_0, and then to that best model investigated parameterization of σ with the same effects as above, and retained the model with optimization of both λ_0 and σ. I retained an intercept-only parameterization for survival probability and modeled variation in rodent density in response to session-specificity (session) or linear temporal trend (Session), and biological covariates (NMDS1, NMDS2, NMDS3, Colony).

Open SCR models failed to converge in estimation of biological effects on density and detection parameters, so I used closed SCR models (package *secr*) for each session separately to explore variation in density, following model notation of (Efford 2020). I used the same decision protocol and buffer width as used in open models for determining the best detection function in closed models. The model structure incorporated detection parameters of intercept (*g0*, analogous to λ_0 of open models), the scale of the detection parameter (σ), the length of the detection 'tail' (*z*), and density (*D*). As for open models, I first optimized the detection parameters *g0* and σ with behavioural (*b, B, bk*) and biological (NMDS1, NMDS2, NMDS3, Colony) effects. If a biological covariate was important, I included the best-supported behavioural covariate in order to account for maximum variation in detection parameters to facilitate accurate estimation of density. I used an intercept-only parameterization of *z*. I modeled density in response to biological effects, and when slope values in models with single effects did not include zero, I considered models with additive effects of such single effects. NMDS axis values and Colony were somewhat confounded so I did not include them in the same models. I report slope values of continuous covariates of NMDS axis values as an indicator of their importance, considering them as significant if confidence intervals did not include zero. I used the *groups*= option to estimate differences in density inside and outside the light goose nesting colony with appropriate models. All density models using 2017 data were inestimable because of low number of captures, so I calculated rodent density inside and outside the nesting colony as number of unique animals captured in each primary session divided by area of trapping grids, including habitat mask (Fauteax et al. 2015).

Insight gained from closed population models suggested a strong divergence in lemming density inside and outside the nesting colony in the final session of 2014. I was motivated to determine the extent to which the increase in density due to recruitment on trapping grids outside the colony was offset by mortality in that year. Thus, I used an open SCR model built on Pollock's robust design to estimate survival (ϕ) and recruitment (*f*, Jolly-Seber-Schwarz-Arnason model *JSSAsecrf*') instead of density (as in the *JSSAsecrD* model). I incorporated the best-supported parameterization of detection parameters from the *JSSAsecrD* model and proceeded to model ϕ and *f* by allowing session-specificity (session) or constancy (~1). I could not directly model biological effects on ϕ and *f* due to nonconvergence and could only estimate these parameters without consideration of biological effects (i.e., all data combined).

4.3 Results

4.3.1 NMDS of vegetation communities

Ordination of 12 species and species groups, that accounted for 98.4% of point-intersect observations (after excluding rare species), resulted in a three-dimensional solution capturing 21.5% of variation in the ranked distance matrix (Table 4.1, Fig. 4.3). I used three axes for the final configuration because convergence was achieved easily (20 iterations over multiple attempts) and was reproducible (plots were very similar). As well, stress was minimal (0.143) and only slightly greater than an ordination using four axes (0.104). In comparison, an ordination using only two axes had stress of 0.215.

Table 4.1. Percent occurrence (%) and resulting axis loadings from nonmetric multidimensional scaling (NMDS) ordination of vegetation community data collected on trap sites (*n*=324) on four live-trapping grids inside and outside of the snow and Ross's goose nesting colony at Karrak Lake, Nunavut in July 2014. Twelve taxa accounted for 98.4% of point-intersect observations, after excluding rare species. The three axes captured 21.5% of variation in the ranked matrix, with axes 1-3 capturing 11.6, 6.0, and 3.9% of variation, respectively.

Species Code	Species or Species Group	Percent Occurrence	NMDS1	NMDS2	NMDS3
PEAT	dead moss species	6.5	0.623	-0.092	0.271
SPHA	*Sphagnum* spp.	1.3	0.086	-0.321	0.538
MOCA	moss carpet (non-*Sphagnum* spp.)	2.9	0.488	-0.248	0.090
GRAS	grass spp.	15.0	-0.677	-0.343	0.032
SEDG	sedge spp.	18.7	-0.807	0.377	-0.135
BIRC	birch *(Betula glandulosa)*	32.5	0.299	0.107	-0.432
WILL	willows (*Salix* spp.)	5.6	-0.169	-0.590	0.102
CRAN	cranberry *(Vaccinium vitis-idaea)*	7.2	0.131	0.379	0.505
LABT	Labrador tea *(Ledum palustre)*	4.4	0.366	0.760	0.166
RAGW	marsh ragwort *(Tephroseris palustris)*	1.0	0.963	-0.239	0.321
MACI	marsh cinquefoil *(Comarum palustre)*	2.3	0.258	-0.928	-0.527
MATA	mare's tail *(Hippuris vulgaris)*	1.0	0.804	-0.182	0.807

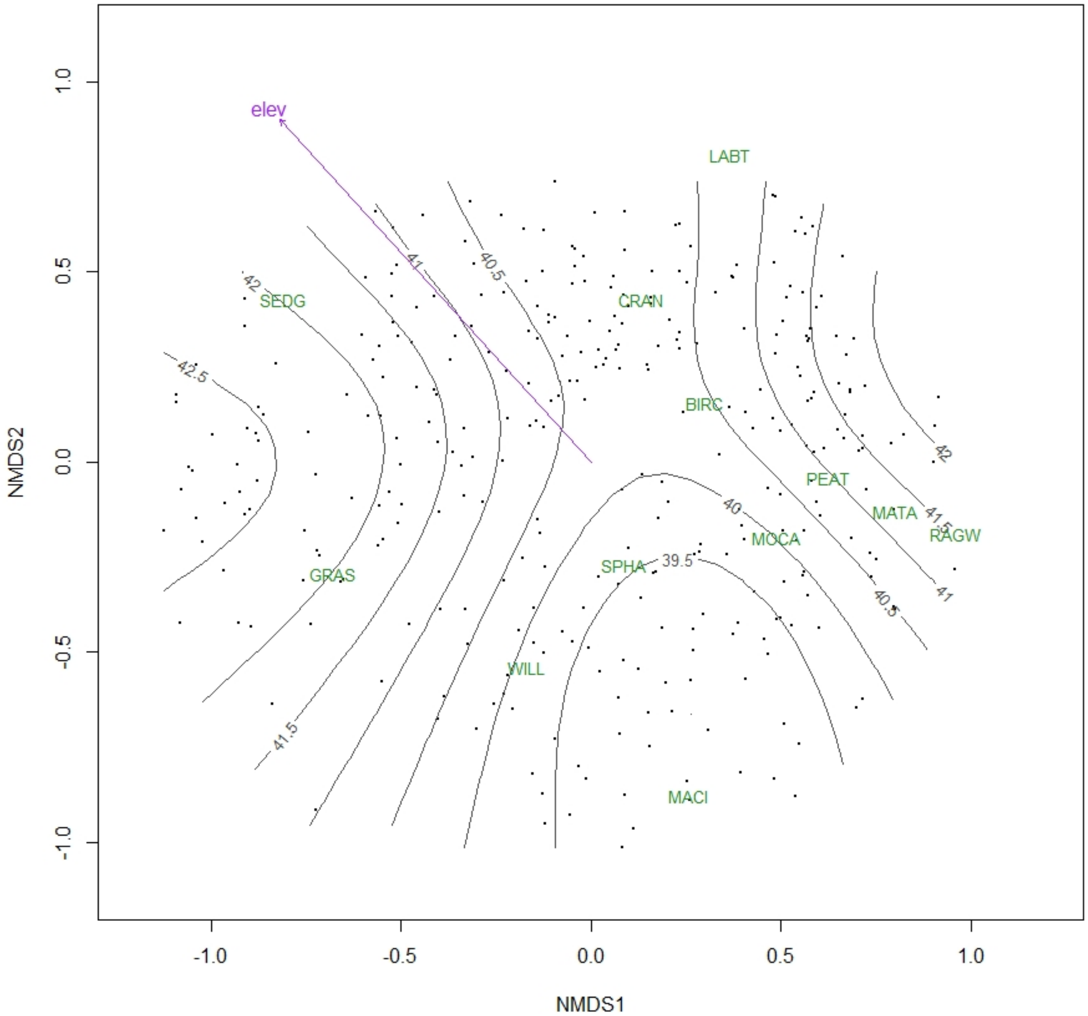

Figure 4.3. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 12 vegetation taxa on trap sites (*n*=324) on four live-trapping grids inside and outside the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2014. The three axes (third axis not shown) captured 21.5% of variation in the ranked matrix, with axes 1-3 capturing 11.6, 6.0, and 3.9% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. The purple arrow represents vector overlay of elevation, with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for elevation. Species and species groups: PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOCA, moss carpet (non-*Sphagnum* spp.); GRAS, grass spp.; SEDG, sedge spp.; BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; LABT, Labrador tea *(Ledum palustre);* RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil *(Comarum palustre)*; MATA, mare's tail *(Hippuris vulgaris)*.

From insight gained in Chapter 3, inspection of the ordination plot suggested a strong correlation between the first axis (NMDS1) and intensity of habitat use by geese (Table 4.1, Fig. 4.3). Negative NMDS1 values were associated with graminoid species typical of intact habitat, whereas positive values were associated with species more common in disturbed landscapes, such as birch *(Betula glandulosa)* marsh ragwort *(Tephroseris palustris)*, mare's tail *(Hippuris vulgaris)*, marsh cinquefoil *(Comarum palustre)*, and exposed peat (Table 4.1, Fig. 4.3). This resembled the ordinations of Karrak Lake and Sanctuary vegetation data presented in Chapter 3 (Figs. 3.2-3.5) where NMDS1 values correlated with covariates that reflected cumulative intensity of habitat use by light geese. As well, high correlation of NMDS1 values with proportion of graminoids at trap locations (r^2=0.951, Fig. 4.1) confirmed that range of NMDS1 values represent changes to habitat quality for brown lemmings. Thus, I proceeded with the assumption that NMDS1 scores from vegetation around rodent traps were a similarly reliable covariate that reflected habitat alteration by nesting light geese.

Elevation was most strongly correlated with the second axis (0.636) than with the first or third axes (-0.578 and 0.511, respectively, r^2=0.214, p<0.001), but none of the three axes appeared to be a decisive indicator of elevation (Fig. 4.3), likely due to low variation in elevation among trap sites. Instead, differences in NMDS2 species scores reflected differences among vegetation communities with positive values reflecting a community composed largely of sedges, cranberry *(Vaccinium vitis-idaea)*, and Labrador tea *(Ledum palustre)*, and negative values reflecting a community consisting of grasses, *Sphagnum* spp., and willow (*Salix* spp., Table 4.1, Fig. 4.3). I did not interpret a clear pattern of NMDS3 species loadings (Table 4.1). I used trap-specific NMDS1-3 scores as habitat covariates in SCR models.

4.3.2 Spatial capture-recapture (SCR)

I monitored trapping grids during four, three, two, and two primary sessions during June and July of 2014-2017, respectively (Table 4.2), and captured 17-256 individual rodents each year. Brown lemmings were the dominant species captured (98.5% of unique animals), so I restricted analyses to this species only. I based analyses on 1025 captures of brown lemmings over 4 seasons.

Table 4.2. Number of secondary sessions, trapping start dates, and number of captures and unique animals of brown and collared lemmings and red-backed voles for each primary trapping session during June and July of 2014-2017 on trapping grids inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut.

Year	Primary	Number of Secondary Sessions	Trapping Start Date		Brown Lemmings		Collared Lemmings		Red-backed Voles	
			Outside Colony	Inside Colony	captures	animals	captures	animals	captures	animals
2014	1	8	12-Jun-14	16-Jun-14	62	29	-	-	-	-
2014	2	8	22-Jun-14	26-Jun-14	119	45	-	-	-	-
2014	3	8	29-Jun-14	02-Jul-14	138	56	-	-	-	-
2014	4	8	22-Jul-14	27-Jul-14	287	126	-	-	-	-
2015	1	14	21-Jun-15	25-Jun-15	110	37	1	1	-	-
2015	2	14	29-Jun-15	03-Jul-15	191	46	-	-	-	-
2015	3	10	20-Jul-15	27-Jul-15	45	24	-	-	-	-
2016	1	14	23-Jun-16	25-Jun-16	10	7	-	-	-	-
2016	2	14	02-Jul-16	05-Jul-16	44	18	-	-	-	-
2017	1	14	22-Jun-17	24-Jun-17	7	4	-	-	1	1
2017	2	14	02-Jul-17	06-Jul-17	12	9	1	1	7	3

4.3.2.1 Open models

Although half-normal (HN) detection functions are often used in SCR models (e.g. Fauteax et al. 2015, Kendall et al. 2019), hazard-rate (HR) detection function was better supported for these data than either HN or negative exponential (EX) in all years (2014: $\text{AIC}_{c\text{HR}} < \text{AIC}_{c\text{EX}}$ and $\text{AIC}_{c\text{HN}}$ by 61.8 and 197.9, respectively; 2015: $\text{AIC}_{c\text{HR}} < \text{AIC}_{c\text{EX}}$ and $\text{AIC}_{c\text{HN}}$ by 104.1 and 391.9, respectively; 2016: $\text{AIC}_{c\text{HR}} < \text{AIC}_{c\text{EX}}$ and $\text{AIC}_{c\text{HN}}$ by 23.7 and 53.2, respectively; 2017: $\text{AIC}_{c\text{HR}} < \text{AIC}_{c\text{EX}}$ and $\text{AIC}_{c\text{HN}}$ by 0.62 and 0.95, respectively). Resulting density estimates of these intercept-only models were very similar among the detection functions (maximum range in estimates <0.132 animals ha^{-1}). *A priori* estimates of σ resulted in applied buffer widths around trapping grids (all grids considered together) of 100, 160, 180, and 80 m, producing habitat masks of 71.1, 103.9, 116.6, and 60.4 hectares for 2014-2017, respectively.

Ninety percent confidence sets of models for each year included only one or two models (Table 4.3). Optimal parameterization of detection functions λ_0 and σ varied slightly among years, variously constrained by effects of parameters of *bk*, *bk*session, session, and Session. In 2014-2016, models that estimated session-specific density were generally favoured over models of constant or temporal trend in density.

Table 4.3. List of most supported models (models with the lowest Akaike Information Criterion adjusted for sample size (AIC_c) scores with cumulative model weights (ω_i) up to 1.0) constructed to estimate density of brown lemmings with open spatial capture-recapture models using data collected at the snow and Ross's goose colony at Karrak Lake, Nunavut, during 2014-2017. Bold fond indicates 90% confidence sets of models for each year. Parameter notation: λ_0: baseline detection probability; σ: spatial scale parameter related to the amount of space used by each individual; z: length of tail of the detection parameter; ϕ: survival; D: density of brown lemmings ha^{-1}; ΔAIC_c: cumulative change in AIC_c; ω_i: weight of model *i*, a measure of support for each model; Cumulative ω: cumulative measure of support for the models. Effect notation: *bk*: detector-specific learned response; *bk*session; session- and detector-specific learned response; session: full temporal session-specificity; Session: linear temporal trend; 1: constant (intercept only).

Year	Model Parameters							
	λ_0	σ	z	ϕ	D	ΔAIC_c	ω_i	Cumulative ω
2014	***bk***	**session**	**1**	**1**	**session**	**0.00**	**1.00**	**1.00**
2015	***bk***	**session**	**1**	**1**	**1**	**0.00**	**0.58**	**0.58**
	bk	**session**	**1**	**1**	**session**	**0.97**	**0.36**	**0.94**
	bk	Session	1	1	1	4.54	0.06	1.00
2016	***bk***	***bk***	**1**	**1**	**session**	**0.00**	**0.92**	**0.92**
	bk	*bk*	1	1	1	5.28	0.07	0.99
	bk	session	1	1	1	8.89	0.01	1.00
2017	***bk*session**	**1**	**1**	**1**	**1**	**0.00**	**0.94**	**0.94**
	bk	1	1	1	1	5.41	0.06	1.00

4.3.2.2 Closed models

For consistency with open SCR modelling, I used hazard-rate detection function and the same buffer widths in closed SCR models. Behavioural effects of *B* and *bk* were generally the most important for *g0* (Table 4.4). In addition to behavioural effect of *bk* explaining variation in σ, the detection parameter scale, σ was also positively influenced by NMDS2 in session 4 of 2014 and NMDS1 in session 3 of 2015 (Table 4.4). The effect of Colony on σ in session 1 of 2015 was non-significant (95%CI of β included zero). An intercept-only model alone converged for the first session of 2016, and no models converged for either session in 2017 (Table 4.4). Such nonconvergence of models presumably was due to low number of captures leading to data sparseness.

Table 4.4. List of closed spatial capture-recapture models of brown lemming density using data from the snow and Ross's goose colony at Karrak Lake, Nunavut, during 2014-2017. Bold fond indicates 90% confidence sets of models for each primary session. Included in model lists are most supported models (models with the lowest Akaike Information Criterion adjusted for sample size (AIC_c) scores with cumulative model weights (ω_i) up to 1.0) as well as all estimable models incorporating habitat effects on density. Model notation: *g0*: baseline detection probability, σ: spatial scale parameter related to the amount of space used by each individual, *z*: length of tail of the detection parameter, *D*: density of brown lemmings ha^{-1}, ΔAIC_c: cumulative change in AIC_c, ω_i: weight of model *i*, a measure of support for each model, Cumulative ω: cumulative measure of support for the models. Parameter notation: *B*: detector-specific transient response, *bk*: detector-specific learned response, NMDS1-3: trap-specific nonmetric multidimensional scaling (NMDS) ordination scores, Colony: inside or outside the light goose nesting colony, 1: constant (intercept only). NMDS axis values and Colony were somewhat confounded so were not included in the same models. †All models inestimable for 2017.

Year	Session	Model Parameters				ΔAIC_c	ω_i	Cumulative ω
		g0	σ	*z*	*D*			
2014	1	***bk***	***bk***	**1**	**Colony**	**0.00**	**0.49**	**0.49**
		bk	***bk***	**1**	**NMDS1**	**1.50**	**0.23**	**0.72**
		bk	***bk***	**1**	**1**	**1.62**	**0.22**	**0.93**
		bk	*bk*	1	NMDS2	4.25	0.06	0.99
		bk	*bk*	1	NMDS3	8.07	0.01	1.00
2014	2	***B***	**1**	**1**	**Colony**	**0.00**	**1.00**	**1.00**
		B	1	1	NMDS1	10.99	0.00	1.00
		B	1	1	NMDS3	16.18	0.00	1.00
		B	1	1	NMDS2	17.61	0.00	1.00

2014	3	***bk***	***bk***	**1**	**Colony**	**0.00**	**0.32**	**0.32**
		bk	***bk***	**1**	**1**	**0.77**	**0.22**	**0.55**
		bk	***bk***	**1**	**NMDS2**	**1.34**	**0.17**	**0.71**
		bk	***bk***	**1**	**NMDS1**	**2.08**	**0.11**	**0.83**
		bk	***bk***	**1**	**NMDS3**	**3.19**	**0.07**	**0.89**
		bk	**1**	**1**	**1**	**4.01**	**0.04**	**0.94**
		bk	Colony	1	1	5.06	0.03	0.96
		bk	NMDS3	1	1	6.40	0.01	0.98
		bk	NMDS1	1	1	6.51	0.01	0.99
		bk	NMDS2	1	1	6.53	0.01	1.00
2014	4	***B***	**NMDS2**	**1**	**Colony**	**0.00**	**1.00**	**1.00**
		B	NMDS2	1	NMDS1+NMDS2	40.77	0.00	1.00
		B	NMDS2	1	NMDS1	53.87	0.00	1.00
		B	NMDS2	1	NMDS2	63.65	0.00	1.00
		B	NMDS2	1	NMDS3	76.49	0.00	1.00
2015	1	***bk***	**Colony**	**1**	**1**	**0.00**	**0.33**	**0.33**
		bk	**NMDS1**	**1**	**1**	**0.49**	**0.26**	**0.59**
		bk	***bk*+Colony**	**1**	**1**	**2.04**	**0.12**	**0.71**
		bk	***bk*+NMDS1**	**1**	**1**	**3.23**	**0.07**	**0.77**
		bk	***bk*+Colony**	**1**	**NMDS1**	**3.68**	**0.05**	**0.83**
		bk	**NMDS3**	**1**	**1**	**4.11**	**0.04**	**0.87**
		bk	***bk*+Colony**	**1**	**NMDS3**	**4.16**	**0.04**	**0.91**
		bk	*bk*+Colony	1	NMDS2	4.84	0.03	0.94
		bk	*bk*+Colony	1	Colony	5.13	0.03	0.97
		bk	1	1	1	5.75	0.02	0.98
		bk	NMDS2	1	1	6.94	0.01	0.99
		bk	*bk*	1	1	8.141	0.01	1.00

2015	2	***bk***	***bk***	**1**	**NMDS1**	**0.00**	**0.95**	**0.95**
		bk	*bk*	1	Colony	5.86	0.05	1.00
		bk	*bk*	1	1	14.34	0.00	1.00
		bk	*bk*	1	NMDS2	16.01	0.00	1.00
		bk	*bk*	1	NMDS3	16.89	0.00	1.00
2015	3	***bk***	**NMDS1**	**1**	**1**	**0.00**	**0.53**	**0.53**
		bk	**NMDS2**	**1**	**1**	**1.71**	**0.23**	**0.76**
		bk	***bk*+NMDS1**	**1**	**NMDS2**	**3.57**	**0.09**	**0.85**
		bk	***bk*+NMDS1**	**1**	**1**	**3.81**	**0.08**	**0.93**
		bk	*bk*+NMDS1	1	Colony	6.32	0.02	0.95
		bk	1	1	1	6.60	0.02	0.97
		bk	NMDS3	1	1	7.68	0.01	0.98
		bk	*bk*+NMDS1	1	NMDS1	8.20	0.01	0.99
		bk	*bk*+NMDS1	1	NMDS3	8.29	0.01	1.00
2016	1	**1**	**1**	**1**	**1**	**0**	**1**	**1**
2016	2	***bk***	**1**	**1**	**NMDS1**	**0**	**0.8693**	**0.8693**
		bk	**1**	**1**	**Colony**	**4.01**	**0.1171**	**0.9864**
		bk	1	1	1	8.311	0.0136	1
		bk	1	1	NMDS3	10.855	0	1
		bk	*bk*	1	1	11.892	0	1
		bk	Colony	1	1	12.84	0	1
		bk	1	1	NMDS2	12.942	0	1
2017†	1	1	1	1	1	all parameters inestimable		
2017†	2	1	1	1	1	all parameters inestimable		

In 2014, density of brown lemmings was greater in areas outside of the nesting light goose colony in all four sessions, and significantly in sessions 2 and 4 (Tables 4.4 and 4.5, Fig. 4.4). Lemming density inside and outside the nesting colony was estimated at <1 and >1 animals ha^{-1} in all sessions, respectively, with a large increase occurring on trapping grids outside the colony in July, to an estimated 3.72 (95%CI: 3.04, 4.56) lemmings ha^{-1} (Table 4.5). Although density models that included Colony were the best-supported in all sessions of 2014, NMDS1 and NMDS2 were also significant predictors of lemming density (Table 4.4). Habitat with more graminoid vegetation (negative NMDS1 values) supported more lemmings in all sessions (significantly so in sessions 2 and 4, Tables 4.4 and 4.6). Density was positively associated with NMDS2 values in all sessions (significantly so in session 4, Tables 4.4 and 4.6), suggesting perhaps a positive influence on lemming density of sedge and/or higher elevation.

Lemming density declined precipitously after 2014 and continued to decline for the duration of the study. In contrast to 2014, lemming densities were very low regardless of location (Table 4.5, Fig. 4.4), and were significantly higher inside the colony only in the second session of 2015. Contrary to expectation, NMDS1 had the opposite effect on density in the second session of 2015 and final session of 2016, so that habitat associated with goose impacts supported somewhat higher lemming densities then (Table 4.4 and 4.6).

Table 4.5. Model-based estimates and 95%CI of density of brown lemmings (animals ha^{-1}) in each primary session inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, estimated with closed spatial capture-recapture models using data collected during 2014-2017. Included are model weights (ω_i), a measure of support for each estimating models. Bold font indicates non-overlapping estimates. †All models inestimable for 2017, with density estimates for inside and outside the light goose nesting colony calculated as number of unique animals captured in each primary session divided by area of live-trapping grids, including habitat mask. NA=not applicable.

Year	Session	Inside Colony		Outside Colony		
		Estimate	95%CI	Estimate	95%CI	ω_i
2014	1	0.836	0.303, 2.302	2.194	0.901, 5.342	0.49
2014	2	**0.304**	**0.165, 0.560**	**1.063**	**0.755, 1.496**	**1.00**
2014	3	0.668	0.393, 1.135	1.23	0.791, 1.912	0.32
2014	4	**0.474**	**0.281, 0.797**	**3.722**	**3.038, 4.560**	**1.00**
2015	1	0.96	0.548, 1.682	0.356	0.172, 0.737	0.03
2015	2	**0.802**	**0.557, 1.154**	**0.283**	**0.160, 0.502**	**0.05**
2015	3	0.707	0.349, 1.436	0.505	0.233, 1.094	0.02
2016	1	0.122	0.033, 0.451	0.163	0.048, 0.554	0.12
2016	2	0.369	0.183, 0.744	0.079	0.025, 0.246	0.00
2017†	1	0.066	-	0.066	-	NA
2017†	2	0.166	-	0.132	-	NA

Table 4.6. Model-based slope estimates (β, with 95%CI) predicting density of brown lemmings in each primary session according to habitat variables NMDS1, NMDS2, and NMDS3 estimated with closed spatial capture-recapture models using data collected at the snow and Ross's goose colony at Karrak Lake, Nunuvut, during 2014-2017. Included are model weights (ω_i) of estimating models. Bold font indicates β estimates in which 95%CI do not include zero. †Only an intercept-only (all parameters constant) was estimable for session 2 of 2016 and all models were inestimable for 2017. ††Estimates from single effect models.

Year	Session	NMDS1			NMDS2			NMDS3		
		β	95%CI	ω_i	β	95%CI	ω_i	β	95%CI	ω_i
2014	1	-0.790	-1.599, 0.019	0.23	0.518	-0.582, 1.618	0.06	0.104	-1.181, 1.389	0.01
2014	2	**-0.719**	**-1.324, -0.113**	**0.00**	0.814	-0.073, 1.700	0.00	0.203	-0.630, 1.035	0.00
2014	3	-0.356	-0.965, 0.253	0.11	0.645	-0.261, 1.551	0.17	0.271	-0.892, 1.434	0.07
2014	4	**-0.897††**	**-1.270, -0.525**	**0.00**	**0.988††**	**0.439, 1.536**	**0.00**	0.159	-0.328, 0.647	0.00
2015	1	0.77	-0.420, 1.960	0.05	0.331	-0.616, 1.277	0.03	0.697	-0.550, 1.945	0.04
2015	2	**1.642**	**0.772, 2.513**	**0.95**	0.424	-0.381, 1.229	0.00	0.251	-1.252, 0.750	0.00
2015	3	0.366	-1.214, 1.947	0.01	1.684	-0.204, 3.571	0.09	-0.262	-1.747, 1.222	0.01
2016†	1		not estimable			not estimable			not estimable	
2016	2	**2.652**	**0.870, 4.433**	**0.87**	-0.056	-1.575, 1.463	0.00	1.554	-0.235, 3.344	0.00
2017†	1		not estimable			not estimable			not estimable	
2017†	2		not estimable			not estimable			not estimable	

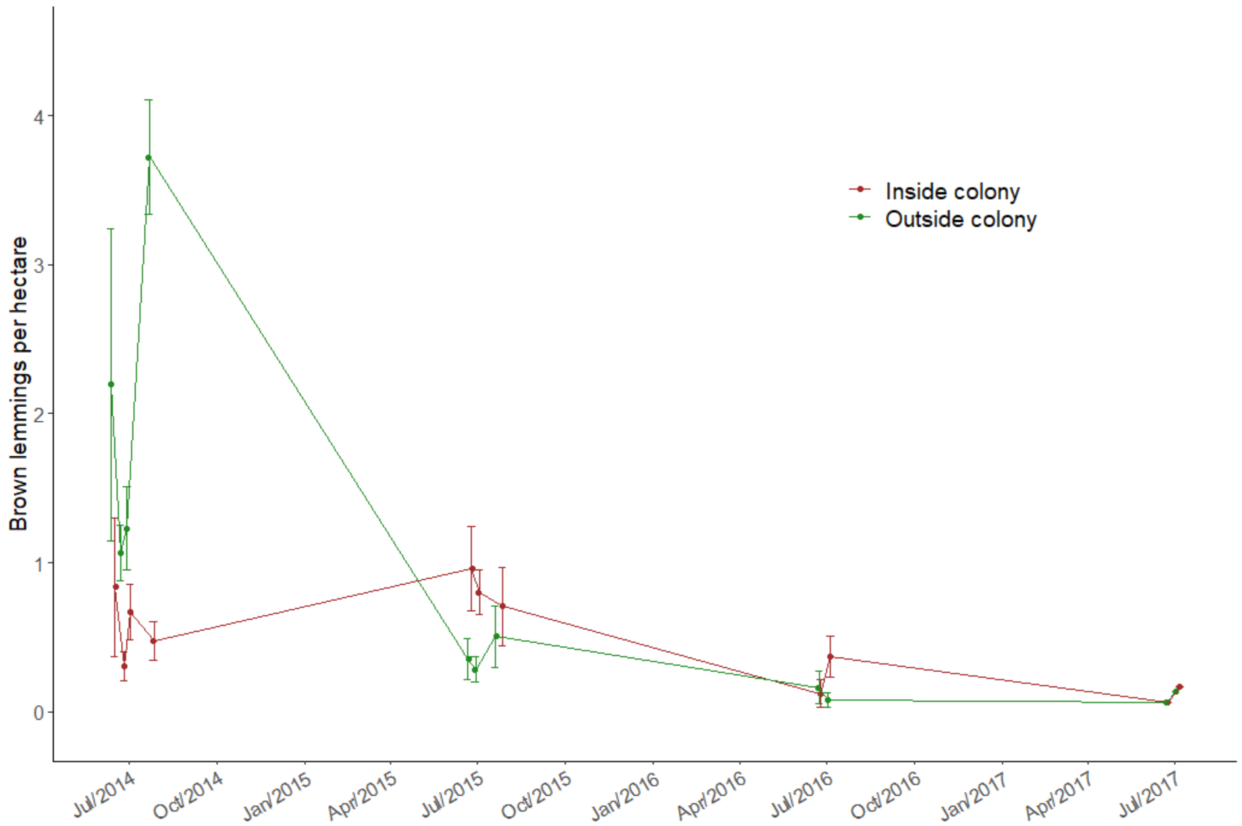

Figure 4.4. Density of brown lemmings (animals ha^{-1}) estimated by closed spatial capture-recapture models inside and outside the snow and Ross's goose colony at Karrak Lake, Nunavut, during 2014-2017. Error bars indicate ±1SE.

4.3.2.3 Survival and recruitment

I used the best-supported parameterization of detection functions (λ_0~*bk*, σ~session, *z*~1) used for density estimation in 2014 in open SCR models to estimate ϕ and *f* in that year. Models with session-specificity (session) for *f* were inestimable, so I modeled *f* with linear temporal trend (Session). The resulting candidate set included four models in which estimates of ϕ were session-specific (session) or remained constant (intercept only, ~1), and *f* followed a linear temporal trend or remained constant (Table 4.7). The best-supported model included temporal effects on both ϕ and *f*, with the second best-supported model (ΔAIC$_c$=0.96) including temporal effects on *f* only (Table 4.7). Estimates of ϕ remained relatively constant throughout June and July in 2014, declining slightly towards the end of the study (Fig. 4.5). In contrast, recruitment remained at low levels during the first two intervals in 2014, and increased substantially in late July (Fig. 4.5). Although I was unable to model age categories separately, high proportion of juvenile individuals captured in the final capture session (65.4%, compared with 0%, 0%, and 3.5% in sessions 1-3, respectively) suggest that increase in recruitment was due to reproduction and not immigration by adult lemmings.

Table 4.7. List of all converged open spatial capture-recapture models for estimation of survival (ϕ) and recruitment (*f*) of brown lemmings at the snow and Ross's goose colony at Karrak Lake, Nunavut, during 2014. Bold fond indicates 90% confidence set of models. Parameter notation: λ_0: baseline detection probability; σ: spatial scale parameter related to the amount of space used by each individual; *z:* length of tail of the detection parameter; ϕ: survival; *f*: recruitment; ΔAIC$_c$: cumulative change in Akaike Information Criterion adjusted for sample size; ω_i: weight of model *i*, a measure of support for each model; Cumulative ω: cumulative measure of support for the models. Effect notation: *bk*: detector-specific learned response; session: full temporal session-specificity; Session: linear temporal trend; 1: constant (intercept only).

Model Parameters					ΔAIC$_c$	ω_i	Cumulative ω
λ_0	σ	z	ϕ	f			
bk	**session**	**1**	**session**	**Session**	**0.00**	**0.69**	**0.69**
bk	**session**	**1**	**1**	**Session**	**0.96**	**0.31**	**1.00**
bk	session	1	session	1	13.33	0.00	1.00
bk	session	1	1	1	15.49	0.00	1.00

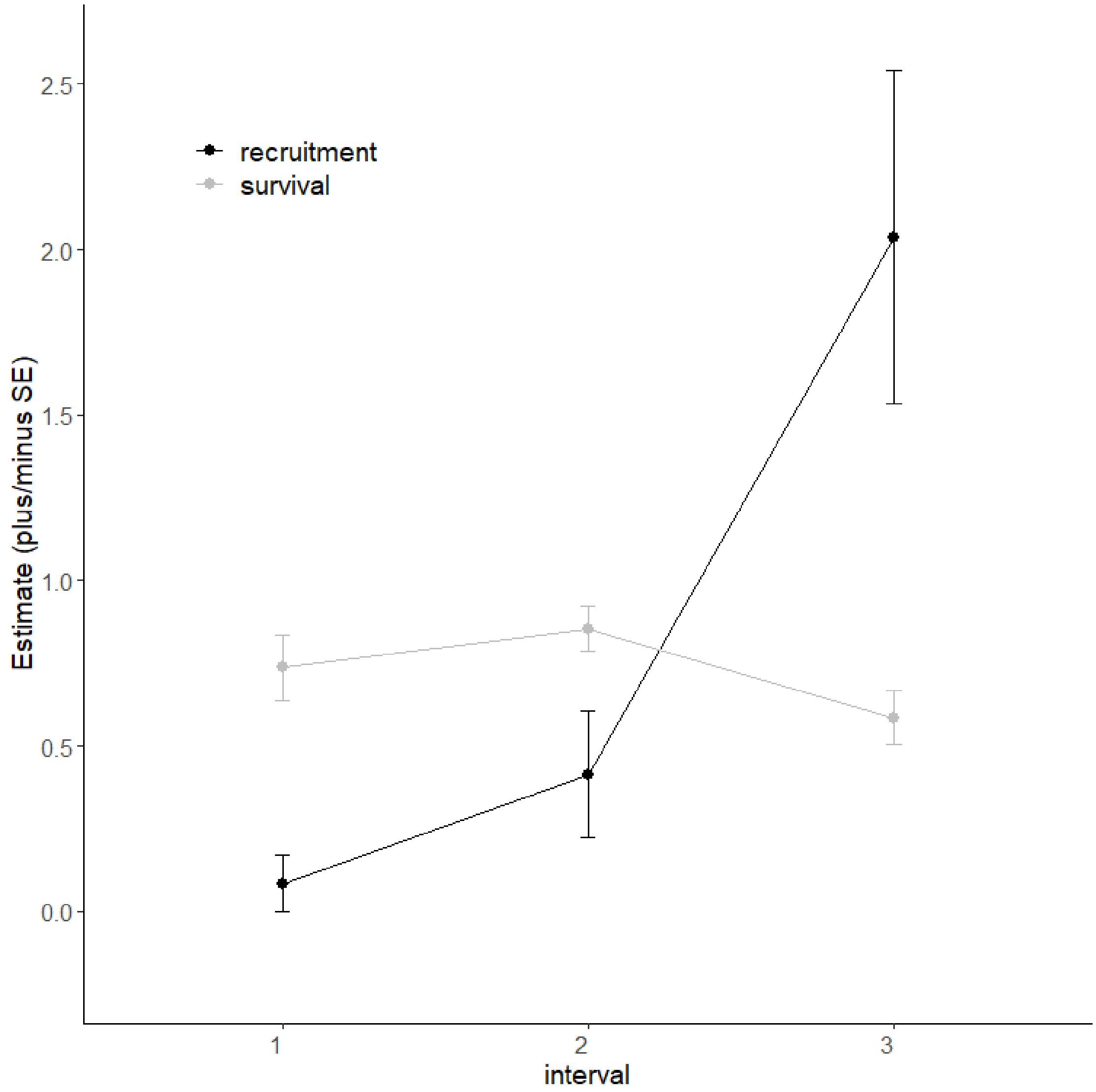

Figure 4.5. Estimates of survival (*ϕ*) and recruitment (*f*) from the best-approximating open spatial capture-recapture model {model λ_0~*bk*, σ~session, *z*~1, *ϕ*~session, *f*~Session} for each primary session in 2014. Error bars indicate ±1SE.

4.4 Discussion

4.4.1 Differences in abundance: habitat or presence of nesting light geese?

Variation in abundance of brown lemmings in lowland habitat in the Karrak Lake region was associated with both species composition of vegetation communities and an effect of light goose presence (Table 4.4, 4.5; Fig. 4.4). However, the intensity and direction of these effects changed over time. In the first year of the study, trapping grids outside the colony with more graminoid vegetation consistently supported higher lemming densities. My planned two-level factorial experimental design crossing effects of colony status (inside versus outside) and goose effects on vegetation (intact versus disturbed), the latter based on assessment of older Landsat imagery, did not capture observed vegetation state as initially expected. Thus, I was unable to discern effects of habitat alteration from effects of goose presence on density of brown lemmings using that initial design. However, it was evident that variation in vegetation communities was largely responsible for differences in lemming abundance (Samelius and Alisauskas 2009). When lemming density was high, relatively intact habitats less altered by geese likely provided greater food availability and superior habitat for breeding and protection from predators than altered communities. Graminoids, willows, and mosses constitute much of brown lemming diets (Batzli and Jung 1980, Batzli and Pitelka 1983, Batzli et al. 1983, Rodgers and Lewis 1986b, Negus and Berger 1998, Soininen et al. 2015, Fauteux et al. 2017), and these species were more abundant in vegetation communities characterized as less affected by light goose use (Chapter 3). Lemmings also rely on adequately vegetated habitats (i.e., high biomass) for nesting material and protection from predators (Batzli et al. 1983). I did not measure aboveground plant biomass on trapping grids (discussed further below), but plant biomass is greater in less disturbed vegetation communities (Chapter 2). Anecdotal observations during field work confirmed that trapping grids without nesting light geese and greater proportion of graminoid species also supported more aboveground graminoid biomass (Fig. 4.6).

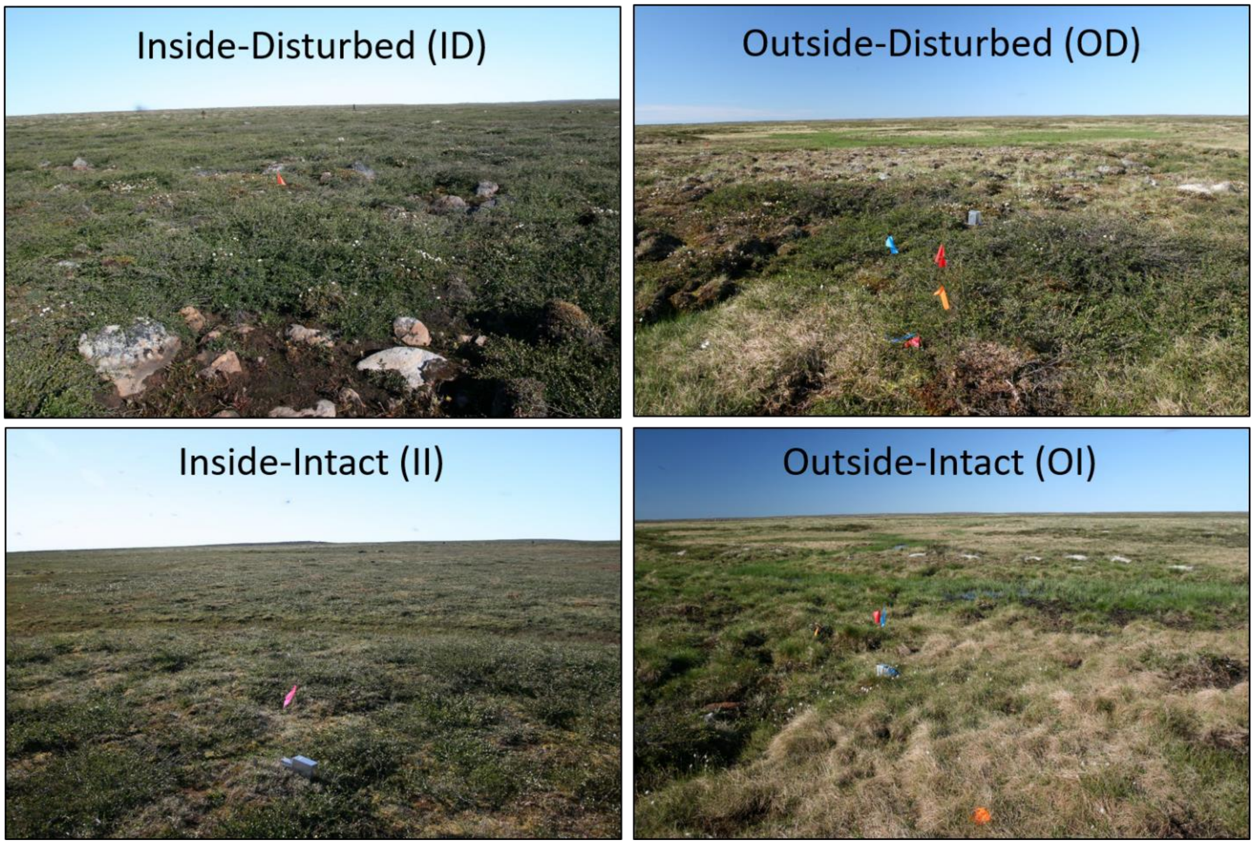

Figure 4.6. Photographs of live-trapping grids used for density estimation of brown lemmings inside and outside the snow and Ross's goose colony at Karrak Lake, Nunavut.

Whereas trapping grids outside the colony were devoid of nesting geese, grids inside the nesting colony contained only very low densities (~14 and ~5 nests ha^{-1} at the beginning and end of the study, respectively (B. Malloure pers. comm., D. Kellett pers. obs.)) relative to core regions of the colony (often >100 nests ha^{-1}, Alisauskas et al. 2012b). Such slight differences in density of nesting light geese among trapping grids likely had little potential for a direct effect on lemming abundance, compared to areas of the colony with 20 times higher densities. Baldwin et al. (2011) reported negative impacts to nest survival for cackling geese (*Branta hutchinsii*) only at high densities of nesting light geese, yet no difference in cackling goose nest density inside and outside the colony, suggesting that disturbance from high density of light geese alone can have negative effects on sympatric species. Even though different species that share habitats with nesting light geese likely respond variably to their presence, disturbance by territorial behaviour of even low densities of light geese can directly influence sympatric species negatively (Flemming et al. 2016), including arvicoline rodents.

Predicted effects of vegetation community structure and goose presence evident during the first year of this study (Table 4.5, 4.6; Fig. 4.4), when lemming abundance was highest, did not hold when lemming densities were low during the rest of the study. Where differences existed during years of low density, vegetation communities with lower proportions of graminoid vegetation reflected in NMDS1 values appeared to support more lemmings, and densities inside and outside the colony were either equivocal or slightly higher inside the colony. As mentioned above, a habitat covariate reflecting quantity of aboveground biomass, in addition to community species composition, may have been a relevant and strong indicator of lemming density. Moreover, I determined species composition of vegetation communities only during the first season, and both species composition and quantity of plant biomass may have changed over the course of this 4-year study. Trapping grids inside the colony in the first year of the study were within about 1.5 km of the boundary of the goose nesting colony. Gradual retraction of the colony boundary (R. Alisauskas unpubl. data) and slightly declining light goose nest densities over time on trapping grids inside the colony may have contributed to unquantified regeneration of vegetation communities (Chapter 2 and 3) in these regions by 2017. However, anecdotal observations in the field suggest that such changes, if present, were not readily apparent. Instead, populations of brown lemmings may persist at low abundance (<1 brown lemming ha^{-1}) during declining phases of population cycles (Fig. 4.4) regardless of habitat quality, and the weak effects of habitat covariates contrary to expectation may simply have been due to chance associated with low number of captures overall.

4.4.2 Population regulation: top-down or bottom-up?

Regulation of multi-annual cycles of northern arvicoline rodent populations, causes of which remain incompletely understood, has been a widely-discussed topic in population ecology. Most evidence suggests that population dynamics of northern lemmings and voles are largely governed by top-down processes through predator-prey interactions, and that bottom-up processes through plant-herbivore interactions are less important (Reid et al. 1995, 1997; Gilg et al. 2003, Krebs et al. 2003, Pitelka and Batzli 2007, Ims et al. 2011, Legagneux et al. 2012, Bilodeau et al. 2014, Therrien et al. 2014, Fauteux et al. 2015, 2016). Recent research suggests that climatic variables, particularly those influencing snow conditions, are important regulators of population dynamics of these species (Kausrud et al. 2008, Bilodeau et al. 2013a, Domine et al. 2018). Fauteax et al. (2015) hypothesized that food-limited rodent populations generally decline during winter, when plants are dormant or snow conditions limits accessibility, whereas predation-limited populations should decline during summer when protective snow cover is absent and avian predators migrate to northern regions to breed. I relate these hypotheses to the results of this study in the following paragraphs.

At Karrak Lake, increase in abundance of brown lemmings on trapping grids outside the colony with high proportion of graminoid vegetation occurred in late summer during 2014, the first year of the study, declined between late summer and the subsequent spring, and remained at low levels for the next three seasons (Fig. 4.4). On trapping grids inside the colony with disturbed vegetation characterized by lower proportions of graminoid species, abundance remained at consistently low levels for the duration of the study. This strong interaction between habitat quality and year on lemming density was the outcome of strong recruitment of juvenile lemmings in late summer 2014, whereas contemporaneous survival probability remained stable (Fig. 4.5). The recruitment was due to reproduction rather than adult immigration. Low numbers of captures precluded separate estimation of recruitment and survival for each trapping grid or habitat. I assume that recruitment caused population increase in habitats with more graminoid vegetation, from the evidence that vegetation structure was responsible for variation in lemming density. Vegetation communities with high proportion of preferred foods of graminoid and willow species may support enhanced recruitment through more abundant or higher quality food and/or protection from predators. Brown lemmings respond reproductively when the plant chemical 6-methoxybenzoxlazolinone becomes available in graminoid vegetation (Negus and Berger 1998), and likely explains strong reproduction on well-vegetated trapping grids in 2014. Survival probability remained relatively constant between 0.59 and 0.74 throughout the snow-free season that I monitored in 2014, suggesting little or no change in predation pressure on lemmings. Predators considered as lemming specialists, such as snowy owls (*Bubo scandiacus*), long-tailed and pomarine jaegers (*Stercorarius longicaudus*, *S. pomarinus*), rough-legged hawks (*Buteo lagopus*), and ermines (*Mustela ermine*; Gilg et al. 2006, Therrien et al. 2014, Bechard et al. 2020, Haven Wiley and Lee 2020, Holt et al. 2020, Wiley and Lee 2020a) were rare in the Karrak Lake region. For example, snowy owls were observed in 17 of 20 years (2000-2019), only rarely in these seasons, and breeding was never reported there (R. Alisauskas, unpubl. data). Instead, generalist predators such as parasitic jaegers (*Stercorarius parasiticus*) and glaucous and herring gulls (*Larus hyperboreus*, *L. argentatus*) and the semi-generalist arctic fox (*Vulpes lagopus*; Gilg et al. 2006, Samelius et al. 2011, Therrien et al. 2014, Weiser and Gilchrist 2020, Weseloh et al. 2020, Wiley and Lee 2020b) show positive responses to presence of geese (Flemming et al. 2016), and were major constituents of the predator community at Karrak Lake (R. Alisauskas, unpubl. data). Brown lemmings may have benefited from mitigated predation when generalist predators may have altered their functional response with focus on abundant seasonal prey such as light geese (Iles et al. 2013, Samelius and Alisauskas 1994), as well as sea ducks such as king eiders (*Somateria spectabilis*) and long-tailed ducks (*Clangula hyemalis*), whose populations are elevated in the region (Kellett et al. 2003, Kellett et al. 2005). However, relatively constant survival probability in 2014 was estimated for the pooled trapping grids without consideration of variation in plant community structure or goose presence, limiting inference.

Population decline between late summer 2014 and the subsequent spring (Fig. 4.4), which may have occurred at any time during this interval, may have resulted from limitations in food abundance or quality, predation, snow conditions affecting survival or food availability, or dispersal. I observed late summer increase in density in the fourth and final session of 2014. Earlier cessation of capture efforts in subsequent years may explain my failure to document annual increases and subsequent declines in abundance, or alternatively, increase in late summer may only have occurred in one year. Regardless, decline in abundance in habitats both with and without graminoid dominance is consistent with normal cycling in arctic arvicoline populations (Angerbjörn et al. 2001, Fauteux et al. 2015, Samelius and Alisauskas 2017). Following high lemming abundance outside the colony in 2014, early summer populations were greater inside the colony in 2015 and 2016 (Fig. 4.4), perhaps an outcome of interacting effects of predation and goose influence. Regular cycles of rodent abundance drive production of arctic fox at Karrak Lake, by affecting recruitment but with no apparent influence on arctic fox survival. Thus, rodent prey are an important driver of local arctic fox dynamics. Overall, lemmings may have experienced increased predation pressure by arctic foxes in autumn or early spring, when protective snow cover (Duchesne et al. 2011, Bilodeau et al. 2013b) was absent and when light geese and their eggs were not available to support locally-elevated arctic fox populations (Samelius et al. 2011). Possibly, reduced lemming densities in spring resulted from greater winter predation by arctic fox or other resident mammalian predators outside the colony. Arctic fox use goose carcasses and caches eggs to supplement their diets during winter and spring (Samelius et al. 2007). Unlike inside the colony, where such ornithogenic foods may serve as alternative (or at least supplementary) prey for arctic fox, there may have been a greater reliance on lemmings as prey outside the colony leading to reduced lemming densities compared to inside. Thus, the apparently paradoxical patterns observed in lemming abundance relative to colony location may have resulted from complex interactions not originally envisaged between lemmings, geese, local plant communities, and predation.

Subnivean spaces important to population persistence are negatively affected by unfavorable microtopography or climatic conditions such as sparse snow cover or rain-on-snow events (Pitelka and Batzli 2007, Kausrud et al. 2008, Duchesne et al 2011, Domine et al. 2018), and such factors may have negatively affected overwinter lemming survival. It seems unlikely that low estimated lemming densities would induce density-dependent dispersal (Soininen et al. 2014). However, lowland habitats with intact vegetation may function as population sources of animals in spatially heterogeneous landscapes such as the Karrak Lake region (Alisauskas et al. 2006, Chapter 2 and 3). Lemmings may move seasonally through such landscape mosaics in response to factors such as spring flooding and snow conditions, further affecting access to food and protection from predators (Batzli et al. 1983).

In habitats within the colony with lower proportions of graminoids, I documented consistently low density of brown lemmings (Fig. 4.4). Foraging and nesting by light geese during the summer reduces food availability to lemmings throughout their entire annual cycle, as aboveground vegetation does not regenerate to an ungrazed state after geese depart northern regions. In addition to removal of aboveground biomass, light geese altered species composition of vegetation communities; in heavily-used lowland areas, geese removed nearly all graminoid vegetation (Alisauskas et al. 2006, Samelius and Alisauskas 2009, Chapter 3). Moreover, willows are important components of brown lemming diets (Soininen et al. 2015, Fauteux et al. 2017), and like graminoids, are replaced in altered communities by non-palatable species such as Labrador tea (Batzli and Jung 1980). Multiseason occupancy by nesting light geese alters microtopography of lowland habitats through trampling of tussocks (D. Kellett pers. obs., Fig. 5 in Alisauskas et al. 2006), and rugged microtopography is integral to maintenance of favorable subnivean spaces to lemmings and protection from predators (Duchesne et al. 2011). Thus, in habitats substantially altered by light geese, plant-herbivore processes may be more important to population dynamics of brown lemmings (Samelius and Alisauskas 2009) than in less disturbed habitats where predator-prey processes are likely more important (Reid et al. 1995, 1997; Gilg et al. 2003, Krebs et al. 2003, Ims et al. 2011, Legagneux et al. 2012, Therrien et al. 2014, Fauteux et al. 2015, 2016).

4.4.3 Characteristics of arvicoline rodent population dynamics at Karrak Lake

Long-term snap-trapping data (1994-2019), a reliable indicator of rodent abundance (Fauteux et al. 2018a), suggests that population dynamics of arvicoline rodents at Karrak Lake were characterized by low-amplitude cycles with 3-4 year periodicity (Samelius and Alisauskas 2017). However, collared lemmings and red-backed voles constitute most snap-captures at Karrak Lake, as trap lines are located in mesic and xeric habitats occupied by these species (Batzli and Jung 1980, Batzli et al. 1983, Rodgers and Lewis 1986a, Samelius and Alisauskas 2009). Although my live-capture study likely only spanned one full population cycle, both live-capture and limited snap-trapping data (brown lemmings constituted only 11% of snap-captures) suggests that brown lemming cycles at Karrak Lake were also characterized by 3-4 year cycles of low amplitude (Samelius and Alisauskas 2017). Density of brown lemmings at Karrak Lake estimated from live-capture data varied from <0.1 to 3.7 animals ha^{-1} over four years, lower than that reported for other regions (Gilg et al. 2006, Bilodeau et al. 2013a, 2014; Fauteux et al. 2015). Regions with similar rodent population dynamics of low abundance (Reid et al. 1997, Wilson and Bromley 2011) reported predator communities composed largely of generalists, and perhaps such regions host sufficiently diverse and abundant prey bases (e.g., supplemented by nesting geese) to sustain generalist predators when rodents are scarce (Reid et al. 1997, Samelius et al. 2011). At Karrak Lake, I suggest that altered vegetation communities were largely responsible for low abundance of arvicoline rodents and a consequential paucity of specialist lemming predators. Similar conditions likely exist throughout the Sanctuary that support high densities of foraging and nesting light geese, including perhaps brood-rearing habitats. Spatial heterogeneity of vegetation communities may result in population cycles varying in amplitude by supporting increases only in higher quality habitats, but predation by resident predators such as arctic fox (Legagneux et al. 2012), as well as other factors such as snow conditions, may dampen such potential increases.

Accumulating evidence from long-term monitoring of arvicoline rodents throughout the circumpolar arctic suggest that climate change may alter population dynamics of these species, and result in cycles of increased periodicity and reduced amplitude (Gilg et al. 2009, Ims et al. 2011, Schmidt et al. 2012). At Karrak Lake, no changes to rodent population cycles have been observed in nearly three decades of monitoring (Samelius and Alisauskas 2017). Here, arvicoline rodent populations of reduced abundance may perhaps be resistant to climate change impacts, but complicated direct and indirect interactions within and among trophic levels, including those interacting with climate change (Gilg et al. 2009), make such predictions only speculative.

4.5 Summary and Transition to Chapter 5

Light geese can have strongly negative impacts on abundance of arvicoline rodents through resource consumption and resulting alteration of shared habitats (Samelius and Alisauskas 2009, this study). Arvicoline rodent communities serve a key role in northern ecosystems, and population oscillations can have strong effects on food webs, through direct effects on plant communities and predators, and indirect impacts on other species through knock-on effects mediated by shared predators or competition for food. Particularly applicable in regions with strongly-oscillating rodent cycles, predators switch to other prey species during low rodent abundance (the alternative prey hypothesis), resulting in predictable effects on productivity or survival of alternative or incidental prey such as nesting birds (Bêty et al. 2001, 2002, Gauthier et al. 2004, McKinnon et al. 2013, 2014). In regions with vegetation communities altered by light geese, consequential low rodent abundance may result in less variable functional and numerical predator responses, with limited effects on alternative or incidental prey. Yet, predator communities supplemented by abundant light geese may still negatively affect other species. More importantly, perhaps, altered vegetation communities encompassing changes to species composition and/or quantity and quality of aboveground plant biomass may directly affect avian species breeding in shared habitats (Flemming et al. 2016), and this is the subject of Chapter 5.

CHAPTER 5: IMPACT OF HABITAT ALTERATION BY LIGHT GEESE ON AVIAN OCCUPANCY

5.1 Introduction

Factors that contribute to declining global biodiversity - including overexploitation, habitat loss, impacts from invasive species, and climate change (Dirzo et al. 2014) - are almost entirely anthropogenic. Of these, habitat fragmentation and loss to human land use has the largest impact on biodiversity in terrestrial ecosystems, largely through conversion of natural landscapes by agricultural intensification (Sala et al. 2000, Dudley and Alexander 2017). However, habitat integral to supporting biodiversity can also be altered by highly abundant herbivore populations at high densities, and modification of vegetation structure and community composition can induce trophic cascades with negative effects on other species (Fuller 2001, Ogada et al. 2008, Martin et al. 2011, Flemming et al. 2016, Rushing et al. 2020). In extreme cases, habitat alteration is considered as degradation, resulting in loss of diversity and abundance of sympatric species, with shifts in ecosystem structure and function (Batt et al. 1997, Abraham et al. 2012). At moderate levels of herbivore abundance, habitat alteration can result in spatial heterogeneity in vegetation communities on a landscape scale, with benefits to biodiversity (Rushing et al. 2020).

High abundance of lesser snow (*Anser caerulescens caerulescens*, hereafter, snow geese) and Ross's geese (*Anser rossii*, collectively with snow geese referred to as light geese) have induced trophic cascades into subarctic and arctic ecosystems where they occur at high densities, with numerous documented effects on other species and ecosystem components. Light geese serving as allochthonous inputs into northern ecosystems have moderated functional and numerical responses of resident and migratory predators (Samelius et al. 2011, Giroux et al. 2012, McKinnon et al. 2013, Lamarre et al. 2017, Flemming et al. 2019a), as well as altered vegetation communities largely through consumption of substantial proportion of annual primary productivity, but also by removal of vegetation for nest construction (Chapters 2 and 3 and references therein). Fidelity of light geese to breeding regions (Wilson et al. 2016) and their occurrence at high densities have hastened cumulative impacts to vegetation over many decades through grazing, shoot-pulling, grubbing, and nesting activities, resulting not only in drastic reduction of plant biomass, but also in changes to richness and species composition of plant communities (Chapters 2 and 3 and references therein). Such habitat alteration has potential to affect sympatrically-breeding migrant and resident birds through changes to nesting cover and food availability.

Avian communities in arctic ecosystems are dominated by shorebird and passerine guilds, and attain greatest species richness and abundance in mesic lowland habitats (Brown et al. 2007, Saalfeld et al. 2013, Flemming et al. 2019c, Smith et al. 2020). Densely-vegetated lowland habitats dominated by grass and sedge species are most heavily impacted by light geese, as graminoid species are their preferred forage (Slattery and Alisauskas 2007). Whereas spatially discrete breeding colonies occupy limited geographical ranges (Flemming et al. 2016), light geese can alter habitat well beyond confines of breeding colonies following post-breeding dispersal, with disproportionate impacts to lowland plant communities (Chapter 2, Slattery and Alisauskas 2007, Fontaine and Mallory 2011, Conkin and Alisauskas 2017.) Yet, lowland habitats are not extensive throughout the circumpolar region, occupying only 36% of the vegetated area (graminoid tundras and wetlands combined, Walker et al. 2005). Removal of protective nesting cover required by many species (Smith et al. 2007, Flemming et al. 2016) that often breed sympatrically with light geese may result in reduced breeding propensity or dispersal in search of suitable habitat elsewhere, resulting in locally depressed densities (Rockwell et al. 2003, Sammler et al. 2008, Latour et al. 2010, Peterson et al. 2014, Flemming et al. 2019b). Alternatively, birds may select nesting habitats with reduced cover and thereby incur greater risk of predation of adults or their nests (Smith et al. 2007, Walpole et al. 2008), with potential impacts to productivity. Moreover, terrestrial arthropod abundance is greatest in lowland habitats (Bolduc et al. 2013), but loss of plant cover results in changes to arthropod prey availability through reduced abundance (Milakovic et al. 2001, Milakovic and Jefferies 2003) or changes to timing of emergence (Park 2017), with potential negative effects on avian nutrition and subsequent productivity (McKinnon et al. 2012).

However, under conditions of incomplete and spatially-variable removal of plant biomass by light geese, as generally occurs in arctic regions, light geese induce spatial heterogeneity to landscapes additive to that produced by topography and related ambient abiotic factors (Chapter 2, Slattery 2000). Variable removal of vegetation likely differentially affects cover-nesting and open-nesting species (Flemming et al. 2019c), and may function to elevate biodiversity across these landscapes, as occurs in prairie ecosystems disturbed by fire and grazing (Fuhlendorf et al.

2006). Moreover, encroachment of shrub species as a result of climate warming (Tape et al. 2006, Post and Pedersen 2008, Olofsson et al. 2009, Fraser et al. 2011, Elmendorf et al. 2012, Carlson et al. 2018), expedited in regions subjected to intense foraging and nesting activities of light geese (Chapter 3), may benefit some species by providing dense nesting cover (e.g. Peterson et al. 2014) or harboring increased abundance of arthropod prey.

I investigated potential effects of habitat alteration by light geese on occupancy of an array of sympatric avian species that breed in the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary (hereafter, the Sanctuary). This region supports high abundance and diversity of passerines and shorebirds (Flemming et al. 2019c), offering an opportunity to investigate occupancy by cover- and open-nesting species with a variety of habitat preferences. I predicted that species-specific occupancy would reflect known habitat preferences (e.g., cover- versus open-nesting, Smith et al. 2007), and therefore habitat alteration by light geese would have species-specific effects. I predicted that cover-nesting specialist species with requirements for heavily-vegetated graminoid-dominated plant communities would be negatively affected by loss of nesting cover (Flemming et al. 2019b). On the other hand, habitat generalist species with flexibility in selection of nesting cover may benefit from increased shrubs in altered habitats. Lastly, I predicted open-nesting species that select sparse vegetative cover (Smith et al. 2007) to be least sensitive to removal of vegetation by light geese. In addition to effects of habitat modification, I also investigated potential effects of nesting density of light geese on occupancy by other avian species. My ability to make predictions about avian response to presence of nesting light geese was confounded by the potential for light geese to attract sympatrically-nesting species through benefits of predator satiation or protective nesting associations (although generally limited to waterfowl species); alternatively, disturbance of nesting birds by light geese may result in their avoidance (Robertson 1995, Kellett et al. 2003, Baldwin et al. 2011, Kellett and Alisauskas 2011, Iles et al. 2013, Flemming et al. 2016, Pederson et al. 2018).

5.2 Methods

5.2.1 Field methods

I conducted avian and vegetation surveys on sample plots within and adjacent to the light goose nesting colony at Karrak Lake in June and July, 2014. I determined locations of systematically-spaced plots using the Universal Transverse Mercator (UTM) grid system

(Alisauskas et al. 2012b). The primary purpose of these circular sample plots, of radius 30 m spaced at 0.5 or 1.0 km intervals, was to facilitate ongoing annual estimation of nest density, species composition, nest initiation date, clutch size, and nest success of snow and Ross's geese (Alisauskas et al. 2012b). The sampling frame for geese was determined each year by mapping the colony boundary from a helicopter (Alisauskas et al. 2012b). I added plots to the avian and vegetation survey sampling design (using the same spacing scheme) to include locations outside the colony without geese and with less altered vegetation.

I recorded detection-nondetection data for avian species at each sample plot. At each plot, I conducted two consecutive 360-degree scans in which I identified all visually observable birds. For each avian sighting, I recorded species, sex if identifiable (sexually dimorphic or dichromatic species only; birds were not classified to sex based on behavior), age (adult or juvenile), and distance (determined with a rangefinder, ±1 m). I considered individuals detected within 100 m of the center of the plot as present for a given sampling occasion. I recorded survey-specific data of date, temperature, wind speed, start time of survey, and duration of survey; surveys were not conducted in inclement weather (precipitation events or high wind). I used handheld weather meters to determine temperature and wind speed. I surveyed a subset of sample plots at 10-day intervals throughout the survey season, and the remainder opportunistically as scheduling allowed.

I conducted point-intersect vegetation surveys described by Alisauskas et al. (2006) on sample plots in July after geese had left the nesting colony. I recorded plant or lichen species or species groups at 1.0 m intervals along 30 m transects extending in each cardinal direction from the plot center, resulting in 120 observations per plot. I did not identify grasses, sedges, lichens, and mosses to species, and instead refer to these categories as species groups.

5.2.2 Statistical analyses

5.2.2.1 Multispecies occupancy models: background

The hierarchical multispecies occupancy model (MSOM; Dorazio and Royle 2005 and extensions) jointly estimates detection and occurrence probabilities of each species in the community, including those species not detected during surveys (reviewed by Devarajan et al. 2020). Nondetection of species is distinguished from species absence through repeated sampling of sites (MacKenzie et al. 2017), and species-specific estimates of occurrence are obtained by using data from all observed species. Thus, this approach is particularly useful for communities that include rarely-observed and unobserved species, which often yield such infrequent observations that render single-species occupancy models (SSOMs) uninformative. This model also estimates species richness and so accounts for species present, but not observed during sampling (Dorazio et al. 2006). For reliable inference, the assumptions of MSOMs are similar to those of SSOMs and include geographic and demographic closure, independence of sample locations, correctness in species identification, and ecological similarity (MacKenzie et al. 2017, Devarajan et al. 2020).

Following Dorazio et al. (2006) and Zipkin et al. (2010), I defined occurrence z for species i at point j as $z(i,j)=1$ if species i occurs within 100 m of point j, and zero if not. The occurrence state z is only partially observed and assumed to be the outcome of a Bernoulli random variable, denoted by $z(i,j) \sim \text{Bern}(\psi_{i,j})$, where $\psi_{i,j}$ is the probability of occurrence of species i at point j. Estimation of $\psi_{i,j}$ is confounded because occurrence is imperfectly observed. However, species absence versus nondetection can be estimated by sampling point j over $k>1$ replicates over a short time period such that closure of the community to colonization or extinction of species at each sampling location is assumed for the duration of sampling (Dorazio et al. 2006). The detection model is specified with the collected data $x(i,j,k)$ as $x(i,j,k) \sim \text{Bern}(p_{i,j,k} * z(i,j))$, where $p_{i,j,k}$ is the detection probability of species i at point j during replicate k, given that species i is present at point j. Both occurrence ($\psi_{i,j}$) and detection ($p_{i,j,k}$) probabilities can be modeled as species-specific and as logit-link functions of covariates across sample plots and survey occasions (Kéry and Royle 2008).

5.2.2.2 Data selection

I restricted my data set to include those species known to be present in the Karrak Lake region throughout the breeding season, based on Birds of the World (Birds of the World 2020) species accounts and species sighting lists maintained annually for the Karrak Lake region since 2000 (R. Alisauskas, unpubl. data). Thus, I excluded one transient species (red knot (*Calidris canutus*)) that migrates through my study area and breeds >200 km north of Karrak Lake (Baker et al. 2020). I also excluded those species known to be area residents but unlikely to be explicitly associated with vegetation measured on sample plots; these included all waterfowl species and predatory species with home ranges much larger than the 100 m sampling radius and typically only observed when flying over sample plots. Such transitory species included herring (*Larus argentatus*) and glaucous (*L. hyperboreus*) gulls, long-tailed (*Stercorarius longicaudus*), parasitic (*S. parasiticus*), and pomarine (*S. pomarinus*) jaegers, common ravens (*Corvus corax*), and peregrine falcons (*Falco peregrinus*). Thus, my restricted data set contained only species unlikely to violate assumptions of closure during the survey period.

I conducted avian surveys on sample plots from 30 May – 3 August of 2014, but truncated survey data to a shorter period for occupancy analyses. I considered the beginning of the survey period to be 9 June, based on the earliest date that I first observed most species on the study area. I chose 15 July as the end of the survey period, because I suspected that assumptions of closure for some species would potentially be violated after that date as species completed nesting and dispersed from the study area. I did not use latest dates that I observed most species on the study area to determine the end of the survey period because I detected some species very infrequently. Thus, my survey period was restricted to 38 consecutive days during which I surveyed sample plots on at least two of the possible approximate four 10-day occasions.

5.2.2.3 Modeling framework: occupancy

I assumed that occurrence ($\psi_{i,j}$) probabilities varied by species and were influenced by plot-specific habitat features. I modeled occurrence probabilities for species *i* at point *j* with habitat covariates that reflected variation in (*i*) vegetation communities influenced by intensity of use by nesting light geese and edaphic state, and (*ii*) physical presence of nesting light geese.

5.2.2.3.1 Vegetation communities. I used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distance (package *vegan*, Oksanen et al. 2019) to characterize patterns in species composition of vegetation communities on sample plots. I compiled input data by summing point-intersect observations of each species or species group per plot for which I collected vegetation data; this sample size was greater than the number of plots on which I conducted avian surveys. I included only those taxa in ordinations for which occurrence across all plots was greater than 1%, as recommended to reduce influence of rare species (Rettie et al. 1997, Elliott and Vose 2016). I first constructed ordinations with 1-9 axes, with a maximum of 500 iterations for each configuration. I determined the appropriate number of axes by seeking low stress values (for ecological community data, stress values between <0.20 are acceptable) and beyond which additional axes resulted in low reductions of stress (McCune and Grace 2002).

I then constructed multiple (>10) ordinations with the chosen number of axes, and visually examined them to ensure reproducibility.

I was particularly interested in how intensity of habitat use by nesting geese, and resulting alteration of vegetation communities from foraging and nest construction (Chapters 2 and 3) influenced avian species occupancy. Thus, I investigated how patterns in vegetation community composition, as characterized by NMDS ordination, were related to sample plot variables of mean number of goose nests (Nests), number of years within the colony (YrsIn), and elevation (Elev) above sea-level (asl), using vector overlays on the NMDS ordination with the function *envfit*. I used Pearson correlation coefficients between biological and environmental variables and NMDS axis scores to define the strength of correlations of covariates with ordination axes, with significance determined using 999 permutations. I derived goose covariates (Nests, YrsIn) for each plot from long-term data described in Chapters 1 and 2. I extracted elevation data for each plot from the Federal Geospatial Platform of Canada (https://maps.canada.ca/), and thus, my analyses contain information licensed under the Open Government License – Canada (https://open.canada.ca/en/open-government-licence-canada). This raster data provided spatial resolution of 20 m, and I used the *bilinear* function to interpolate elevation from the four nearest cells for each plot (±0.1 m).

The resulting vector overlays on the ordination suggested that the second NMDS axis strongly reflected differences in community structure due to intensity of habitat use by light geese (see Results). Thus, I modeled occurrence probabilities with the second NMDS axis scores (NMDS2) for each sample plot as a covariate reflecting effects of intensity of habitat use by light geese on vegetation community composition. I included both linear and quadratic terms of NMDS2 so that species associations with this habitat covariate could maximize or minimize at intermediate levels, but the model did not converge with the quadratic term so I used only the linear term of NMDS2. Plot elevation was most strongly correlated with the first NMDS axis (see Results) so I used NMDS1 as an additional covariate to account for differences in vegetation community composition due to elevation and associated edaphic state. Although I was not explicitly interested in the effect of elevation *per se* on avian occupancy, such influences are important predictors of species distribution patterns because of linkages to vegetation communities influenced by moisture regimes (reviewed by Devarajan et al. 2020).

5.2.2.3.2 Presence of nesting geese. I used the recorded number of light goose nests on sample plots as a covariate reflecting density of light geese (goose density, GD) in 2014. I reasoned that this covariate represented the potential immediate effects of physical presence of light geese on avian species occurrence. Such effects could arise from (*i*) a positive influence of goose presence through effects of predator swamping and reduced probability of predation through aggression against predators, or (*ii*) a negative influence such as direct aggression by nesting geese on sympatric species (Robertson 1995, Kellett et al. 2003, Baldwin et al. 2011, Kellett and Alisauskas 2011, Iles et al. 2013, Pederson et al. 2018). This differed from Nests (used in vector overlay on NMDS ordination, above) which reflected long-term impacts of habitat use by geese on vegetation communities. I included both linear and quadratic terms of GD so that species associations could maximize or minimize at intermediate levels of light goose density, but as with NMDS2, the model did not converge with the quadratic term so I used only the linear term of light goose nesting density.

Thus, I specified the occurrence model of species *i* at point *j* as:

$$\mathrm{logit}(\psi_{i,j}) = \mu\mathrm{spp}_i + \alpha1_i\mathrm{NMDS2}_j + \alpha2_i\mathrm{NMDS1}_j + \alpha3_i\mathrm{GD}_j$$

In this parameterization, $\mu\mathrm{spp}_i$ is the occurrence probability on the logit scale for species *i* in the study area, at average values of NMDS2, NMDS1, and GD. The coefficients for the three α terms are the effects of NMDS2 ($\alpha1$) and NMDS1 ($\alpha2$) axis values and goose density ($\alpha3$) on species *i*. I standardized all covariate data to a mean of zero.

5.2.2.4 Modeling framework: detection

I assumed that detection ($p_{i,j,k}$) probabilities also varied by species and were influenced by survey-specific and plot-specific habitat effects. I modeled detection probabilities for species *i* at point *j* during replicate *k* with survey-specific covariates of survey date, ambient temperature, wind speed, survey duration, and survey start time (hours after 06:00), and plot-specific habitat effects of NMDS2, NMDS1, and GD. However, exploratory analyses revealed that all covariates except for survey duration (TimeScan) explained little variation in detection probability and their inclusion resulted in non-convergence, so I modeled detection probability against survey duration only, expecting that detection probability would increase with survey duration.

Thus, I specified the detection model of species *i* at point *j* during replicate *k* as:

$$\text{logit}(p_{i,j,k}) = \nu\text{spp}_i + \beta 1_i \text{TimeScan}_{j,k}$$

In this parameterization, νspp_i is the detection probability on the logit scale for species *i* in the study area, at average values of the TimeScan covariate. The coefficients for the β term is the effect of TimeScan ($\beta 1$) on species *i*. I standardized detection covariate data to a mean of zero.

5.2.2.5 Species-specific parameters as random effects

A benefit of the multispecies approach in modeling occupancy is that species-specific occurrence and detection parameters were assumed to be drawn from a common (community-level) distribution; combining species data is an improvement over single-species models providing that it is reasonable to assume that individual species parameters are drawn from a common distribution (Sauer and Link 2002, Zipkin et al. 2010). By connecting individual species occurrence and detection probabilities through a community hierarchical component, efficient use of data allows for better precision of species-specific estimates (Kéry and Royle 2008, Zipkin et al. 2009). Each of the species-specific occurrence (μspp_i, $\alpha 1$-$\alpha 3$) and detection (νspp_i, $\beta 1$) parameters are random effects governed by 'hyper-parameters'. As an example, I assumed that $\mu\text{spp}_i \sim \text{norm}(\mu_{\mu\text{spp}}, \sigma_{\mu\text{spp}})$ where $\mu_{\mu\text{spp}}$ is the mean occurrence across the community and $\sigma_{\mu\text{spp}}$ is the standard deviation among species.

5.2.2.6 Data augmentation to estimate N

I estimated species richness, *N*, using the method of data augmentation by populating the data with several all-zero encounter histories to represent species present but never observed during sampling (Dorazio et al. 2006, Royle et al. 2007, Kéry and Royle 2009). Analysis by data augmentation assumes a uniform prior (0,*M*) for *N* in which I fixed *M* to an arbitrary constant much greater than the observed number of species in the community (*n*), such that the resulting posterior distribution for *N* was not at risk of truncation. On the other hand, high values of *M* incur higher computational costs (Dorazio et al. 2006). I detected *n*=14 species during sampling, and initially set M=34. I augmented the data set with (M-n)=20 all-zero encounter histories such that the model for the augmented data was a zero-inflated model where N is estimated as a derived parameter (Dorazio et al. 2006, Royle et al. 2007, Kéry and Royle 2009, Devarajan et al. 2020). I then modified the occurrence process from $z(i,j) \sim Bern(\psi_{i,j})$ to $z(i,j) \sim Bern(\psi_{i,j} * w_i)$, where w_i were latent indicator variables assumed to be independent and Bernoulli-distributed indexed by the estimated parameter Ω, the probability that species i is a member of the metacommunity of size N (Dorazio et al. 2006, Zipkin et al. 2010, Devarajan et al. 2020). A value of w_i=1 corresponds to species that were either observed or that were unobserved but available for sampling, and zero otherwise. It is important to note that N is not the number of species that occur in a particular landscape, but is equivalent to the asymptote of a species-accumulation curve (Dorazio et al. 2006, Kéry and Royle 2009, Zipkin et al. 2010). Initial trials determined that N was estimated at <20, so I augmented the data set with five all-zero encounter histories (M=19) for subsequent evaluations of the model, in order to improve convergence.

5.2.2.7 Model implementation

I analysed my multispecies occupancy model in a Bayesian framework with Markov Chain Monte Carlo (MCMC) methods implemented in WinBUGS (Spiegelhalter et al. 2003) through R package *R2WinBUGS* (Sturtz et al. 2005) in Program R (R Development Core Team 2018). Following Zipkin et al. (2010), I used vague prior distributions for all parameters. I used 3 chains of length 50,000, with burn-in of 25,000 and thin of 25, saving 3000 posterior samples for each parameter to be used in post-modeling analysis. I assessed convergence with R-hat (Brooks and Gelman 1998), and stored posterior samples when R-hat <1.1 in order to draw reliable inference for parameters of interest. R-hat statistics for most parameters were <1.1 (mean R-hat of all parameters=1.10). I found poorer convergence of species-specific detection parameters (mean R-hat=1.71), but increasing number of iterations did not improve convergence.

5.3 Results

5.3.1 Avian surveys

I conducted avian surveys at 144 plots within or near the light goose colony at Karrak Lake between 9 June and 15 July, 2014 (Fig. 5.1). I visited 42 plots during all four sampling occasions, but surveyed most plots less frequently (63 and 39 plots surveyed on 2 and 3 occasions, respectively). I observed 24 avian species during sampling, but included 14 species in my MSOM (Table 5.1, and see Methods for rationale). I observed a maximum of five of 14 possible species at any individual plot, and observed no species on any occasion at four plots. I observed Lapland longspurs (*Calcarius lapponicus*) most frequently, on 537 occasions, but 7 of 14 species (Baird’s sandpiper (*Calidris bairdii*), black-bellied plover (*Pluvialis squatarola*), dunlin (*Calidris alpina*), pectoral sandpiper (*Calidris melanotos*), red phalarope (*Phalaropus fulicarius*), semipalmated plover (*Charadrius semipalmatus*), and white-crowned sparrow (*Zonotrichia leucophrys*)) on <5 occasions.

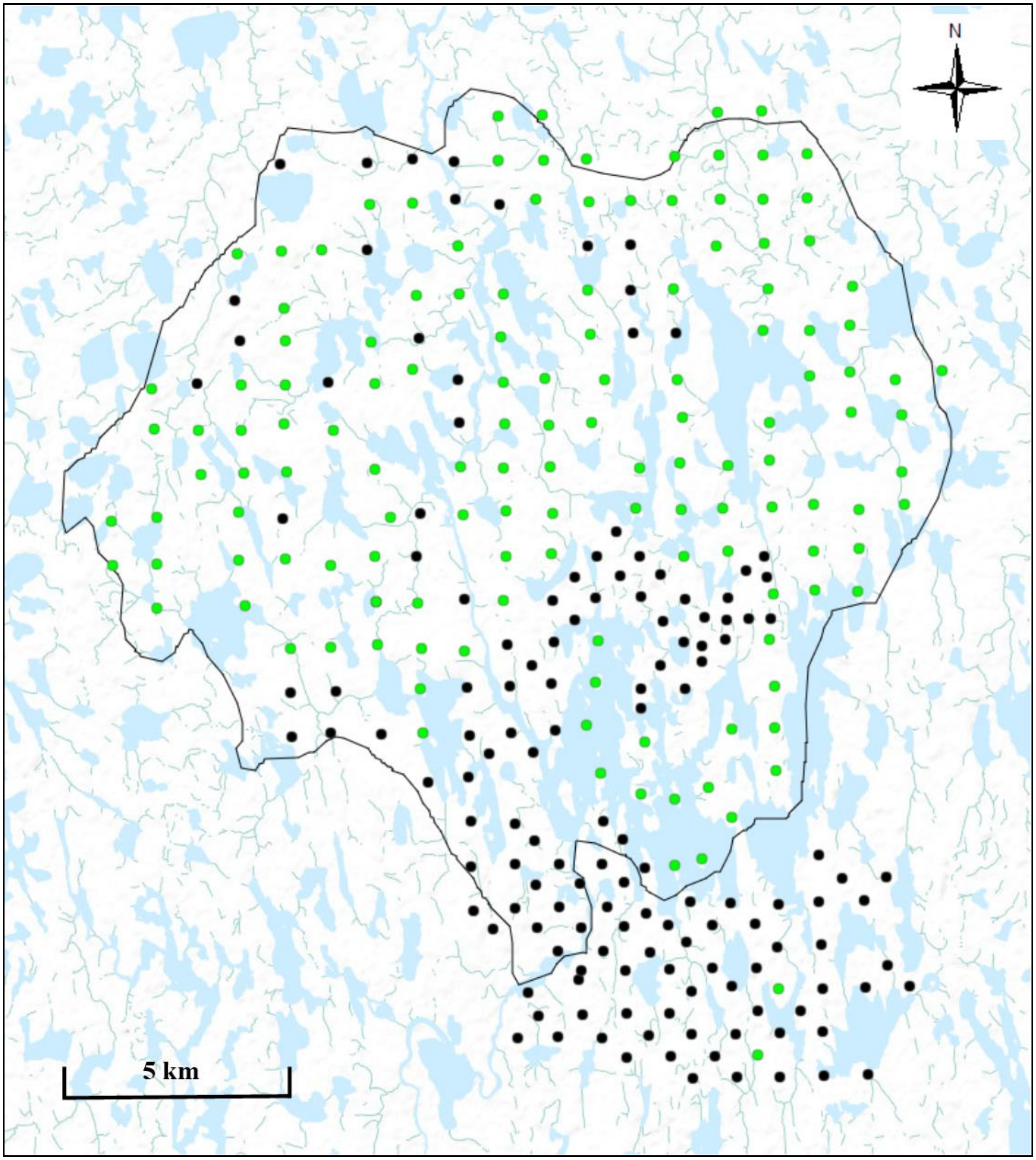

Figure 5.1. Map of study area showing locations of sample plots (green and black dots) inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut. The black line depicts the colony boundary in 2014. The green dots depict those plots on which only vegetation surveys (30 m sampling radius) were conducted, and the black dots depict those plots on which both vegetation and avian surveys (100 m sampling radius for avian surveys) were conducted.

Table 5.1. All avian species observed at Karrak Lake, Nunavut, during May-August, 2014. The first 14 species listed were included in the multispecies occupancy model (MSOM). The remainder were either (superscript b) detected during surveys at distances of <100 m but excluded for reasons listed in text, or (superscript c) not detected during surveys but observed in study area. Nest type was determined according to Birds of the World (2020) species accounts. †Species whose distributional ranges do not include the Queen Maud Gulf (Ahiak) Migratory Bird Sanctuary, Nunavut, according to species accounts of Birds of the World (2020). Species codes follow American Ornithological Society.

Common Name	**Scientific Name**	**Taxonomic Family**	**Species Code**	**Included in MSOM**	**Nest Type**
Horned Lark	*Eremophila alpestris*	Alaudidae	HOLA	yes	open
Lapland Longspur	*Calcarius lapponicus*	Calcariidae	LALO	yes	cover
Snow Bunting	*Plectrophenax nivalis*	Calcariidae	SNBU	yes	cover
Black-bellied Plover	*Pluvialis squatarola*	Charadriidae	BBPL	yes	open
American Golden Plover	*Pluvialis dominica*	Charadriidae	AGPL	yes	open
Semipalmated Plover	*Charadrius semipalmatus*	Charadriidae	SEPL	yes	open
White-crowned Sparrow	*Zonotrichia leucophrys*	Passerellidae	WCSP	yes	cover
Savannah Sparrow	*Passerculus sandwichensis*	Passerellidae	SAVS	yes	cover
Rock Ptarmigan	*Lagopus muta*	Phasianidae	ROPT	yes	open
Semipalmated Sandpiper	*Calidris pusilla*	Scolopacidae	SESA	yes	cover
Baird's Sandpiper	*Calidris bairdii*	Scolopacidae	BASA	yes	open
Pectoral Sandpiper	*Calidris melanotos*	Scolopacidae	PESA	yes	cover
Dunlin	*Calidris alpina*	Scolopacidae	DUNL	yes	cover
Red Phalarope	*Phalaropus fulicarius*	Scolopacidae	REPH	yes	cover
Lesser Snow Goose	*Anser caerulescens*	Anatidae	LSGO	no^{b}	
Ross's Goose	*Anser rossii*	Anatidae	ROGO	no^{b}	
Pacific Loon	*Gavia pacifica*	Gaviidae	PALO	no^{b}	

Sandhill Crane	*Antigone canadensis*	Gruidae	SACR	no[b]
Glaucous Gull	*Larus hyperboreus*	Laridae	GLGU	no[b]
Red Knot†	*Calidris canutus*	Scolopacidae	REKN	no[b]
Parasitic Jaeger	*Stercorarius parasiticus*	Stercorariidae	PAJA	no[b]
Long-tailed Jaeger	*Stercorarius longicaudus*	Stercorariidae	LTJA	no[b]
Snowy Owl	*Bubo scandiacus*	Strigidae	SNOW	no[b]
Rough-legged Hawk	*Buteo lagopus*	Accipitridae	RLHA	no[c]
Northern Harrier†	*Circus hudsonius*	Accipitridae	NOHA	no[c]
Golden Eagle†	*Aquila chrysaetos*	Accipitridae	GOEA	no[c]
Bald Eagle†	*Haliaeetus leucocephalus*	Accipitridae	BAEA	no[c]
Tundra Swan	*Cygnus columbianus*	Anatidae	TUSW	no[c]
Greater White-fronted Goose	*Anser albifrons*	Anatidae	GWFG	no[c]
Cackling Goose	*Branta hutchinsii*	Anatidae	CACG	no[c]
Northern Pintail	*Anas acuta*	Anatidae	NOPI	no[c]
King Eider	*Somateria spectabilis*	Anatidae	KIEI	no[c]
Long-tailed Duck	*Clangula hyemalis*	Anatidae	LTDU	no[c]
Red-breasted Merganser	*Mergus serrator*	Anatidae	RBME	no[c]
Green-winged Teal†	*Anas crecca*	Anatidae	AGWT	no[c]
Canada Goose	*Branta canadensis*	Anatidae	CAGO	no[c]
Common Raven	*Corvus corax*	Corvidae	CORA	no[c]
Peregrine Falcon	*Falco peregrinus*	Falconidae	PEFA	no[c]
Gyrfalcon	*Falco rusticolus*	Falconidae	GYFA	no[c]
Redpoll spp. (Common, Hoary)	*Acanthis flammea, A. hornemanni*	Fringillidae	REDPOLL	no[c]
Red-throated Loon	*Gavia stellata*	Gaviidae	RTLO	no[c]

Herring Gull	*Larus argentatus*	Laridae	HEGU	no[c]
Sabine's Gull†	*Xema sabini*	Laridae	SAGU	no[c]
Arctic Tern	*Sterna paradisaea*	Laridae	ARTE	no[c]
Ruddy Turnstone†	*Arenaria interpres*	Scolopacidae	RUTU	no[c]
Least Sandpiper†	*Calidris minutilla*	Scolopacidae	LESA	no[c]
White-rumped Sandpiper	*Calidris fuscicollis*	Scolopacidae	WRSA	no[c]
Stilt Sandpiper†	*Calidris himantopus*	Scolopacidae	STSA	no[c]
Wilson's Snipe†	*Gallinago delicata*	Scolopacidae	WISN	no[c]
Red-necked Phalarope	*Phalaropus lobatus*	Scolopacidae	RNPH	no[c]
Whimbrel†	*Numenius phaeopus*	Scolopacidae	WHIM	no[c]
Buff-breasted Sandpiper†	*Calidris subruficollis*	Scolopacidae	BBSA	no[c]
Pomarine Jaeger†	*Stercorarius pomarinus*	Stercorariidae	POJA	no[c]
Short-eared Owl†	*Asio flammeus*	Strigidae	SEOW	no[c]

5.3.2 Vegetation surveys

I conducted vegetation surveys at 282 plots within or near the goose colony at Karrak Lake in 2014 (Fig. 5.1). Ordination of 13 species or species groups accounting for 97.3% of point-intersect observations resulting in a four-dimensional solution capturing 25.9% of variation in the ranked distance matrix (Table 5.2, Fig. 5.2). I used four axes for the final configuration because convergence was achieved easily (<280 iterations over multiple attempts), reproducible (plots were very similar) and stress was minimal (0.106) and only slightly greater than an ordination using five axes (0.089). In comparison, a three-dimensional solution had stress of 0.133. The second axis of the ordination represented the biological covariates of number of years in colony (YrsIn) and mean number of goose nests (Nests, Fig. 5.2). Number of years in colony was strongly correlated with the second axis (0.815) and less so with the first, third, or fourth axes (0.003, -0.520, and -0.257, respectively, $r^2=0.333$, $p<0.001$, Fig. 5.2). Likewise, Nests was most strongly correlated with the second axis (0.814) compared with the first, third, or fourth axes (0.076, -0.376, and -0.435, respectively, $r^2=0.416$, $p<0.001$, Fig. 5.2). Thus, positive values of NMDS2 represented communities composed of taxonomic groups typically associated with disturbance by geese (Table 5.2, Fig. 5.2). Elevation was most strongly correlated with the first axis (-0.715) and less so with the second, third and fourth axes (-0.075, 0.339, and 0.606, respectively, $r^2=0.179$, $p<0.001$, Fig 5.2), and was largely orthogonal to the NMDS2 axis representing disturbance by geese. Thus, positive NMDS1 values were associated with vegetation communities composed of species in moister habitats at lower elevations (Table 5.2, Fig. 5.2).

Table 5.2. Percent occurrence of species and species groups and resulting axis loadings from nonmetric multidimensional scaling (NMDS) ordination of vegetation community data collected on *n*=282 sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 2014. Thirteen species and species groups accounted for 97.3% of point-intersect observations.

Species Code	Species or Species Group	Percent Occurrence	NMDS1	NMDS2	NMDS3	NMDS4
LICH	all lichen species	9.6	-0.552	-0.348	-0.076	0.114
PEAT	dead moss species	9.1	0.417	0.223	-0.227	0.208
SPHA	*Sphagnum* spp.	3.4	0.598	-0.328	0.398	0.147
MOCA	moss carpet (non-*Sphagnum* spp.)	6.7	0.349	0.171	0.169	-0.152
GRAM	graminoids (grass and sedge spp.)	6.9	0.674	-0.689	-0.063	-0.097
BIRC	birch *(Betula glandulosa)*	13.5	0.288	0.213	-0.107	0.044
WILL	willows *(Salix* spp.)	3.5	0.680	-0.413	-0.218	-0.026
CRAN	cranberry *(Vaccinium vitis-idaea)*	15.9	-0.116	0.081	0.176	0.147
CROW	crowberry *(Empetrum nigrum)*	1.3	-0.628	-0.022	0.178	-0.747
BEAR	bearberry (*Arctous*spp.)	1.4	-0.518	0.073	0.694	-0.137
LABT	Labrador tea *(Ledum palustre)*	18.4	-0.318	0.077	-0.038	0.113
HEAT	white heather *(Cassiope tetragona)*	6.7	-0.428	0.022	-0.276	-0.062
RAGW	marsh ragwort *(Tephroseris palustris)*	0.8	0.652	0.754	-0.162	-0.261

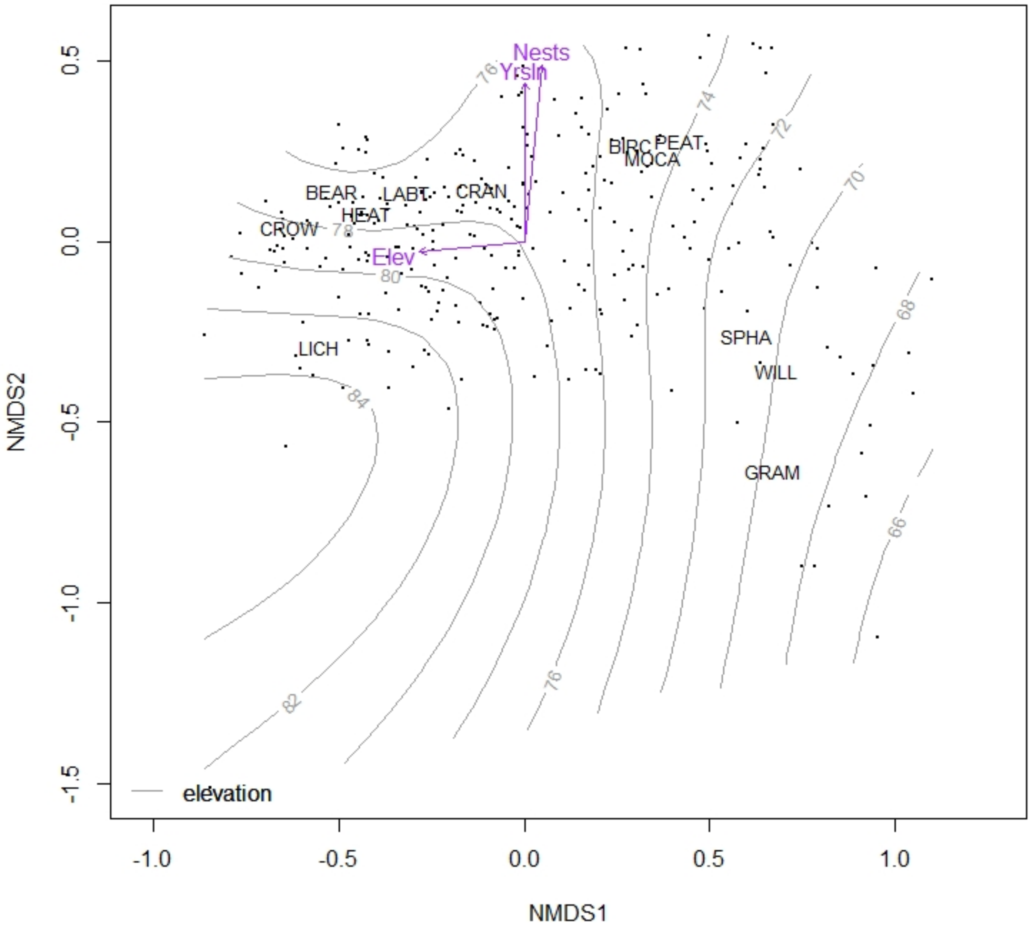

Figure 5.2. Four-dimensional nonmetric multidimensional scaling (NMDS) ordination of 13 taxonomic groups of vegetation on 282 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2014. The four axes (third and fourth axis not shown) captured 25.9% of variation in the ranked matrix, with axes 1-4 capturing 12.4, 5.9, 4.2, and 3.4% of variation, respectively. Black dots and text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays of environmental and biological covariates of elevation (Elev), number of years in colony (YrsIn), and mean number of goose nests (Nests), are depicted by purple arrows, with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for elevation. Species and species groups: LICH, all lichen species; PEAT, dead moss species; SPHA, Sphagnum spp.; MOCA, moss carpet (non-*Sphagnum* spp.); GRAM, graminoids (grass and sedge spp.); BIRC, birch (*Betula glandulosa*); WILL, willows (*Salix* spp.); CRAN, cranberry (*Vaccinium vitis-idaea*); CROW, crowberry

(*Empetrum nigrum*); BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea (*Ledum palustre*); HEAT, white heather (*Cassiope tetragona*); RAGW, marsh ragwort (*Tephroseris palustris*).

5.3.3 Multispecies occupancy estimates

My MSOM estimated 16.5 avian species in the surveyed region (95% posterior interval (PI): 14, 19); this is the estimate of number of species unlikely to violate assumption of closure during the survey period, and thus excludes transient species and those typically observed flying over sample plots. Species-specific occupancy probabilities at mean covariate values were highly variable, ranging between ~1.000 (0.989, 1.000) for Lapland longspur and 0.002 (0.000, 0.041) for Baird's sandpiper (Table 5.3). With the exception of Lapland longspur, species-specific detection probabilities at mean covariate values were generally low, ranging between 0.919 (0.876, 0.953) for Lapland longspur and 0.078 (0.037, 0.175) for rock ptarmigan (*Lagopus muta*; Table 5.3).

Table 5.3. Species-specific estimates of occupancy (ψ) and detection (p) probabilities (mean and 95% posterior interval (PI)), at mean values of explanatory covariates, for 14 avian species (species codes follows Table 5.1) observed during point count surveys on sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 2014.

Species	Occupancy (ψ)			Detection (p)		
Code	mean	L95%PI	U95%PI	mean	L95%PI	U95%PI
LALO	1.000	0.989	1.000	0.919	0.876	0.953
SESA	0.942	0.427	1.000	0.098	0.060	0.153
ROPT	0.748	0.128	1.000	0.078	0.037	0.175
SAVS	0.613	0.172	1.000	0.117	0.052	0.210
HOLA	0.607	0.280	0.944	0.178	0.104	0.282
SNBU	0.264	0.144	0.484	0.363	0.205	0.502
REPH	0.070	0.005	0.912	0.120	0.020	0.453
AGPL	0.047	0.005	0.364	0.112	0.031	0.313
PESA	0.010	0.000	0.260	0.123	0.016	0.363
DUNL	0.010	0.000	0.102	0.175	0.055	0.488
WCSP	0.005	0.000	0.061	0.212	0.046	0.371
BBPL	0.003	0.000	0.033	0.285	0.089	0.624
SEPL	0.003	0.000	0.021	0.592	0.190	0.899
BASA	0.002	0.000	0.041	0.208	0.058	0.801

Detection probabilities of individual species were positively influenced by survey duration (Fig. 5.3) as expected, although nearly all 95% confidence intervals bounded zero. Lapland longspur showed very high detection probabilities, with detection probability nearing ~1.0 after 12 minutes of surveying. All other species showed an increasing linear trend of detection probability with survey duration within the range of survey duration used in this study (3-17 minutes).

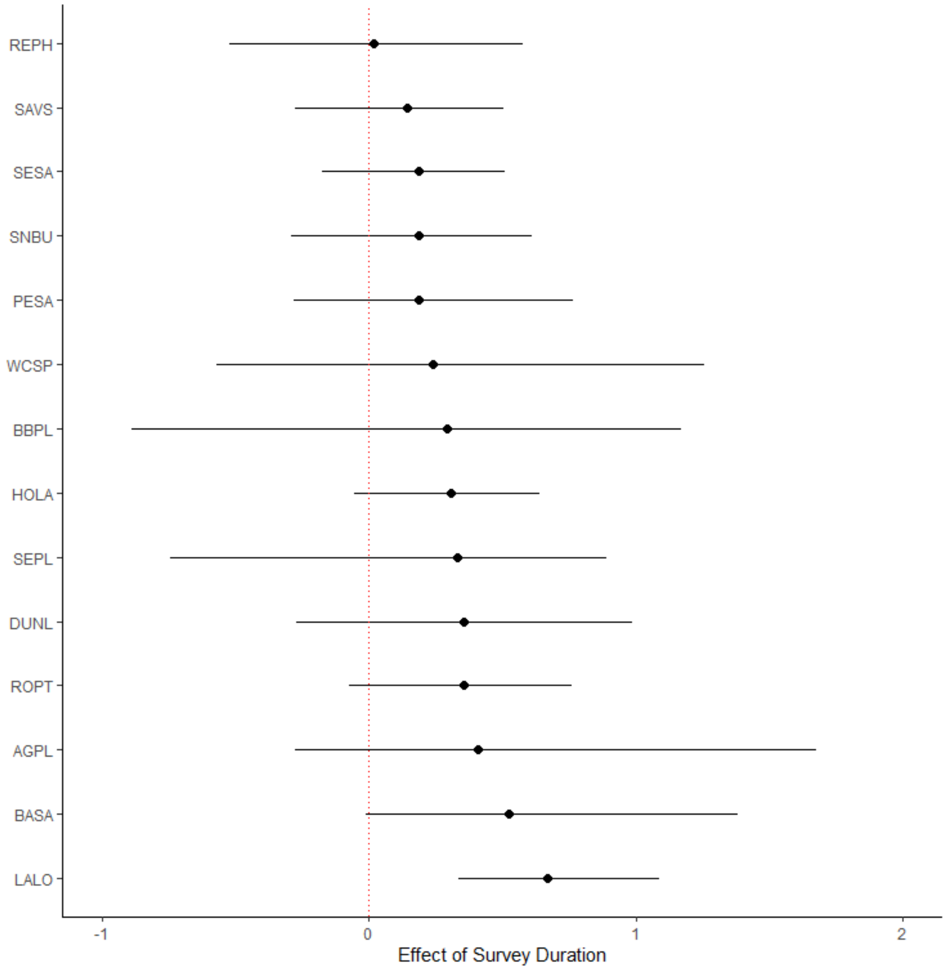

Figure 5.3. Species-specific effect of survey duration on detection probability of avian species observed on sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 2014. Shown are species-level responses to survey duration: the black dots and bars represent mean coefficient estimates and 95% posterior interval, respectively, in which points to the right of the vertical red line indicates that all species showed positve response to longer survey duration. Species names are shown on the y-axis as four-letter alpha codes (see Table 5.3 for full species names).

Individual species occurrence was influenced differentially by vegetation community composition reflected by NMDS axis scores (Fig. 5.4). Nearly all 95% confidence intervals of species-specific coefficients of NMDS2 and NMDS1, which reflected vegetation differences due to long-term use by nesting light geese and elevation, respectively, bounded zero. However, horned lark and snow bunting showed strong positive association between occupancy and increasing NMDS2 scores, occurring more frequently in habitat with long and intense history of use by nesting geese. Dunlin, on the other hand, showed strong negative association between occupancy and increasing NMDS2 scores, occurring more frequently in habitat less disturbed by nesting geese dominated by graminoids and intact moss communities. Effects of NMDS1 on species occupancy were more pronounced than were effects of NMDS2. Shared effects of moisture and elevation reflected in species composition of vegetation communities, best described by NMDS1, on avian occupancy were in the directions expected. Specifically, American golden plover (*Pluvialis dominica*), black-bellied plover, horned lark (*Eremophila alpestris*) and snow bunting (*Plectrophenax nivalis*) showed higher occupancy in xeric upland habitats, whereas Baird’s sandpiper, dunlin, savannah sparrow (*Passerculus sandwichensis*), and semipalmated sandpiper (*Calidris pusilla*) occurred more frequently in moist lowland habitats.

All species showed lower occupancy with increasing nesting density of light geese (Fig. 5.4), although all 95% confidence intervals bounded zero. With the exception of two species, occupancy declined to nearly zero when number of light goose nests on sample plots exceeded 30, equating to a nest density of about 106 nests ha^{-1}.

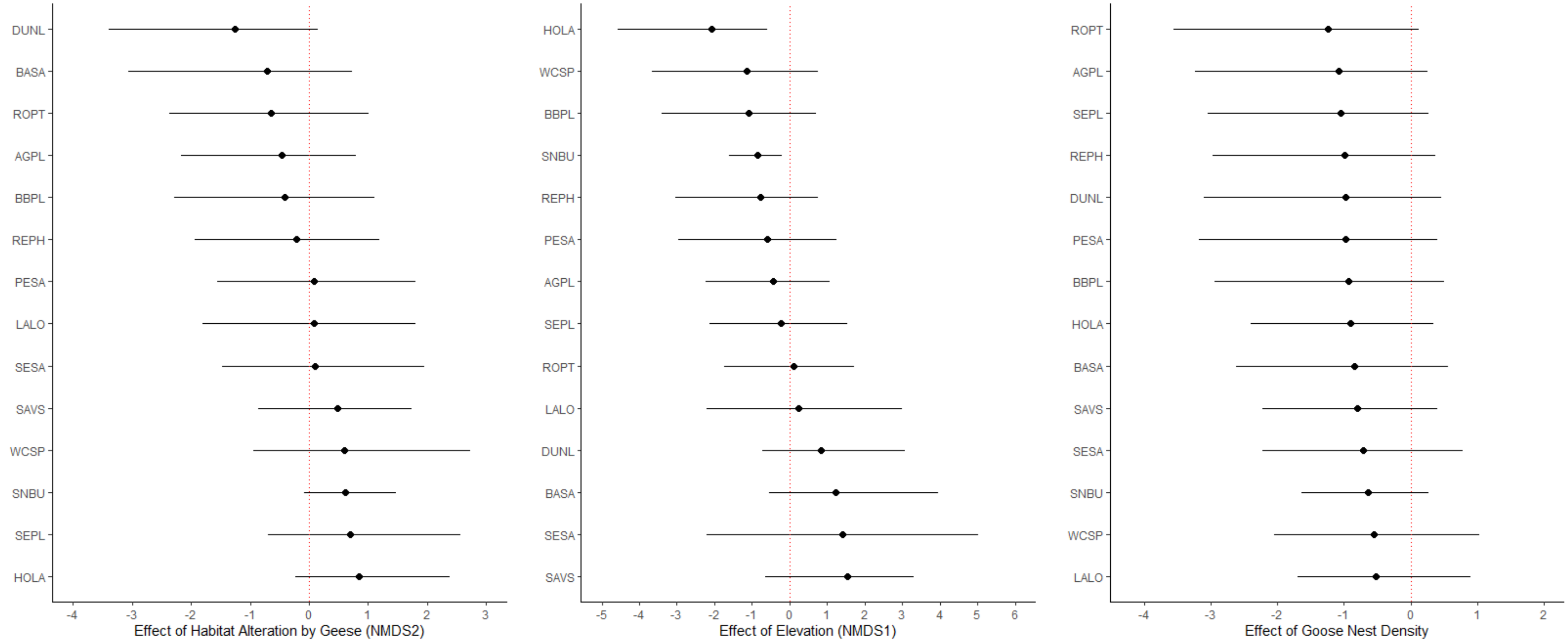

Figure 5.4. Species-specific habitat and biological effects on occupancy probabilities of avian species observed on sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, during 2014. Shown are species-level responses to covariates: the black dots and bars represent mean coefficient estimates and 95% posterior interval, respectively. Left panel indicates species response to habitat alteration by geese (second-axis nonmetric multidimensional scaling (NMDS) ordination scores, NMDS2), in which points to the left and right of the vertical red line indicate species with negative and positive response to habitat alteration respectively. Middle panel indicates species response to habitat elevation (first-axis NMDS ordination scores, NMDS1), in which points to the left and right of the vertical red line indicate species with greater occupancy at higher and lower elevations, respectively. Right panel indicates species response to density of nesting snow and Ross's geese, in which points to the left of the vertical red line indicates that all species showed negative response to increasing densities of nesting geese. Species names are shown on the y-axis as four-letter alpha codes (see Table 5.3 for full species names).

I observed 0-5 species on sample plots, whereas model estimates of number of species on sample plots ranged 1.0-2.8 (Fig. 5.5). Plot-specific species richness was not influenced by NMDS1 scores, which reflected vegetation community differences largely due to elevation. Species richness declined very slightly with increasing NMDS2 scores, suggesting that plots with habitat subjected to longer and more intense use by nesting light geese perhaps supported fewer avian species. In contrast, density of nesting geese had a strong negative effect on species richness.

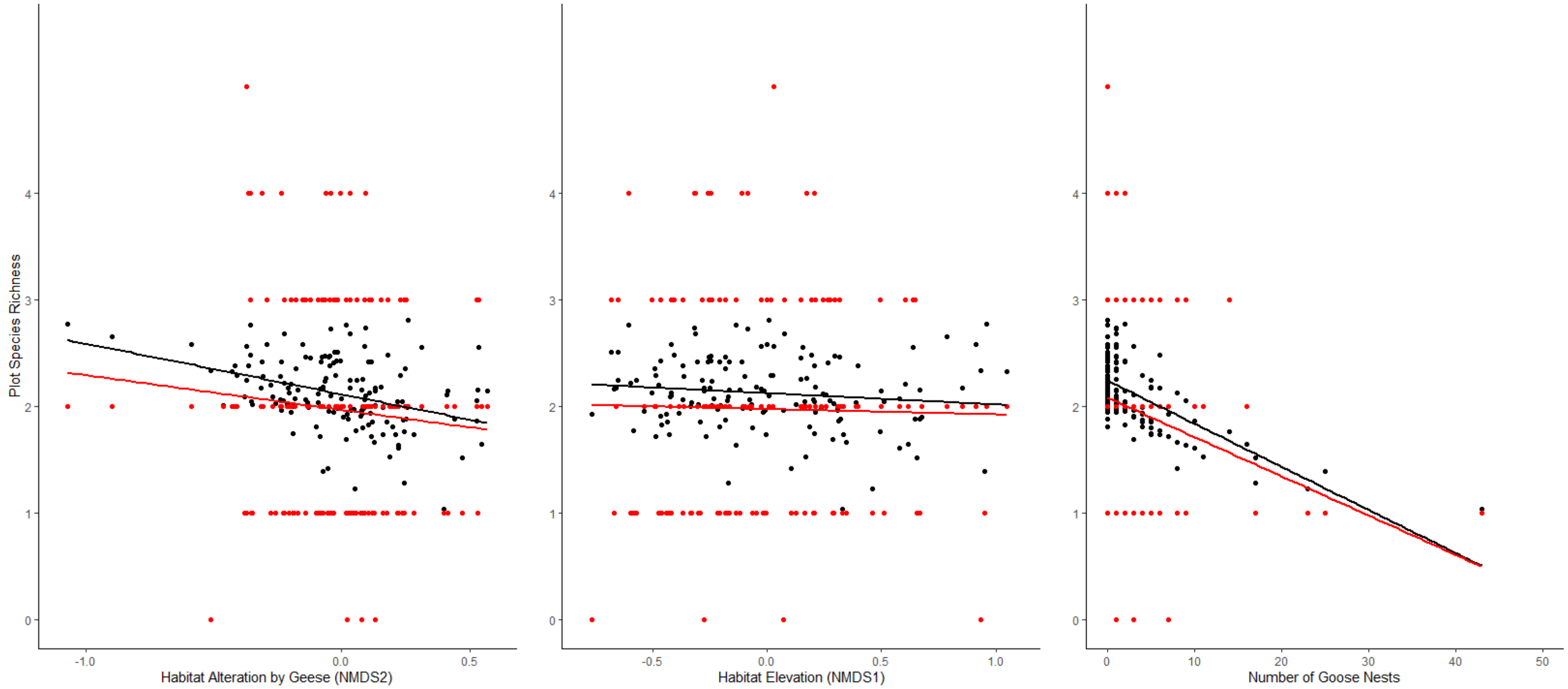

Figure 5.5. Model-based estimates (black circles) versus observed (red circles) plot-specific avian species richness in relation to environmental and biological covariates measured on sample plots inside and outside the snow and Ross's goose nesting colony at Karrak Lake, Nunavut, 2014. Left panel: second-axis nonmetric multidimensional scaling (NMDS) ordination scores (NMDS2), representing habitat alteration by geese; middle panel: first-axis NMDS ordination scores (NMDS1) representing habitat elevation; and right panel: number of snow and Ross's geese nests (30 m radius sample plot).

5.4 Discussion

Whereas extinction of species is important to defining the current decline of global biodiversity, extinctions begin with a reduction in population abundance that can also have profound effects on ecosystem structure and function (Rosenberg et al. 2019). Throughout the circumpolar arctic region, many shorebird species are believed to have declined in abundance, although only the Eskimo curlew (*Numenius borealis*) is presumed to be extinct (Downes et al. 2011, NABCI 2012, Zöckler et al. 2013, Smith et al. 2020). As well, limited data suggest declines in abundance of passerines, although several broadly-distributed species show long-term increasing population trends (Downes et al. 2011, Smith et al. 2020). Most threats to shorebird and passerine populations likely originate outside arctic regions, and are largely identified as habitat loss and degradation along migratory routes and wintering areas (NABCI 2012). However, threats that occur on northern breeding grounds might induce additive stressors to already declining populations.

Within arctic regions, climate-related mismatch is expected to have the greatest negative impacts on avian reproduction, as accelerated rate of climate change at high latitudes (Allen et al. 2018) may exceed ability of many species to adapt (NABCI 2012, Smith et al. 2020, but see Weiser et al. 2018). Light geese, as dominant herbivores in many northern ecosystems (Gauthier et al. 2004, Alisauskas et al. 2006, Kerbes et al. 2014, Legagneux et al. 2014, Conkin and Alisauskas 2017, Flemming et al. 2019b), can have knock-on effects to sympatrically-breeding birds (this study) and resident rodents (Chapter 4) through changes to vegetation communities (Chapters 2 and 3 and references therein). As arctic-nesting shorebirds may interact with light geese during the breeding season, Flemming et al. (2016) suggested that geese could result in regional declines in abundance and diversity of shorebirds and passerines.

Several avian guilds are appreciably less abundant near light goose colonies (Latour et al. 2010, Lamarre et al. 2017, Flemming et al. 2019c), and decline in abundance of cover-nesting versus open-nesting species close to goose colonies suggests that reduction of vegetative cover is responsible for these trends (Latour et al. 2010, Flemming et al. 2019b, 2019c, but see Lamarre et al. 2017, Flemming et al. 2019a). This motivated my investigation of species-specific probability of occupancy in response to alteration of vegetation communities at Karrak Lake. Using analytical methods that accounted for incomplete and species-specific probability of detection, these results showed that shorebird and passerine species varied in their response to habitat alteration (Fig. 5.4), largely in predicted directions based on known habitat preferences. The direction of any response in occupancy should vary by species depending on its feeding ecology and requirements for nest crypsis. All species showed negative responses to increased densities of nesting light geese (Fig. 5.4, discussed further below). Trophic cascades initiated by light geese can affect avian species through a variety of mechanisms in addition to habitat alteration, such as changes to predator communities and arthropod prey (Flemming et al. 2016), which I did not investigate but discuss further below.

5.4.1 Changes to predator communities

Large aggregations of breeding birds can attract predators (e.g. Iverson et al. 2014), providing predictable resources for both migratory and resident predators (e.g., Samelius and Alisauskas 1999, Iles et al. 2013). I did not investigate avian occupancy in relation to potential changes to predator communities associated with breeding light geese. However, documented changes to functional and numerical responses of predators in response to availability of geese as prey (Samelius et al. 2011, Giroux et al. 2012, McKinnon et al. 2013, Lamarre et al. 2017, Flemming et al. 2019a, but see Flemming et al. 2019c) also likely had an effect on occupancy of sympatric avian species at Karrak Lake, as has been reported in other regions (Lamarre et al. 2017, Flemming et al. 2019a). On Bylot Island, enhanced primary productivity as a result of climate change coupled with moderate abundance of breeding greater snow geese (*Anser caerulescens atlantica*) has not resulted in severe alteration of vegetation communities (Gauthier et al. 2004, Legagneux et al. 2014). Yet, Lamarre et al. (2017) demonstrated that abundance of nesting shorebirds was lower near the nesting colony where there was increased risk of predation due to attraction of predators by nesting geese. Likewise, Flemming and coauthors (2019a), in addition to demonstrating habitat effects on abundance of sympatric birds (2019b, discussed further below), also reported decline in predation risk with increasing distance from light goose nesting areas.

Despite generally low lemming densities, breeding by arctic fox at Karrak Lake is determined by lemming abundance (Samelius et al. 2011, Samelius and Alisauskas 2017), and risk of predation for nesting birds may be more pronounced during low phases of multiannual rodent oscillations when predators seek alternative prey (Bêty et al. 2002, McKinnon et al. 2014). As well, predation risk likely differs among geese, shorebirds, and passerines. As light geese actively defend nests from predators (Bêty et al. 2002, Samelius and Alisauskas 2006), they are likely less susceptible to nest loss than are smaller passerine and shorebird species. Moreover, because risk of predation varies with location within nesting aggregations (e.g., Lecomte et al. 2008), birds that avoid high densities of geese (Baldwin et al. 2011, this study) or select nest sites in less altered habitats, both of which typically exist on peripheries of nesting colonies (Alisauskas et al. 2012b, Chapters 2 and 3), may incur additional predation risk.

On the other hand, although predators may be more abundant near goose colonies, extremely large aggregations such as at Karrak Lake may overwhelm ability of predators to respond functionally. Certain species may choose to nest in the vicinity of light geese (often waterfowl, e.g., Kellett et al. 2003, Kellett and Alisauskas 2011), motivated by predator satiation (Baldwin et al. 2011, Iles et al 2013, Pedersen et al. 2018)) or protective nesting associations (most often associated with raptors, gulls and terns (reviewed by Quinn and Ueta 2008), but see Robertson (1995) for light geese). However, despite potential benefits, all avian species investigated in this study showed lower occupancy probabilities with higher densities of nesting light geese. Further, projected occupancy rates declined to zero at light goose densities that are not uncommon throughout the colony (Alisauskas et al. 2012b); territorial aggression between light geese may result in increased disturbance or abandonment of nests by sympatric species (Baldwin et al. 2011) or outright avoidance of such densities (this study).

5.4.2 The role of arthropod prey

Although climate warming has the greatest potential to alter arctic arthropod communities (Bolduc et al. 2013, Smith et al. 2020), changing prey availability (both abundance and phenology) for insectivorous birds is also likely a knock-on effect of alteration of vegetation communities by light geese. On Hudson Bay’s western coast, diversity and abundance of beetles, spiders, and midges declined in response to near-complete removal of vegetation by light geese (Milakovic et al. 2001, Milakovic and Jefferies 2003). Further, grubbing by light geese increased evaporation rates of ephemeral ponds, constricting their temporal availability, with consequences to diversity and timing of emergence of mosquito species (Park 2017). However, in arctic regions where substantial vegetative cover remains, severe alteration of arthropod communities due to nesting and foraging light geese has not yet been investigated and may be unlikely. In fact, large aggregations of waterfowl can enrich aquatic environments through faecal nutrient inputs (Mallory et al. 2006, Côté et al. 2010, R. Alisauskas unpubl. data), and have potential to increase abundance of aquatic invertebrate prey available to nesting birds such as sea ducks. However, more research is needed in this area.

5.4.3 Changes to nesting habitat

Like light geese, abundant deer and other large herbivores can modify cover, structure and species composition of vegetation communities, with variable response by avian species to such alteration (Fuller 2001, Ogada et al. 2008, Martin et al. 2011, Rushing et al. 2020). In forested ecosystems, for example, birds that nest or forage near the ground are negatively affected by altered vegetation communities resulting from high deer populations, whereas impacts to other guilds can be neutral or even positive (Fuller 2001, Martin et al. 2011, Rushing et al. 2020). In grassland communities, fire and herbivore grazing can increase avian species diversity (Fuhlendorf et al. 2006), suggesting species-specific responses to such disturbances. Despite moderate to high herbivory by light geese within the Sanctuary, nesting and foraging activities by geese increased spatial heterogeneity of vegetation communities, additive to that produced by topography and related abiotic factors (Chapters 2 and 3, Slattery 2000). In this study, species richness did not vary with respect to the vegetation ordination axis representing elevation (Fig. 5.5), suggesting that avian species richness was similar in hydric, mesic, and xeric habitats. Species richness declined only slightly in response to the vegetation ordination axis representing habitat alteration (Fig. 5.5), suggesting that alteration at the extent documented near Karrak Lake did not severely negatively affect passerine and shorebird species richness (but see below). However, species responded differently to both elevation gradient and extent of vegetation alteration.

5.4.3.1 Elevation

Species that showed greater occupancy in vegetation communities associated with higher elevations included the passerines horned lark, snow bunting, white-crowned sparrow, and shorebirds black-bellied plover, American golden plover, pectoral sandpiper, and red phalarope (Fig. 5.4). Species that showed greater occupancy in vegetation communities associated with lower elevations included the passerine savannah sparrow and shorebirds semipalmated sandpiper, Baird’s sandpiper, and dunlin (Fig. 5.4). A few species, including semipalmated plover, rock ptarmigan, and the ubiquitous Lapland longspur, showed no response to vegetation communities varying by elevation. Occupancy of vegetation communities governed by factors associated with elevation were as expected according to documented species-specific nesting habitat preferences (Birds of the World 2020), except for some species with few detections and thus low power for inference (white-crowned sparrow (*n*=1 detection), red phalarope (*n*=3), Baird's sandpiper (*n*=1), and sempalmated plover (*n*=1)). I expected the first two species to show greatest occupancy in lowland habitats and the last two species to show greatest occupancy in upland habitats. Occupancy estimates and response to measured covariates were based on visual observations of adult birds and not of nest locations, so species were undoubtedly occasionally observed in non-typical nesting habitat, such as during foraging bouts in which birds may occupy a wider habitat range. However, for these infrequently detected species, observations in non-typical habitat likely produced unexpected and spurious results.

5.4.3.2 Habitat alteration

Probability of occupancy by five species declined with increased habitat alteration by light geese, five species increased, and four species showed no response (Fig. 5.4). Similar to elevation, slope estimates overlapped zero for all species, but horned lark (+), snow bunting (+), and dunlin (-) showed the strongest responses, with 95% confidence intervals barely including zero.

Although many cover-nesting species actively select sites with more vegetation for nest sites (Smith et al. 2007, Walpole et al. 2008, Swift et al. 2017, Flemming et al. 2019b), not all modeled cover-nesting species responded negatively to habitat alteration in this study. Only dunlin demonstrated a negative response to habitat alteration, likely due to removal of graminoid vegetation in their preferred hydric sedge meadow habitats (Warnock and Gill 2020). All four passerine cover-nesting species showed neutral (Lapland longspur) or positive (snow bunting, savannah sparrow, white-crowned sparrow) responses to habitat alteration, likely a result of increased abundance of birch in altered habitats. Lapland longspurs are highly abundant throughout arctic regions (Latour et al. 2010, Smith et al. 2020), and demonstrated very high occupancy (and detection) rates at Karrak Lake. In addition to occurring in a wide range of vegetation communities, Lapland longspurs were least negatively affected by density of nesting geese, demonstrating remarkable habitat flexibility and tolerance to apparent disturbance.

Availability of nest sites in rock crevices, preferred by snow buntings, are not limited by vegetation alteration by geese. However, snow buntings are reportedly plastic in nest site selection where rock crevices are limited (Montgomerie and Lyon 2020), and may therefore frequently take advantage of dense shrubby vegetation (D. Kellett pers. obs.) in altered habitats. Savannah sparrows have declined in coastal subarctic regions where light geese have largely eliminated shrub communities in some areas (Rockwell et al. 2003, Peterson et al. 2014), their preferred habitat in the northern edge of their range (Wheelwright and Rising 2020). However, increasingly abundant birch-dominated habitat, at least partly in response to long and intense history of goose nesting (Chapter 3), may explain positive response of savannah sparrows to altered communities at Karrak Lake. The largely neutral response to habitat alteration demonstrated by the cover-nesting shorebirds pectoral sandpiper and semipalmated sandpiper may be explained by their relative flexibility in nest site selection, choosing both graminoid and shrub vegetation (Farmer et al. 2020, Hicklin and Gratto-Trevor 2020). The neutral response of red phalarope to habitat alteration was unexpected and may be explained by low number of detections (*n*=3), as this species, like dunlin, is likely to respond negatively to removal of graminoid vegetation by geese in hydric habitats (Tracy et al. 2020).

Although only one cover-nesting species demonstrated a negative response to habitat alteration, infrequent detections of some cover-nesting species (i.e., low apparent abundance; dunlin (*n*=3), pectoral sandpiper (*n*=3), red phalarope (*n*=3), and white-crowned sparrow (*n*=1)) might suggest that such species were uncommon because they avoided the light goose nesting colony at Karrak Lake. Importantly, several cover-nesting species (white-rumped sandpiper, red-necked phalarope, and hoary and common redpolls) were rarely observed at Karrak Lake and were not observed during surveys, also suggesting their avoidance of the light goose colony. Likewise, Flemming et al. (2019b) reported that all shorebirds, but particularly cover-nesting species, were largely absent from areas with high density of nesting light geese. Species with requirements for graminoid-dominated nesting habitat may avoid unsuitable areas such as light goose nesting colonies, whereas generalist species may choose suboptimal nest sites with less graminoid cover (Flemming et al. 2019b) and suffer increased risk of predation (Smith et al. 2007, Walpole et al. 2008). On the other hand, high proportion of birch in altered habitats at Karrak Lake may appeal to habitat generalists such as many passerines and some shorebirds (this study), with little or no consequence of nest failure resulting from predation. Birch-dominated altered habitats at Karrak Lake contrasts starkly with light goose-induced habitat change on coastal marshes of western Hudson Bay, where an alternative stable state of bare sediment induced local population declines of passerines and shorebirds (Rockwell et al. 2003, Sammler et al. 2008, Peterson et al. 2014).

Open-nesting species that select sparse vegetative cover for nest sites (Smith et al. 2007) were expected to be least affected by removal of vegetation by light geese, and both horned lark and semipalmated plover, species that generally select barren habitats for nesting (Beason 2020, Nol and Blanken 2020), responded positively to habitat alteration. Likewise, semipalmated plover was one of only two species that nested in altered habitats dominated by moss carpets and exposed substrate at Southampton Island (Flemming et al. 2019b). Despite flexibility of rock ptarmigan in nest site selection and occurrence in a wide variety of habitats (Montgomerie and Holder 2020), this species responded negatively to habitat alteration at Karrak Lake. Black-bellied plover, American golden plover, and Baird's sandpiper, shorebirds that also select sparse vegetation cover for nesting, similarly showed negative response to habitat alteration at Karrak Lake, which may be explained by low number of detections, particularly for black-bellied plover (n=1) and Baird's sandpiper (n=1). Alternatively, in the case of rock ptarmigan and American golden plover, species that were detected more frequently, factors such as predation risk or food availability separate from or in conjunction with habitat change may have been responsible for such negative response to habitat alteration (Lamarre et al. 2017, Flemming et al. 2019a, 2019b).

5.5 Summary and Conclusions

At Karrak Lake, avian species richness was affected very little by intensity of habitat alteration by light geese (Fig. 5.5), suggesting that spatial heterogeneity in vegetation removal and species composition changes to plant communities did not have severe negative impacts to avian guilds investigated here. However, whereas some passerine and shorebird species demonstrated positive response to habitat alteration, occupancy by others was lower in altered habitats (Fig. 5.4). Moreover, low frequency of detections during surveys for some species, and notable omission of others in analyses due to their rarity at Karrak Lake, suggest that some species likely avoided the nesting colony or persisted at low abundance.

All modeled species demonstrated negative responses to high densities of nesting light geese (Fig. 5.4), and projected occupancy of nearly all species declined to zero at high goose nesting densities that occurred throughout the colony. Consequently, species richness was negatively correlated with light goose density (Fig. 5.5). However, extremely high light goose nesting densities, and nesting colonies in general, occupy discrete areas with small spatial extents, and thus disturbance of sympatrically-breeding birds is expected to have negligible impacts on a population or landscape scale.

Relative to vegetation change and removal at large nesting colonies, less severe alteration of vegetation communities and ephemeral and transient disturbance by foraging geese in molting and brood-rearing habitats is expected to have smaller impacts on sympatric bird communities. Other authors have speculated that abundant light geese may have wide-ranging negative effects to many avian species. Certainly, habitat alteration and knock-on effects (e.g., changes to arthropod communities) coupled with changes to predator communities have potential for synergistic effects on sympatrically-breeding birds, adding further stress to species suffering habitat loss on migration and wintering areas and climate-related mismatch effects in arctic regions.

5.6 Acknowledgements

I adapted code from Zipkin et al. (2010), available online at doi:10.1016/j.biocon.2009.11.016. Scott Wilson kindly supplied analytical advice.

CHAPTER 6: SYNTHESIS

6.1 A summary

Anthropogenic food wastes and surpluses available from crop residuals, garbage dumps, fishing discards, and other sources are consumed by a diversity of Earth's organisms, ranging from decomposers to herbivores to tertiary consumers. Consumption of such anthropogenic foods often facilitates increased survival and recruitment of behaviorally plastic species able to exploit such spatiotemporally predictable resources, and results in their elevated population abundance (Oro et al. 2013). Crop residuals have increased carrying capacity for many Holarctic goose populations in agricultural landscapes, and in North America, snow and Ross's geese have broadened their distributional ranges and responded numerically to agricultural production (Abraham and Jefferies 1997, Abraham et al. 2005a, Abraham et al. 2012, Fox and Madsen 2017, Lefebvre et al. 2017, Fox and Leafloor 2018).

Migratory animals link geographically distant ecosystems, and even moderately abundant migrant animals can have profound impacts on ecosystems through trophic effects and transport of nutrients, energy, propagules, toxins, parasites and pathogens (Bauer and Hoyle 2014). Midcontinent light geese connect temperate and arctic ecosystems through seasonal migration, and their high abundance has created trophic cascades in northern ecosystems in which these species reproduce. Changes to soil properties, vegetation communities, and vertebrate and invertebrate biodiversity in subarctic regions are well-documented (Kerbes et al. 1990, Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996, Abraham and Jefferies 1997, Kotanen and Jefferies 1997, Chang et al. 2001, Handa et al. 2002, Jefferies and Rockwell 2002, Rockwell et al. 2003, Walker et al. 2003, McLaren and Jefferies 2004, Abraham et al. 2005a, b; O et al. 2005, Jefferies et al. 2006, Sammler et al. 2008, Abraham et al. 2012, Peterson et al. 2013, 2014). In arctic ecosystems, where most midcontinent light geese breed (Kerbes et al. 2014), emerging evidence suggests similar but less severe impacts than those to subarctic ecosystems (Alisauskas et al. 2006, Fontaine and Mallory 2011, Flemming et al. 2016, Conkin and Alisauskas 2017, Flemming et al. 2019a, 2019b, 2019c; this study).

In an important arctic breeding area for midcontinent light geese, this research documented changes to plant community structure (Chapters 2 and 3) and responses to those changes by resident rodents (Chapter 4) and sympatrically-breeding birds (Chapter 5). In a landscape mosaic created by variation in topography, moisture, and soil properties, foraging and nesting by light geese increased spatial heterogeneity of vegetation communities. Specifically, in the brood-rearing and molting region north of Karrak Lake, their sustained foraging over multiple decades created a landscape composed of lightly and intensely foraged grazing lawns, but with little change to species composition of plant communities. Instead of widespread devegetation, as observed in coastal subarctic habitats and establishment of an alternative stable state of bare sediment, aboveground biomass in some areas in the Sanctuary was significantly depleted, but bare sediment was less common than in disturbed subarctic habitats, depending on the scale of observation (Conkin and Alisauskas 2017). Moreover, belowground plant stores in these graminoid-dominated lowland plant communities were largely intact and had strong potential for regeneration.

Within the nesting colony at Karrak Lake, I documented evidence of severe reduction of biomass of both graminoid vegetation (preferred forage of light geese) and fruticose and foliose lichens (not consumed by light geese but often incorporated into nests) in regions with high nest densities and long-term occupancy by light geese. In coastal subarctic regions, removal of vegetation resulted in exposure of mineral soils, desiccation, hypersalinity, and limited establishment of halophytic species. In terrestrial freshwater communities near Karrak Lake, colonizing plant species established on bare sediment or peat exposed by vegetation removal by nesting and foraging geese, resulting in shifts in species composition of plant communities to altered communities composed of colonizing species. High densities of nesting light geese resulted in transition of lowland communities dominated by graminoids, *Sphagnum* spp., and willows to those comprised of exposed peat, birch, non-*Sphagnum* mosses, marsh ragwort, and mare’s tail. In naturally less vegetated upland regions where community change from nesting by geese was less apparent, fruticose lichens, crowberry and white heather dominated undisturbed plant communities whereas crustose lichens and bearberry were more dominant in disturbed communities. Thus, although light geese altered upland and lowland habitats at Karrak Lake, this landscape remained largely vegetated, contrasting sharply with altered subarctic coastal habitats consisting of bare sediment.

Reduction of biomass and plant community shifts from graminoid-dominated to those with high proportions of exposed peat and birch near Karrak Lake had negative effects on abundance of brown lemmings and occupancy by graminoid-specialist shorebirds. Although intact graminoid communities are important to many resident and migratory arctic vertebrates, some open-nesting and generalist cover-nesting avian species showed neutral or positive responses to habitat alteration by light geese, likely due to high proportions of birch in altered habitats. Independent from variable effects of habitat alteration, all avian species demonstrated lower occupancy at high densities of nesting geese. Light geese nest in localized, dense aggregations in the Sanctuary, and thus negative impacts on sympatric species are expected to be somewhat limited spatially (but see Flemming et al. 2019c), and confined to large nesting colonies and severely altered brood-rearing and molting regions.

6.2 Suggestions for future research

This research illuminated patterns of vegetation change, and patterns of response of selected vertebrate species to those changes, produced by foraging and nesting of hyperabundant lesser snow and Ross's geese in one terrestrial arctic ecosystem. However, I only speculated in Discussion sections of data chapters on potential mechanisms responsible for these observed patterns. I describe them briefly here, as suggestions for future research about the mechanistic role of these migratory avian herbivores as important species in arctic ecosystems.

Changes to soil chemistry have been described for altered subarctic coastal ecosystems (references given above), but in arctic ecosystems, future research might include investigations of soil chemistry, microbial communities and nutrient cycling. Differential responses by plant species to intense grazing and high fecal nutrient inputs may determine mechanisms for community change, which may be in part responsible for the widespread establishment of birch in areas heavily used by geese, alongside other potential processes such as positive response to climate warming. The hypothesis that birch-dominated communities represent an alternative stable state produced by cumulative and intense nesting and foraging by geese (and perhaps exacerbated by climate warming) remains untested. This hypothesis is worthy of examination, along with investigations of its potential resilience and conditions (such as severe winters with high winds and little protective snow cover) required for reversion to former graminoid-dominated communities. As well, loss of graminoid-dominated communities likely negatively affect graminoid specialist species such as lemmings and cover-nesting shorebirds by a variety of mechanisms. These include reduced food availability provided by graminoid vegetation and arthropod prey, and thermoregulatory benefits and protection from predators of nests, young, and adult individuals. Functional and numerical responses of predators to allochthonous inputs represented by light geese have been investigated by several authors (Samelius and Alisauskas 2007, 2011; Lamarre et al. 2017, Flemming et al. 2019a, 2019c; Bédard et al. *in review*), and future research might continue to investigate species-or guild-specific response of prey to changes in predator dynamics and communities (see Flemming et al. 2019a). For example, shorebirds that rely on intact graminoid vegetation to evade detection of nests by predators may suffer increased predation in devegetated habitats (Smith et al. 2007) or avoid light goose nesting colonies (Flemming et al. 2019a, 2019c; this study). In contrast, sea ducks and other goose species that select nest sites in birch and on islands may accrue thermoregulatory benefits and reduced detection and accessibility by predators, and may further benefit from predator satiation provided by light geese (Kellett et al. 2003, Kellett and Alisauskas 2011, Baldwin et al. 2011).

Large annual influxes of migratory light geese transport absolutely more nutrients, energy, propagules, toxins, parasites and pathogens (Bauer and Hoyle 2014, Hessen et al. 2016) to northern ecosystems than do less abundant populations of geese. Yet, unlike seabirds that nest in highly concentrated aggregations and continually transport nutrients from donor marine ecosystems to recipient terrestrial ecosystems throughout the breeding season (Michelutti et al. 2009), geese deposit comparatively fewer fecal nutrients originating from outside ecosystems on breeding areas, and dilute these nutrients by distribution across broader spatial regions. As well, low mortality of adult light geese (Calvert et al. 2017, Alisauskas et al. *in review*) ensures few nutrients in the form of carcasses remain on arctic breeding and feeding grounds. Nutrient transport between southern and northern terrestrial ecosystems by light geese is likely inconsequential compared to nutrient transfer between northern terrestrial and aquatic ecosystems (see below). As herbivorous light geese occupy low trophic levels, they accumulate few toxins with negligible transport between ecosystems (K. Gurney unpubl. data), but complexities of parasite and pathogen transmission between light geese and arctic resident and migratory fauna is an active area of research (e.g., Elmore et al. 2014). Light geese may aid in dispersal of plant species from southern landscapes through transport of propagules in feces, which may have increased success at establishment in northern ecosystems with recent climate warming.

Finally, several studies have documented nutrient enrichment of aquatic ecosystems in arctic regions by large aggregations of birds (Mallory et al. 2006, Hessen et al. 2016), including light geese (Côté et al. 2010, Mariash et al. 2018). Such ornithogenic enrichment of aquatic ecosystems has potential to change their trophic status and initiate trophic cascades. Feedbacks associated with such cascades may affect abundance and diversity of aquatic microflora and fauna, as well as invertebrates, with direct and indirect knock-on effects to other trophic levels both within aquatic (e.g., fishes) and terrestrial (e.g., birds) ecosystems.

6.3 Current population status of midcontinent light geese

The midcontinent light goose population, designated as overabundant beginning in 1999 (for snow geese, with Ross's geese designated in 2014 (CWS 2013, 2014)), has been subjected to greatly liberalized harvest regulations for over 20 years in an attempt to reduce abundance (Batt 1997, Alisauskas et al. 2011). However, survival remained high during the period of harvest liberalization (Calvert et al. 2017) and despite failure at population reduction through harvest-mediated modulation of adult survival (Alisauskas et al. 2011), midcontinent light geese have declined precipitously in the last decade due to declining recruitment (Calvert et al. 2017, Alisauskas et al. 2018, Weegman et al. *in review*). Effects of density dependence, climate-related mismatch between timing of hatch and peak forage availability, and extreme weather events have resulted in negligible production at Karrak Lake in recent years (Ross et al. 2017, 2018; R. Alisauskas unpubl. data). As well, dispersal between subpopulations within the midcontinent metapopulation has resulted in net movement of geese from the Sanctuary (Alisauskas et al. *in review*, Weegman et al. *in review*), likely motivated at least in part by nesting failure and eastward shifts in winter distribution, and perhaps declining carrying capacity (Wilson et al. 2016, Alisauskas et al. *in review*). In fact, low per capita *in situ* recruitment coupled with high probability of emigration ensures the Queen Maud Gulf subpopulation of snow geese cannot sustain itself (Alisauskas et al. *in review*). Lower abundance of light geese will release grazing and nesting pressure on vegetation communities, perhaps allowing revegetation of and reversion to formerly graminoid-dominated communities, contingent on the extent and resilience of encroaching shrub communities dominated by birch.

6.4 Anthropogenic trophic cascades

Humans have modulated distribution and abundance of many of Earth's organisms for millennia (Boivin et al. 2016). Whereas Holarctic geese, and light geese in particular, have been described as keystone herbivores (Kerbes et al 1990, Fox and Leafloor 2018) and responsible for trophic cascades detrimental to northern ecosystems, humans as a 'hyperkeystone' species have overarching effects that drive complex interaction chains through influence of other keystone species across different habitats (Worm and Paine 2016). Both humans and light geese have escaped natural carrying capacities through increased food production fueled by inorganic fertilizers and fossil fuels, and trophic cascades initiated by light geese in northern ecosystems ultimately originated with *Homo sapiens*.

Anthropogenic-subsidized species are sensitive to changes in anthropogenic food resources (Oro et al. 2013), and present-day agricultural landscapes and the energy and nutrient subsidies they provide to geese may change in the future (Fox and Abraham 2017). This, coupled with human-mediated effects of climate change on arctic ecosystems, may ultimately govern abundance and distribution of snow and Ross's geese in North America.

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APPENDIX A: SUPPORTING INFORMATION FOR ACKNOWLEDGEMENTS

Table A.1. Research personnel at Karrak Lake Research Station, Nunavut, 1991-2019.

Amy Adair
Ian Adams
Al Afton
Jorgan Aitoak
Ron Akhok
Guillermo Alba
Pat Algona
Andrea Alisauskas
Ray Alisauskas
Kale Anderson
Ryan Askren
Dale Assmus
Melanie Bakker
Bart Ballard
Jason Bantle
Christoffer Bergmann
Amie Black
Anne Blondin
Ray Bon
Émilie Bouchard
Éveline Boudreau
Tim Brace
Keith Brady
Colin Brayton
Todd Buckley
Kayla Buhler
Lothian Buss
Gary Calleja
David Carr
Maliya Cassels
Jason Charlwood
Vanessa Charlwood
Bob Clark
David Clark
Jan Clark
John Conkin
Malcolm Conly
Lea Craig-Moore
Melissa Cunningham
Jeff Danielson
Jonathan D'Autrechy
Robert de Carle
Cécile de Sérigny
Simon Demaio
John Denton
Jean-Luc DesGranges
Deanna Dixon
Joshua Dooley
Kiel Drake
Kevin Dufour
Stacey Elmore
Kimberly Epp
Kirsten Ermel
Jessica Evans
Bellarose Eyegetok
David Farmer
Greg Fenech
Rory Fenech
Nina Finley
Scott Freeman
Marie-Christine Frenette
David Fronczak
Julie Gailius
Michel Gendron
Garry Gentle
Karen Gesy
Murray Gillespie
Mark Gloutney
Andrew Greenawalt
Ruth Greuel
Brendan Griebel
Mark Grovijahn
Bill Gummer
Kirsty Gurney
Jenn Guy
Nadine Haalboom
Doug Halliwell
Christy Hansen
Vanessa Harriman
Myles Hartman
Deborah Hawkshaw
Kevin Hawkshaw
Jeremiah Heise
Chris Hendrickson
Kent Hensley
Justin Heseltine
Deke Hobbick
Keith Hobson
Danica Hogan
Adrian Hopkins
Naomi Huig
Oksana Izio
Emily Jenkins
David Johns
Leon Johnson
Toren Johnson
Dennis Kaleta
Dana Kellett
Elaine Kennedy
Richard Kerbes
Blake Klema
Joanna Klima

Stephanie Koch
Elsie Krebs
Kammie Kruse
Wolf Kurz
Tony Lau
Shona Lawson
Steve Leach
Jim Leafloor
Nicolas Lecomte
Craig LeSchack
Kelly Likos
Mark Lindberg
Crissy Linstead
Mike Lippsmeyer
Steele Logan
Brian Long
Ryan Lorenz
Katelyn Luff
Ella Lunny
Alain Lusignan
Brandon Lyall
Samantha Lynch
Edith MacHattie
Glenn Mack
Cliff Mallard
Brian Malloure
Lisa May
Kevin McCracken
Jerry McKeating
Katherine Mehl
Stéphane Menu
Chantel Michelson
Nathaniel Mimialik
Bill Moore
Ferguson Moore
Corrine Morhan
Tim Moser
Edward Moss
Claire Mussells
Lisa Myndio
Teija Nakashook
Troesch Nate
Mialisa Nuna
Rich Olsen
Anders Östergren
Robin Owsiacki
Christopher Palmer
Sara Pearce Meijerink
Shyla Perreault
Delia Person
Chad Peterson
Kimberly Phipps
Justin Pitt
Adam Potts
Kailee Price
Eric Reed
Kim Régimbald-Bélanger
Matt Roberts
Melanie Rose
Megan Ross
Sasha Ross
John Ryder
Gustaf Samelius
Nicholas Sanchez
Keaton Schmidt
Mike Schwitters
Peter Scully
Nathan Shirley
Mungla Sieck
Howie Singer
Stuart Slattery
Matt Smith
Dan Spencer
Kyle Spragens
Colin Starkevich
Doug Stern
Walter Sturgeon
Wade Sumners
Kevin Swiechowicz
Cindy Swoboda
Win Sim Tan
Michael Thomas
Joshua Traylor
Audrey Tremblay
Laurent Von Allmen
Amos Wamikon
Keith Warner
Thea Warren
Mark Wayland
Mitch Weegman
Kristin Weers
Joshua White
Nathan Wiebe
Jonathan Willans
Scott Wilson
Credence Wood
Carma Woof
Noel Worden
Ron Zega

APPENDIX B: SUPPORTING INFORMATION FOR CHAPTER 3

B.1 NMDS 1998

I sampled 185 plots within or near the goose colony at Karrak Lake in 1998, and used 12 species or species groups in NMDS ordinations. I used three axes for the final configuration because convergence was achieved easily (20-48 iterations in four attempts), reproducible (plots looked similar) and stress was minimal (0.123) and only slightly greater than an ordination using four axes (0.094). In comparison, an ordination using only two axes did not achieve convergence after 1000 iterations, and estimated stress was 0.169. Elevation was more strongly correlated with the first axis (0.981) than with the second axis (0.195, r^2=0.114, p<0.001, Fig. B.1). Number of years in colony was strongly correlated with the second axis (-0.999) and not with the first axis (-0.035, r^2=0.337, p<0.001, Fig. B.1). Likewise, mean number of nests was strongly correlated with the second axis (-0.999) and not with the first (0.036, r^2=0.366, p<0.001, Fig. B.1).

B.2 NMDS 2010

I sampled 302 plots within or near the goose colony at Karrak Lake in 2010, and used 15 species or species groups in NMDS ordinations. I used three axes for the final configuration because convergence was achieved easily (25-92 iterations over four attempts), reproducible (plots looked similar) and stress was minimal (0.126) and only slightly greater than an ordination using four axes (0.097). In comparison, an ordination using only two axes did not achieve convergence (after 1000 iterations) and estimated stress was 0.171. Elevation was strongly correlated with the first axis (-0.996) than with the second axis (0.094, r^2=0.191, p<0.001, Fig. B.2). Number of years in colony was strongly correlated with the second axis (0.970) and less so with the first axis (-0.244, r^2=0.271, p<0.001, Fig. B.2). Likewise, mean number of nests was strongly correlated with the second axis (0.994) and less so with the first (-0.114, r^2=0.323, p<0.001, Fig. B.2).

B.3 NMDS 2014

I sampled 282 plots within or near the goose colony at Karrak Lake in 2014, and used 15 species or species groups in NMDS ordinations. I used four axes for the final configuration because convergence was achieved easily (80-326 iterations, although one attempt did not converge), reproducible (plots looked similar) and stress was minimal (0.109) and only slightly greater than an ordination using five axes (0.089). In comparison, an ordination using only three axes did not achieve convergence (after 1000 iterations) and estimated stress was 0.1350. Elevation was strongly correlated with the first axis (-0.999) and not with the second axis (0.007, r^2=0.148, p<0.001, Fig B.3). Number of years in colony was strongly correlated with the second axis (0.999) and not with the first axis (0.006, r^2=0.236, p<0.001, Fig. B.3). Likewise, mean number of nests was strongly correlated with the second axis (0.994) and less so with the first (0.102, r^2=0.327, p<0.001, Fig. B.3).

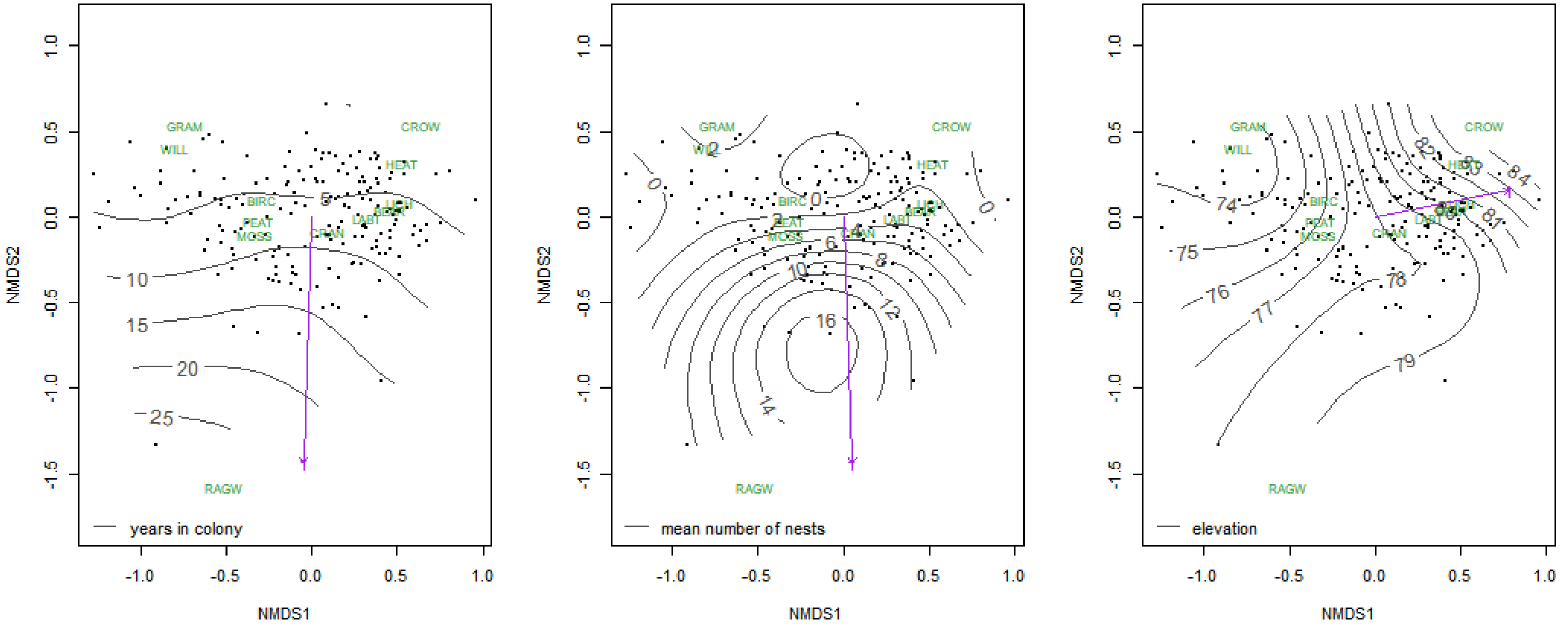

Figure B.1. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 12 vegetation taxa on 185 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 1998. The three axes (third axis not shown) captured 28.2% of variation in the ranked matrix, with axes 1-3 capturing 17.3, 6.6, and 4.3% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel (left: years in colony, middle: mean number of nests, right: elevation), with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for each covariate. Species and species groups: LICH, lichen species; PEAT, dead moss species; MOSS, live moss species; GRAM, graminoids (grass and sedge spp.); BIRC, birch (*Betula glandulosa*); WILL, willows (*Salix* spp.); CRAN, cranberry (*Vaccinium vitis-idaea*); CROW, crowberry (*Empetrum nigrum*); BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea (*Ledum palustre*); HEAT, white heather (*Cassiope tetragona*); RAGW, marsh ragwort (*Tephroseris palustris*).

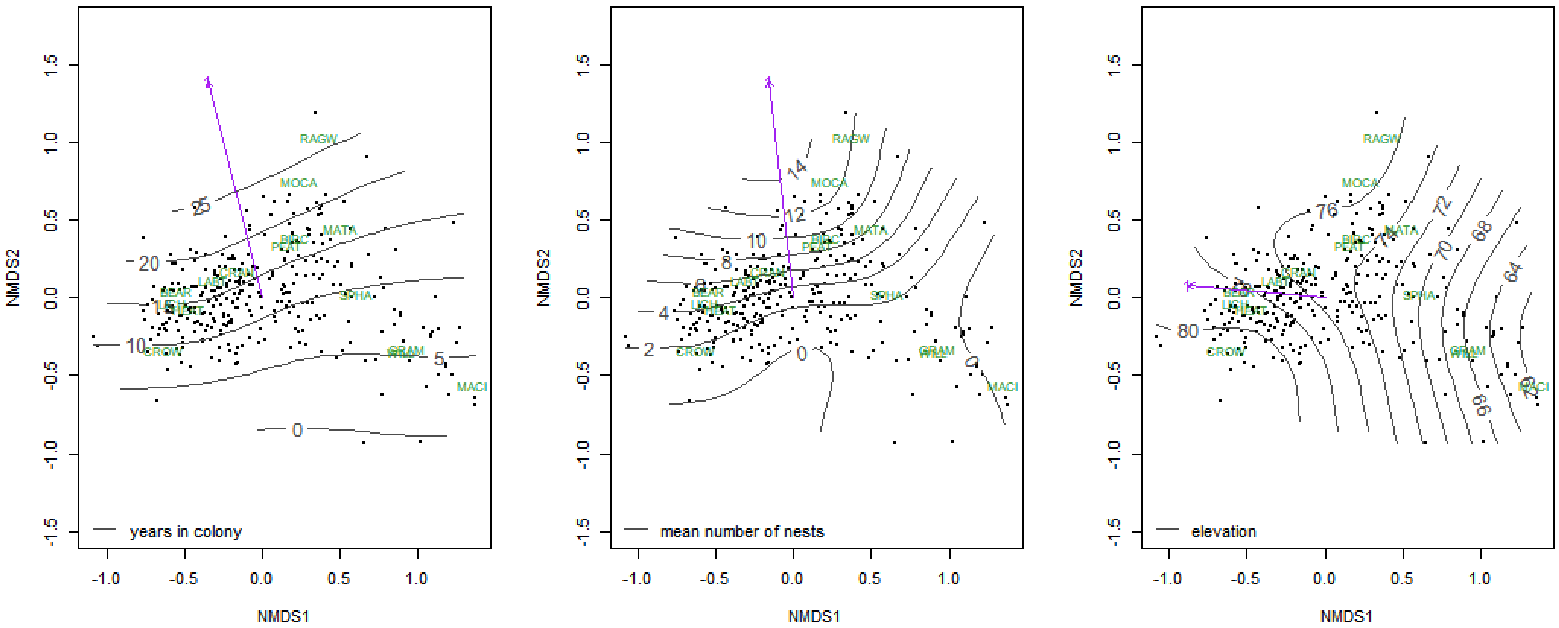

Figure B.2. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 15 vegetation taxa on 302 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2010. The three axes (third axis not shown) captured 22.7% of variation in the ranked matrix, with axes 1-3 capturing 12.6, 6.3, and 3.8% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel (left: years in colony, middle: mean number of nests, right: elevation), with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for each covariate. Species and species groups: LICH, lichen species; PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOCA, moss species other than *Sphagnum* spp.; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; CROW, crowberry *(Empetrum nigrum)*; BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*).

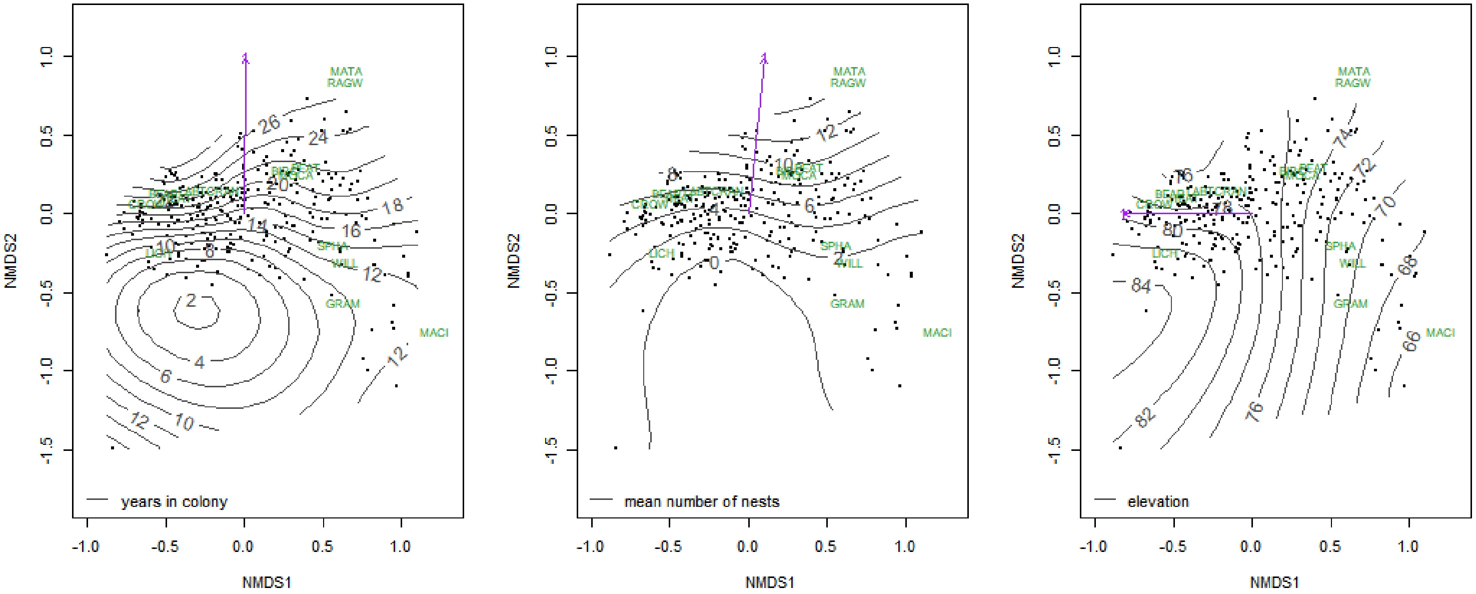

Figure B.3. Three-dimensional nonmetric multidimensional scaling (NMDS) ordination of 15 vegetation taxa on 282 sample plots inside and near the snow and Ross's goose colony at Karrak Lake, Nunavut, in 2014. The four axes (third and fourth axes not shown) captured 26.1% of variation in the ranked matrix, with axes 1-4 capturing 12.2, 6.1, 4.4, and 3.4% of variation, respectively. Black dots and green text specify locations of individual sample plots and taxa (species and species groups), respectively, on the ordination with respect to axes 1 and 2. Vector overlays (purple arrows) of environmental and biological covariates are depicted separately in each panel (left: years in colony, middle: mean number of nests, right: elevation), with strength and direction of correlation given by the length of the vector-line and vector-arrow, respectively. Grey contour lines are shown for each covariate. Species and species groups: LICH, lichen species; PEAT, dead moss species; SPHA, *Sphagnum* spp.; MOCA, moss species other than *Sphagnum* spp.; GRAM, graminoids (grass and sedge spp.); BIRC, birch *(Betula glandulosa);* WILL, willows *(Salix* spp.); CRAN, cranberry *(Vaccinium vitis-idaea)*; CROW, crowberry *(Empetrum nigrum)*; BEAR, bearberry (*Arctous* spp.); LABT, Labrador tea *(Ledum palustre);* HEAT, white heather *(Cassiope tetragona)*; RAGW, marsh ragwort *(Tephroseris palustris);* MACI, marsh cinquefoil (*Comarum palustre*); MATA, mare's tail (*Hippuris vulgaris*).