LANDSCAPE FACTORS INFLUENCING MOOSE (ALCES AMERICANUS) DENSITY AND BROWSING IN NEWFOUNDLAND, CANADA

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Landscape factors influencing moose (*Alces americanus*) density and browsing in Newfoundland, Canada.

by

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Abstract

I investigated landscape scale processes and factors that influence moose (*Alces americanus* syn. *Alces alces*) browsing and density in Newfoundland, Canada. I tested whether moose density and management designation were related to browsing patterns on the landscape, and if browsing has the potential to change forest regeneration. I quantified landscape composition and configuration in areas of different moose density (low vs. high).

Moose browsing was quantified using vegetation indices in areas of different moose density (low vs. high) and management designation (crown land vs. National parks). Landscape scale processes and factors (management designation, moose density, forage species, and sapling height) were incorporated into linear regression models to explain browsing patterns, and compared using the information theoretic approach. At a broader scale, landscape scale processes and factors (hunter access, success, forest cuts, and natural disturbances) as well as landscape composition and configuration were mapped and categorized using a GIS. Landscape processes and factors were included into regression models to explain moose density and compared using the information theoretic approach. Results indicate that forest regeneration was altered through selective browsing but did not differ according to moose density or management designation. Further, moose density did differ with landscape composition and configuration. There was high variance observed in moose browsing in relation to forest regeneration not explained by either moose density or management designation. Because of a sustained high moose density across Newfoundland, the current vegetation may be reflecting the legacy of previously high impact periods of moose browsing. My research supports previous findings that moose browsing and density are regulated by a complex interaction of landscape scale processes and factors. An understanding of the role of these landscape scale processes and factors can help guide the

management of non-native overabundant moose populations in a nearly predation free ecosystem.

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Chapter 1. General introduction

1.1 Overabundant non-native large herbivores on the landscape

One of the outcomes of changing landscape patterns and processes has been an increase in overabundant populations of large herbivores through one or more of the following mechanisms: 1) introduction of non-native herbivores, 2) extirpation of large carnivores, and 3) anthropogenic development and activities (McShea et al. 1997). Three research themes are prevalent in the literature on overabundant large herbivores: 1) their capacity to alter forest dynamics, which if sustained, has the potential to alter the trajectory of forest succession (Nugent et al. 2001, Martin et al. 2010, Ruzicka et al. 2010); their capacity to alter ecosystem processes (Pastor et al. 1988, McInnes et al. 1992, Pastor and Danell 2003, Butler and Kielland 2008, Côté et al. 2004, Stewart et al. 2009, Martin et al. 2010, Randall and Walters 2011); and 3) management of large herbivore populations (Brown et al. 2000, Giles and Findley 2004, Fryxell et al. 2010). Gaps remain in our knowledge of landscape scale processes and factors that affect density of overabundant large herbivores populations, which in turn modify forest dynamics via herbivore browsing (Olff and Ritchie 1998, Denyer et al. 2010). Landscape scale processes and factors include natural and anthropogenic mechanisms that alter ecosystem functions of the landscape (Turner 1989). Caughley (1981) described four classes of overabundance as those that: (1) threaten human life or livelihood; (2) depress other species that may be economically or aesthetically important; (3) are too numerous for their "own good"; or (4) one where the population is out of equilibrium. In this study, overabundant population is defined in the sense of Gosse et al. (2011) as one that been observed to alter forest regeneration through browsing rather than a numerical value of a population. This definition of an overabundant population touches on three (2, 3, and 4) of the four classes of overabundance defined by Caughley (1981).

My research focuses on indices of ecological processes and management decisions, which I refer to as landscape scale processes and factors, that influence browsing (Chapter 2) and density (Chapter 3) of moose (*Alces americanus* syn. *Alces alces americana*) in Newfoundland and Labrador, Canada. I focused on the insular portion of the province, Newfoundland, has it harbours a non-native overabundant moose population in a nearly predator free ecosystem. I also quantified the response of vegetation to the browsing (Chapter 2). My study is unique because I conducted my analysis at a larger spatial extent than previous studies carried out in Newfoundland. I included areas across Newfoundland with different management designation and moose densities. The first strength of my research is that my research quantifies the impact of the overabundant moose population. However, it also explores predictors of the processes and factors that have resulted in the observed impacts. The second strength is that moose density was not classified as low or high based on the management designation of the study areas; rather, moose density was represented by actual survey numbers within each area. The moose management area (MMA) and national park on the west coast of Newfoundland harbours a higher moose density than the eastern MMA and national park, thus enabling me to treat the effects of moose density and management regime (hunting/forestry vs. protection) as independent variables in my analyses.

1.2 Invasive Species: Background and Theoretical Context

The introduction of non-native species influences interactions between flora and fauna and can lead to states of disequilibria within ecosystems (Wilcove et al. 1998); classic examples include cane toads (*Rhinella marina*) in Australia (Tingley and Shine 2011) and Asian carp (*Hypophthalmichtys nobilis* & *H. molitrix*) in North America (Patel et al. 2010). Island ecosystems are especially influenced by introduced plants (Richardson and Rejmánek 2011) and mammals (Courchamp et al. 2003) resulting in reduced biodiversity, altering forest structure and regeneration. Invasive mammals are often successful competitors for island resources, capitalizing on native species' lack of exposure to competition and predation (Courchamp et al. 2003).

The impacts that non-native large herbivores have on island ecosystems will vary depending on processes regulating population density (Messier 1994) which in turn influence browsing and forest dynamics (Olff and Ritchie 1998, Denyer et al. 2010). The processes regulating population density can be top-down or bottom-up, and I will discuss each of these in turn.

Top-down regulation of large herbivore populations results from factors including top carnivores (McLaren and Petersen 1994, Berger 1999), hunting (Ferguson and Messier 1996), and/or wintering conditions (Telfer and Kelsall 1984). One way that wildlife managers attempt to manage large herbivore populations is by taking advantage of top-down processes through managed hunts (Ferguson and Messier 1996), however, hunter access influences hunter success and their effectiveness in regulating moose densities (Ferguson et al. 1989, Rempel et al. 1997, Courtois and Beaumont 1999, McLaren and Mercer 2005).

Bottom-up processes may also play an important role in herbivore population regulation (McLaren and Petersen 1994, Messier 1994). Bottom-up factors include food availability (Telfer 1978), natural disturbances (Crête 1989), road density (Child 1998), wintering conditions (Telfer and Kelsall 1984), and anthropogenic activities (Kramer et al. 2006). While variations do exist, in general high browse production results in higher moose population density (Telfer 1978). Natural disturbances such as fire, windfall, and insect disturbance have been shown to result in increased moose density by providing preferred early successional habitats (Crête 1989). Large herbivores have also been seen to adjust their behaviour to the presence of roads, and may avoid using roads due to noise pollution, use by predators, and direct mortality (Forman and Alexander 1998). Alternatively, some large herbivores prefer habitats adjacent to roads as they provide early successional habitats (Child 1998), salt licks (Laurian et al. 2008), and corridors that funnel winds and provide relief from insects (Kelsall and Simpson 1987). Wintering conditions such as snow depth (Telfer and Kelsall 1984) and snow hardness (Pruitt 2005) can lead to large herbivore mortality (Ballard et al. 1991) through increased energetic demands to accommodate mobility and metabolism demands (Schwab and Pitt 1991), reduced availability of importance forage (Stephenson et al. 2006) and increased reliance on lower quality coniferous species (Augustine and McNaughton 1998, Spalinger et al. 2010). Further, certain types of anthropogenic development and activities can create or supplement preferred habitats for large herbivores (Kramer et al. 2006), by creating edge habitats preferred by most *Cervidae*, especially white-tailed deer (*Odocoileus virginianus*; Crête 1989). Forestry activities in particular produce preferred early successional habitats which are associated with increased densities of large herbivores (Crête 1989, Sinclair 1997, Fuller and Gill 2001, Kramer et al. 2006).

In addition to the relative importance of top-down vs. bottom-up processes, the degree to which browsing by large herbivores influences forest dynamics is largely dependent on population density (Brandner et al. 1990), consumption rates (Renecker and Hudson 1986), forage availability (Messier 1994, van Beest et al. 2010), habitat selection (Senft et al. 1987), and feeding behaviour (Augustine and McNaughton 1998, Spalinger et al. 2010). Sustained browsing from overabundant large herbivores can reduce the abundance of preferred species, leading to a change in forest composition (Risenhoover and Maass 1987, McInnes et al. 1992, Brandner et al. 1990, Thompson and Curran 1993, Connor 2000).

The influence of sustained browsing on forests dynamics is dependent on habitat selection and forage preferences of large herbivores. Large herbivores select habitats within landscapes in a hierarchical manner and have been shown to be less selective at the landscape level, more selective at the patch level, and highly selective at the plant level (Senft et al. 1987, Wallace et al. 1995, Schiwart et al. 2003 Bee at el. 2009, DeJager et al. 2009). At the plant level, moose appear to exhibit a preference for deciduous over coniferous species (Peterson 1955, Chamberlin 1972, Dodds 1960, Krefting 1974, Wiens 1976, Hundertmarkt et al. 1990) dependent on the relative availability of species on the landscape (Telfer 1978, Osko et al. 2004, van Beest et al. 2010). Selecting deciduous rather than coniferous species may be attributed to the presence of secondary metabolites in the latter, which can inhibit digestive properties of the bacteria within the rumen (Bryant et al. 1991). Large herbivores browse new growth which has more nutrients and less lignin, allowing for easier digestion (Augustine and McNaughton 1998, Martin et al. 2010, Mathisen et al 2010, Spalinger et al. 2010).

Habitat selection, and consequently forage selection, of large herbivores is dependent on the spatial arrangements of suitable habitats across landscapes (i.e. the landscape pattern) (Riitters et al. 1997). The landscape pattern is measured by the configuration, connectivity, and scale of individual habitat patches (Owen-Smith 2004). Landscape pattern can be analyzed quantitatively to explain variations in space and time (Gustafson 1998). Landscape composition and configuration are the basis of landscape pattern and can be quantified using landscape indices (McGarigal and Marks 1994, Haines-Young and Chopping 1996), which are well known in landscape ecology. Landscape indices are used to compare landscapes in space and/or time, identify significant temporal changes, and relate patterns to function (Turner 1989). Additionally, the patches which make up a landscape can differ in quality which will lead to individuals to be selective (Wiens 1976) where the relative preference for habitat patches is dependent on the relative abundance and/or quality of the preferred plants (Senft et al. 1987).

Habitat selection quantifies areas of use relative to availability or use versus non-use (Mayor at el. 2009) and has traditionally focused on individual habitat patches. The analysis of landscape pattern has been suggested to be useful in improving predictions of species occupancy (Mazerolle and Villard 1999). The probability that large herbivores will occupy a habitat patch depends strongly on the patch itself but also on the spatial arrangement and dynamics of all required habitat types in landscape (Pastor et al. 1988). As well, it is important to remember habitat selection is not static and fluctuates with relative availability of habitats (Osko et al. 2004).

1.2 The introduction of non-native moose to Newfoundland

Moose are not indigenous to Newfoundland, where the only native large herbivore is the caribou (*Rangifer tarandus terraenovae*), but rather were introduced to provide a source of protein when caribou populations were low. The successful establishment of moose is attributed to abundance of habitat with a lack of predators, competitors, and epidemic diseases. In 1878, two moose were introduced from mainland Nova Scotia to the Gander region in Central Newfoundland (Pimlott 1953). A second introduction followed in 1904 where four moose were brought to Newfoundland from New Brunswick and released in the Howley region on the western part of Newfoundland (Pimlott 1953). After the introduction, the moose population steadily began to increase, reaching its first peak in the 1960s (Pimlott 1959, Mercer and Manual 1974; Figure A.1.1) then peaked again in the 1980s at approximately 217 000 individuals (Newfoundland and Labrador Wildlife Division, unpublished data). The population declined in the 1990s to reach approximately 117 000 animals, similar to the 2010 population estimates (Newfoundland and Labrador Wildlife Division, unpublished data). The current densities within moose management areas (MMAs) are 0.25 to 14 moose·km^{-2} with an island wide density of 2 moose·km^{-2} within forested areas and scrub (Newfoundland and Labrador Wildlife Division, unpublished data). In contrast, indigenous North American moose densities are 0.5-1.5 moose·km^{-2} (Karns 1998).

The forested areas to which moose were introduced were composed of approximately 75 % white birch - balsam fir and also contained bogs and barrens, both considered to be prime moose habitat (Pimlott 1953). The Newfoundland wolf (*Canis lupus beothucus*) was extirpated shortly after the introduction (Allen and Barbour 1937), limiting the natural predators of moose calves to black bear (*Ursus americanus hamiltoni*) and possibly lynx (*Lynx canadensis subsolanus*) (Pimlott 1953). In addition to the lack of predators on adults and limited herbivore competition from snowshoe hare (*Lepus americanus*; Dodds 1960), the lack of epidemic diseases, such as those caused by winter tick (*Dermacentor albipictus*; Welche et al. 1991, Delgiudice et al. 1997) and meningeal worm (*Parelaphostrongylus tenius*; Anderson 1972), enabled the moose population to rapidly increase and spread throughout Newfoundland.

With the increase in moose population, changes to Newfoundland's forest composition became apparent. Balsam fir is important forage for moose on Newfoundland especially during late winter (Dodds 1960) and is reduced in abundance within the understory if subjected to continuous moose browsing (Connor 2000, Gosse et al. 2011). Bergerud and Manual (1968) reported evidence of moose winter browsing leading to stunted balsam fir and white birch along with the uprooting of balsam fir seedlings. Humber and Hermanutz (2011) observed low balsam fir seedling densities in areas subjected to moose browsing pressure which had been previously disturbed by spruce budworm in Gros Morne National Park. Within MMAs, forestry activities may be influencing browsing impacts as forest cuts in coastal areas on Newfoundland naturally regenerate as balsam fir and white birch, providing ideal moose winter foraging habitats five years after cutting (Bergerud and Manual 1968). The influence of moose winter browsing on forest composition and structure can be long lasting. For example, in exclosure experiments, where moose are prevented from accessing the vegetation within the plot following initial browsing, the influences from previous browsing were still apparent after five years (McLaren et al. 2009).

High moose densities on Newfoundland have resulted in elevated levels of browsing that have altered forest composition and structure (Connor 2000, McLaren et al. 2004) at large spatial scales in both protected areas and within MMAs (Gosse et al. 2011). Protected areas and MMAs are the two primary management designations which concern moose on Newfoundland. These two management designations can be defined as: (1) those that are in national parks, which are protected; and (2) those that are Crown land in MMAs where hunting and forestry activities are legal. Crown land is managed for a variety of purposes by various agencies; the management allocation of interest is within MMAs which are under the jurisdiction of the provincial Wildlife Division. The Wildlife Division uses managed hunts as its main management tool of the moose population. The forestry activities permitted within the boundary of these areas are managed by the Forestry Division through 17 Forestry Districts, which do not coincide with the MMA boundaries.

Newfoundland's two national parks, Terra Nova (TNNP) and Gros Morne (GMNP), are managed with the goal of maintaining ecological integrity of the ecosystems within park boundaries (Parks Canada 2008). Generally, National parks do not allow for hunting and forest harvesting. There is an exception to the forest harvests within Gros Morne where residents within the park enclaves have domestic cutting privileges. These are limited to individuals who were residents of the area during the time of the establishment of the park in 1973 and privileges are grandfathered to their children, but not to subsequent generations. These enclaves were omitted from my study. Historically, there has been no hunting within the national parks; however, a hunt was opened for the fall of 2011 (outside of my study period) in both parks in an attempt to address the issue of high moose densities (J. Gosse and T. Knight, Parks Canada, pers. comm.).

1.3 Thesis Overview

My research considers a broader spatial extent with respect to the impacts of moose density and browsing on forest regeneration processes on Newfoundland than previous studies. Identifying landscape scale processes and factors that affect moose density and browsing dynamics will assist wildlife managers in more effectively managing moose populations no longer naturally controlled by predators. My thesis has the following two objectives:

The first objective was to compare the response of vegetation exposed to browsing from an overabundant moose population in areas having different management designations and moose densities (Chapter 2). The vegetation response (percent browsed) of preferred forage species was measured using browse plots in MMAs and Terra Nova and Gros Morne National Parks, where the MMA and national park (GMNP) in western Newfoundland has a higher moose densities than eastern Newfoundland's MMA and national park (TNNP). I determined the availability, use, and palatability (Dodds 1960) of winter forage species in these areas. Further, I focused on the influence of moose browsing on balsam fir, a species integral to both moose winter diet and dominant coastal species, via seedling densities. I quantified landscape composition and configuration in areas with high and low moose densities across Newfoundland to determine the feasibility of identifying stands that will attract moose which could result in high moose densities (Chapter 3).

The second objective was to identify landscape scale processes and factors that influence moose browsing (Chapter 2) and density (Chapter 3). In both chapters, an information theoretic approach was applied to test multiple competing hypotheses of the landscape scale processes and factors. In Chapter 2, I compared logistic regressions with browsing as the responsible variable and landscape scale processes and factors (including management designation, moose density, stand type, species, and sapling height) as the explanatory variables. In Chapter 3, I compared logistic regressions with moose density as the responsible variable and the landscape scale processes and factors (i.e., natural disturbances, cut blocks, hunter success, and hunter access) as the explanatory variables.

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Co-Authorship Statement

Both Chapters 2 and 3 will be submitted for publication and will be co-authored by Drs. Yolanda Wiersma and Luise Hermanutz. As such, there will be necessary repetition between Chapters 1, 2, and 3. I was responsible for project development, design, field sampling, analysis, and writing, but co-authors guided all aspects of the project.

Chapter 2. Impacts of moose (*Alces americanus*) browsing on forest structure in response to landscape processes and factors in Newfoundland, Canada.

2.1 Abstract

Overabundant large herbivore populations can alter ecosystem processes, and change forest dynamics thereby influencing the trajectory of forest regeneration. This study determined whether moose (*Alces americanus* syn. *Alces alces americana*) density (high vs. low) and management designation (protected vs. managed) explained moose winter browsing patterns at the landscape level, and if these patterns have the potential to change the trajectory of forest regeneration on Newfoundland. I focused on known preferred winter forage species but particularly on balsam fir (*Abies balsamea*) which is integral to both moose winter diet and is a dominant species of coastal forest ecosystems on the island. Overall balsam fir seedling density was lower than necessary for mature stands to be fully stocked but did not differ with moose density or management designation. Percent browsing was significantly higher in protected areas for wild raisin (*Viburnum nudum* var. *cassinoides*), but did not vary for other species with moose density or management designation. I compared regression models using the Akaike Information Criterion (AIC_c) and found that the global model (management designation, moose density, stand type, species, and sapling height) best explained the variance in the observed browsing percentages. The results suggest that moose forage selectively in winter, and that deciduous species have higher odds of being browsed than coniferous species. This study supports other studies suggesting that moose browsing has the capacity to alter the trajectory of forest regeneration, but in my study, browsing did not vary with management designation or moose density. The best model indicates that a combination of landscape scale processes and factors may play a role in regulating the regeneration of the vegetation community through both top-down and bottom-up processes.

2.2 Introduction

Overabundant large herbivore populations are receiving attention globally because of their pervasive impacts on ecosystems. These populations can alter ecosystem processes by changing the trajectory of vegetation regeneration patterns that modify soil properties (Pastor et al. 1988, Pastor and Danell 2003, Butler and Kielland 2008) and forest dynamics (Brandner et al. 1990, McInnes et al. 1992, Côté et al. 2004, DeJager and Pastor 2009). There are increasingly common occurrences of non-native overabundant populations of large herbivores on islands devoid of top carnivores leading to ecosystem disequilibria including black-tailed deer on the islands of Haida Gwaii, British Columbia, Canada (Martin et al. 2010), deer and goats to New Zealand (Nugent et al 2001), and moose in the Cape Breton Highlands, Nova Scotia, Canada (Smith et al. 2010). On the Haida Gwaii Archipelago, black-tailed deer were introduced, reached high densities due to the lack of predators, and consequently have reduced forest community diversity to coniferous browse-tolerant species (Martin et al. 2010). Introduced deer and goats to New Zealand were shown to negatively influence forest composition by browsing preferred forage (Nugent et al 2001). In the Cape Breton Highlands where moose (*Alces americanus americanus*) occur at high density due to the extirpation of their main predator the grey wolf (*Canis lupus*), severe browsing on balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) has altered forest regeneration, and has resulted in changes to cyclical insect herbivores such as spruce-budworm (*Choristoneura fumifera*), an important component of the forest regeneration processes (Smith et al. 2010).

Foraging is further influenced by patch size, shape, and diversity (Turner 1989). The presence, composition, and configuration of the habitat patches available in the landscape exploited by large herbivores are often influenced by anthropogenic factors. Simulation models for white-tailed deer showed that size of habitat patches and corresponding productivity can be influenced by habitat fragmentation from human development which, in turn can influence deer foraging behaviour and their impacts on landscape processes (Augustine and McNaughton 1998, Walters et al. 2001). One of the main anthropogenic factors altering habitat in a number of ways is forest harvesting (Kramer et al. 2006). Forest harvests reverts stands to an early successional stage, improving forage for herbivores (Crête 1989, Kramer et al. 2006). Moose have been shown to be present in higher abundance in stands 7-10 years following harvests (Parker and Morton 1978, Collin and Schwartz 1998, Potvin and Courtois 2004, Potvin et al. 2005). Young saplings contain a high amount of nutrients (especially proteins) and less secondary metabolites which allow for easier digestion than older stems (Spalinger et al. 2010). Thus forest harvest may contribute to increased moose densities. However, forest harvest resource roads also provide access for human harvesting of large herbivores (Ferguson et al. 1989, Rempel et al. 1997, McLaren and Mercer 2005) which can contribute additive mortality to the population (Ferguson & Messier, 1996, Mercer and McLaren 2002, Sæther et al. 2009). There still remain gaps in the understanding of the complex interplay between ecosystem processes, human activities, and their influence on large herbivore populations (Hobbs 1996).

Many large herbivores are adaptable generalists that forage in a hierarchical manner (Senft et al. 1987). Large herbivores select individual trees within these stands. Normally they show a preference for deciduous species over coniferous species selecting based on what is available (Petersen 1955, Dodds 1960, Proulx and Kariz 2005). Further, large herbivores have been shown to selectively forage at an even finer level, choosing particular stems from available species (Senft et al. 1987). It is through selective foraging that large herbivores can influence forest composition when at high densities (Brandner et al. 1990, McShea et al. 1997, Côté et al. 2004). Browsing by large herbivores at high densities can also influence forest regeneration through the reduction of seedling density. Browsing influences seedling density by either interfering directly with recruitment via eating reproductive structures/tissues (Mathisen et al 2010, Ruzicka et al. 2010) and new growth (Martin et al. 2010), or indirectly via trampling and/or uprooting of seedlings and changes in soil composition (Naimen 1988, Pastor et al. 1993, Pastor and Danell 2003).

The moose population of Newfoundland is referred to as overabundant because they have altered forest regeneration (Gosse et al. 2011). Although the island-wide density is 2 moose·km^{-2}, there is wide variation across the island. Moose density ranges from 0.25 to 14 moose·km^{-2} of forest and scrub area (Newfoundland and Labrador Wildlife Division, unpublished data) across Moose Management Areas (MMAs). Currently, the west coast has higher moose densities than the east coast of Newfoundland (Newfoundland and Labrador Wildlife Division, unpublished data; Figure A.1.1). Compared to the moose's indigenous North American range of densities of 0.5-1.5 moose·km^{-2} (Karns 1998), moose density in Newfoundland is generally high. Along with the increase in moose density, there is increasing evidence to indicate that browsing pressure influenced forest composition and structure. Various studies have suggested that winter browsing has caused a decrease in abundance of balsam fir, white birch, and other preferred deciduous browse below 2 m in height (Bergerud and Manuel 1968, Connor et al. 2000,), as well as a shift in dominance to black spruce (*Picea mariana*) and white spruce (*P. glauca*) (Thompson and Curran 1993, McLaren et al. 2009, Gosse et al. 2011). Balsam fir is of particular interest as it is integral to both moose winter diet and forest dynamics on Newfoundland (Dodds 1960, Bergerud and Manuel 1968). Balsam fir is reduced in abundance within the understory if subjected to continuous moose browsing (Connor 2000, Gosse et al. 2011). Humber and Hermanutz (2011) observed low balsam fir seedling densities in areas subjected to high moose browsing pressure that had been previously disturbed by spruce budworm (*Choristoneura fumiferana*) in Gros Morne National Park.

Currently on Newfoundland, there are two main management designations for moose and forests on the landscape which may influence forest regeneration patterns; protected areas and moose management areas (MMAs). Within protected areas, moose hunting or logging are not permitted. On the island, these include the two national parks, Gros Morne (GMNP) and Terra Nova (TNNP) as well as Rodney Pond, a proposed provincial Ecological Reserve (WERAC 2007). During this study, the national parks did not allow hunting and logging within their boundaries. Rodney Pond is Crown Land, where logging is currently banned; however, moose hunting is permitted in this area. The MMAs refer to the areas designated by the Wildlife Division (Department of Environment and Conservation, Government of Newfoundland). The forestry activities permitted within the boundary of the MMAs are managed by the Forestry Division through 17 forestry districts, which do not coincide with the MMA boundaries.

My research aims to identify landscape scale processes and factors that influence moose browsing, as well as describing moose browsing patterns. I conducted my research at a larger spatial extent than previous studies on Newfoundland by including areas across the island with different management designation and moose densities. Moose density was not deemed low or high based on the management designation of the study areas; rather, moose density was represented by actual survey numbers within each area. The moose management area and national park on the west coast of Newfoundland harbours a higher moose density than the eastern MMA and national park, thus enabling me to treat the effects of moose density and management regime (hunting/forestry vs. protection) as independent variables in the analysis.

In this chapter, I 1) describe moose winter browsing patterns in areas exposed to varying moose density and management designation, and 2) determine if the browsing patterns have the potential to alter forest regeneration. I focused on known preferred winter forage species, but particularly on balsam fir, which is integral to both moose winter diet (Dodds 1960) and is dominant in coastal forests on Newfoundland (Bergerud and Manual 1968).

I tested the following three hypotheses: 1) Balsam fir seedling density is influenced by varying moose density and management designation on Newfoundland (i.e., top-down regulation). Thus, I predict that if balsam fir seedling density is influenced by moose density and management designation, then my national park study sites ("protected management designation") that have a higher moose density will have low balsam fir seedling density; 2) The proportion by which preferred species are browsed will vary with moose density and management designation. If moose are regulating the vegetation community (i.e. top-down regulation), then preferred forage species will be reduced in height in areas where moose are present at high density and in protected areas compared to areas with low moose density and in MMAs; and 3) How moose populations are regulated (i.e., top-down via hunting, or bottom-up via food limitation) within management areas will influence moose browsing impacts on vegetation. If regulation of moose densities in a particular management area (MMA or protected area) are regulated primarily by top-down processes (i.e., hunting), then I predict that, all else being equal, there will be a lower percentage of winter forage species browsed in the MMAs where moose are hunted than in protected areas, where they are not. Alternatively, if moose densities are regulated primarily by bottom-up processes (i.e., available forage species and stand type), then I predict that there will be higher percent of winter forage species browsed in areas with high moose densities (based on the assumption that there is abundant year-round food to support moose at high densities), independent of whether the area has moose hunting or not.

To test hypotheses 1 and 2, I quantified moose winter browsing through the establishment of browse plots within dominant habitats types of two moose management areas adjacent to the two national parks and a proposed ecological reserve within one of the moose management areas. I measured balsam fir seedling (<10 cm) densities in areas of different management designations and moose densities. I quantified moose browsing patterns as percent of forage sapling (>10 cm and < 200 cm) browsed on the landscape, the use and availability of forage species by moose, palatability of forage species by stand types, and the odds of forage species being browsed. I addressed hypothesis 3 by analyzing moose browsing in relation to landscape scale processes and factors using statistical models. The statistical models were compared via model selection through an information-theoretic (IT) approach (Burnham and Anderson 2002) to determine which landscape scale processes and factors (management designation, moose density, habitat type, species, and height of forage sapling) best explained observed moose winter browsing.

Identifying browsing patterns as well as landscape scale processes and factors that influence moose browsing and density at the management unit scale will help forestry and wildlife managers more effectively manage moose populations that are not naturally controlled by predation more effectively. These landscape scale processes and factors can then be incorporated into management strategies during MMA harvest quota development to deal with time-lags in responses to decreases and increases in large herbivore populations.

2.3 Study Areas

Moose Management Area 02 (MMA 02) and Gros Morne National Park (GMNP) are situated on the west coast of Newfoundland (Figure 2.1 & Table A.1.1). GMNP and MMA 02 encompass portions of the Northern Peninsula Forest, Western Newfoundland Forest and the Long Range Barrens Ecoregions. Damman (1983) describes the Northern Peninsula and Western Newfoundland Ecoregions as balsam fir dominated, except at higher elevations where black spruce is dominant. The Western Newfoundland Ecoregion has an abundance of mountain maple (*Acer spicatum*), with red maple (*A. rubrum*) and trembling aspen (*Populus tremuloides*) as sub-dominants. The Northern Peninsula (NP) Ecoregion has few deciduous species present because their northern limits approach the southern border of the ecoregion. Yew (*Taxus canadensis*) is present in higher abundance on the NP than anywhere else on the island. The Long Range Barrens are characterized by ericaceous shrubs with scattered balsam fir and black spruce stands (Damman 1983). GMNP had an overall density of 5.47 moose$\cdot$km^{-2} of forested area (Parks Canada 2007 unpublished data) and MMA 02 had a current density of 2.63 moose$\cdot$km^{-2} of forest and scrub (Newfoundland and Labrador Wildlife Division 2008 unpublished data) (Figure A.1.1).

Moose Management Area 42 (MMA 42), Rodney Pond, and Terra Nova National Park (TNNP) are located in eastern Newfoundland, Canada (Figure 2.1 & Table A.1.1). These areas are within the Central Newfoundland Ecoregion (Damman 1983). This ecoregion has historically been disturbed by fire, resulting in forests dominated by black spruce interspersed with stands of white birch and trembling aspen, albeit in lesser amounts. Terra Nova also overlaps with the North Shore Forest Ecoregion. This forest is described as being similar to the Central Newfoundland Forest but with a few notable differences including a higher occurrence of white spruce and trembling aspen. The moose population density is currently 0.27 moose$\cdot$km^{-2} of forested and scrub areas in TNNP (Parks Canada 2008, unpublished data), MMA 42 and Rodney

Pond currently have a density of 0.51 moose·km^{-2} of forested and scrub areas (Newfoundland and Labrador Wildlife Division 2009, unpublished data) (Figure A.1.1).

2.4 Methods

Quantifying Moose Browsing via Browse Plots

I used browse plots to assess the extent of damage due to moose browsing activity on seedlings and saplings of preferred winter forage in each study area. The locations of the browse plots within each study area were chosen using a random point generation tool in Hawth`s Analysis Tool (Beyer v.3.26) in Geographic Information Systems software, ArcGIS (ESRI v. 9.3). The XY coordinates generated represented the centre of the browse plots. Five browse plots were established in each of the study areas within the dominant stand types for a total of 25 browse plots (Figure A.2.1-A.2.5). To determine an appropriate number of browse plots, I examined the number of stems (± standard deviations) of two main winter forage species (Figure A.2.6), balsam fir and white birch, from browse plot measurements collected by TNNP staff during 2008 (Parks Canada unpublished data). I examined the curve generated and determined where it levelled off (asymptote) to determine the number of browse plots necessary, given the temporal limitations for extensive samples across such a large extent over two short field seasons.

The browse plot, designed by J. Gosse (Parks Canada unpublished data), is circular with a radius of 11 m encompassing an area of 400m^2 (Figure A.2.7). The measurements within the browse plots were based on methods used in Terra Nova (Gosse, J., Parks Canada unpublished data) and Gros Morne (Connors et al. 2000, Parks Canada unpublished report). Balsam fir, mountain maple, red maple, striped maple (*A. pensylvanicum*), trembling aspen, white birch, wild raisin (*Viburnum nudum* var. *cassinoides* (L.) Torr & A. Gray), willow (*Salix spp.*), and yew were the winter forage species (Bergerud & Manual 1968, Dodds 1960, Connors et al. 2000) sampled in the browse plots. For each sapling (all species; >10 cm and <200 cm in height) encountered, the following measurements were recorded: height (cm; stem base to end of terminal leader), stem basal diameter (mm), stem diameter of the terminal leader (mm; at the point of browse which will vary depending on browsing condition), and whether the terminal leader was browsed (Yes or No). All balsam fir saplings within the entire browse plot were counted. A 1 m wide belt transect in the middle of the browse plot was surveyed for saplings of deciduous species. To minimize bias, all balsam fir seedlings (<10 cm) were counted in a 1 m x 1 m square facing the northeast, and were expressed as seedling per hectare.

Forage availability on the Landscape

Species availability was calculated for each study site (protected areas and MMAs) in a GIS (ArcGIS v. 9.3) from stand composition data in the Forest Resource Inventory (FRI) available as Geographic Information Systems layers. For the MMAs, I used provincial FRI data (Forestry Division, Newfoundland and Labrador Government Department of Natural Resources) while in the national parks I used FRI data developed by Parks Canada (Parks Canada, unpublished data). However, both agencies use the same sampling techniques and classification scheme so the FRIs for all study sites were comparable. Stand composition is restricted to tree species; thus, shrubs, such as wild raisin, were omitted from some analyses as species composition was not available within the FRI database.

Statistical Analysis

All statistical analyses were carried out with the R statistical package (R base package v. 12.0; R Development Core Team 2012). I used the car package to conduct all of the Analysis of Variance (ANOVA) tests (Fox and Weisberg, 2011). Sampling occurred on the east coast of Newfoundland in 2009 and 2010 so I conducted a t-test to determine if these data could be pooled. The t-tests showed that there was no inter-annual variation so all data were pooled for further analyses (Table A.4.1). To test hypothesis 1 (balsam fir seedling density is top-down regulated), I used one-way ANOVA ($\alpha = 0.05$). To test hypotheses 2 (proportion of browsing on preferred species influenced by moose density and management designation) and 3 (moose population regulation within management areas influences moose browsing impacts on vegetation), I conducted several frequentist analyses to quantify moose browsing patterns on winter forage species. First it was necessary to quantify browsing damage. Since continually browsed saplings exhibit stunted heights with increasing basal diameter sizes (Bergerud and Manual 1968), damage to saplings from moose browsing was assessed using linear regressions based on the relationship between height and basal diameter described by Bergerud and Manual (1968). These linear regressions were graphed for visualization using the lattice package (Sarkar 2008). Regressions were done only on species that had a large enough sample size to be statistically robust ($n \geq 10$ saplings). Second, moose browsing patterns were examined by: 1) the percent browsing of saplings from the amount of terminal leaders browsed and the total available stems in the browse plot; 2) a use versus availability analysis using a chi-square test where the observed percent browsed indicated the use of the saplings and the species composition of stands was used to determine the availability of stands of different types for moose in all study areas; and 3) the palatability of browse species found within the browse plot was calculated using Dodd's palatability index (1960). Browsing percentages were analyzed using an odds ratio and one-way ANOVAs. Odds ratios (R base package v. 12.0; R Development Core Team 2012) were computed from logistic regressions of browsing percentages with a binomial distribution to examine whether some species of saplings had higher odds of being browsed over others in relation to different moose density and management designation. I carried out one-way

ANOVAs ($\alpha = 0.05$) of percent browsing of each encountered forage species with respect to management designation (hypothesis 2) and moose density (hypothesis 3). Lastly, to determine which factors best explained the observed browsing patterns, I created general linear models (with a binomial distribution) to test for the relationship of moose percent browsing to landscape scale processes and factors (management designation, moose density, stand type, forage species, and sapling height). Candidate models were derived using the landscape scale processes and factors described in the introduction and hypothesized to influence moose browsing patterns (Table 2.4.a). To address my third hypothesis, I developed models 2 and 3 (see Table 2.4a) that include factors that are top-down regulators (e.g., moose density or management designation). I chose not to include the model with moose density and management designation together, but rather analyzed them separately in different models to see if one over the other would be better model. I developed models 10 and 11 that included bottom-up regulation factors (e.g., available forage as described by species types and stand types). Finally, models 4-9 are a combination of bottom-up and top-down regulation factors. The combinations of factors were based on the interactions of top-down and bottom-up factors described in the introduction (e.g., moose density and available forage species or management designation and available forage species). I carried out model selection to test these multiple competing hypothesis (sensu Chamberlin 1965) using the information-theoretic (IT) approach (Burnham and Anderson 2002). I calculated log-likelihood, parameters (K), AICc values, Akaike weights (w_i), and delta AICc (Δ_i) according to the methods outlined in Burnham and Anderson (2002). I determined plausibility of the models using Δ_i values. Models with $\Delta_i < 2$ are considered highly plausible, models with Δ_i between 2- 4 are plausible and any model with Δ_i larger than 4 is not very plausible (Burnham and Anderson 2002). I computed parameter weights ($\sum w_i$) of the plausible models where each parameter was present) to determine the weight of each parameter across all plausible models. I calculated parameter estimates with standard errors for the plausible models to determine how these parameters and moose densities interact. The models were verified for normality using the Shapiro-Wilk test ($\alpha=0.05$) and tested for fit using the adjusted r-squared which takes into account the variance resulting in lower values than r-squared (Crawley 1997). Multi-collinearity was tested for by comparing the estimated effects of highly correlated explanatory variables via relative odds ratios in univariate versus multivariate analysis of the logistic regressions from the AIC analysis.

2.5 Results

Balsam Fir Seedlings

Overall balsam fir seedling density (Figure 2.2) was lower than the estimated 10,000 seedlings ha^{-1} necessary to reach a mature stand stocked at 2500 stems ha^{-1} (Tremblay et al. 2007). Seedling density did not differ with management designation ($F_{1,3}=1.11$; $p=0.36$) or moose density ($F_{1,3}=0.34$; $p=0.59$).

Moose Browsing Patterns

In both MMA 02 and Gros Morne, balsam fir fit the expected relationship between basal diameter and height well (Figure 2.3) indicative of limited browsing. In MMA 02, maples and yew displayed a poor fit of the expected linear relationship of basal diameter and height which confirms severe browsing damages (Figure 2.3). Maple spp. and yew in Gros Morne had very small sample sizes so browsing effects could not be statistically compared. In MMA 42 and Rodney Pond, the height to basal diameter relationship suggested little browsing of balsam fir while in Terra Nova it appeared that balsam fir was severely browsed (Figure 2.4). In both MMA 42 and Terra Nova, moose intensely browsed on maples (Figure 2.4). Regression slopes of balsam fir from Terra Nova, MMA 02, and Gros Morne had similar slopes which were lower than MMA 42 and Rodney Pond indicating that these areas had lower heights in relation to basal diameter (Figure 2.3 & 2.4). Thus, Terra Nova, MMA 02, and Gros Morne had a higher browsing intensity than MMA 42 and Rodney Pond as they had the most stunted balsam fir saplings. MMA 02 had a lower slope value for maples indicating a higher browsing intensity as there was more stunted sapling stems present compared to MMA 42 and Rodney Pond (Figure 2.3 & 2.4).

The proportion of saplings transitioning into taller size class gives a good indication of browsing intensity. For example, in MMA 42 approximately 10% of balsam fir saplings were not counted in the second year of the study as they had grown beyond 2 m sapling height limit, confirming the lower browsing intensity, while maples showed the opposite trend as no sapling in 2010 surpassed the 2009 height and basal diameter because of browsed leaders. In Terra Nova, the overall heights for balsam fir were very low and no balsam fir saplings in 2010 exceeded the heights recorded in 2009 since leaders were browsed. Maples in Terra Nova showed similar heights and basal diameters between 2009 and 2010. In Rodney Pond, balsam fir saplings were distributed fairly evenly among the heights and basal diameters with approximately 7% of the saplings measured in 2009 exceeding the 2 m mark in 2010.

When analysing differences between the forage species used compared with their availability on the landscape, I found that moose were foraging in a significantly selective manner at all study sites except Rodney Pond (Table 2.1). Across study sites, the palatability factor index of maple spp., white birch, and wild raisin were higher than balsam fir regardless of stand type (Table 2.3). However, the palatability factor index varied for balsam fir within different stand types similarly in each study area. Balsam fir saplings found in a balsam fir or black spruce dominant stand had a higher palatability factor index than balsam fir in a hardwood or mixedwood dominant stand (Table 2.3). Yew had a high palatability factor index in one hardwood stand and mixedwood stands but was low when found in a black spruce stand, however, the abundance of yew across all stands types was low (Table 2.2).

Browsing by moose was generally higher for maple spp., white birch, wild raisin, and yew compared to balsam fir in eastern Newfoundland (Figure 2.5). Percent browsing was significantly higher in protected areas than managed areas ($F_{1,5}= 75.5$; $p<0.0001$) for wild raisin, but did not differ with moose density ($F_{1,4}= 0.16$; $p=0.70$). Percent browsing did not differ with management designation or moose density for balsam fir ($F_{1,27}=0.91$; $p=0.34$ & $F_{1,27}= 0.47$; $p=0.49$), maple spp. ($F_{1,15}= 3.54$; $p=0.079$ & $F_{1,15}= 0.24$; $p=0.62$), white birch ($F_{1,6}= 0.79$; $p=0.40$ & $F_{1,5}= 2.28$; $p=0.19$), and yew ($F_{1,4}= 0.34$; $p= 0.58$ & $F_{1,4}= 5.40$; $p= 0.080$).

Regardless of moose density or management designation, deciduous species had higher odds of being browsed than coniferous species (Table 2.3). In terms of moose density, balsam fir had higher odds of browsing in higher density areas. Maple spp. and yew had higher odds of being browsed in low moose density areas (Table 2.3a). On the west coast of Newfoundland, balsam fir had lower odds of being browsed in MMA 02 than GMNP (Table 2.3b). Maple spp. and yew had higher odds of being browsed in MMA 02 than GMNP. On the east coast of Newfoundland, balsam fir in MMA 42 had a higher likelihood of being browsed than in TNNP and Rodney Pond. However, maple spp. and yew had lower odds of being browsed in MMA 42 than in TNNP and Rodney Pond (Table 2.3c).

Explaining Variation in Moose Browsing on the Landscape

Model selection results suggested that the global model (which included management designation, moose density, stands type, forage species, and height) was the most plausible model (AIC weight of 0.96) explaining observed browsing patterns (Table 2.4.b). There was only one plausible model from all of the candidate models so parameter weights were equal (Table 2.5). Moose browsing had a positive association with management designation, forage species, stand types, and forage height; however these parameter estimate values were low (Table 2.6). Moose browsing had a negative association with moose density again with low parameter estimate values. The best model does not show normality and the adjusted r-squared indicates a poor fit (Table 2.6). This result could be due to some multi-collinearity present in some of the explanatory variables (Table A.9.1; Appendix 9).

2.6 Discussion

Balsam Fir Seedling Density

There was evidence of low balsam fir seedling densities in all study areas, which, contrary to my hypothesis, did not differ with moose density or management designation. It appears that the both the history of site browsing and the plant community context mediate browsing intensity and impacts. The lack of variation in seedling densities between areas that have different moose density or management designation may be a result of past browsing by moose and a myriad of other consumers. In Newfoundland, red squirrels (*Tamiasciurus hudsonicus*) consume female and male cones of balsam fir, while rodents and slugs consume newly establishing seedlings (Gosse et al. 2011). In addition, intense herbivory by moose on saplings prevent them from reaching the adult stage, further limiting seed productivity (Gosse et al. 2011). A previous study in GMNP found low balsam fir seedling densities where moose are present in high densities (Humber and Hermanutz 2011). On Isle Royale, McLaren and Janke (1996) attributed the variation in balsam fir seedling density to severe moose browsing and natural disturbances such as fire and wind-throw. Tremblay et al. (2007) found that balsam fir seedling mortality decreased with decreasing white-tailed densities in both clear-cut and uncut forests. However, to my knowledge, there is limited research on large herbivore browsing in relation to balsam fir seedling densities.

Moose Browsing Patterns

In agreement with my hypothesis, moose are foraging selectively with a higher probability of deciduous species being browsed than coniferous species. There was an observed gradient of selective moose winter forage browsing patterns of deciduous species over coniferous species; however, the gradient was not completely explained by moose density or management designation (Figures 2.3 & 2.4; Tables 2.2, 2.3, & 2.4). Moose exhibited preferences for species in terms of palatability and used balsam fir, maple species, and white birch in a higher proportion than the proportion available on the landscape (Table 2.2 & 2.3).

Rodney Pond showed little browse damage of balsam fir saplings with a strong height to basal diameter relationship. Rodney Pond is dominated by mature forest so there are few saplings available within the moose's browsing range of below 2 m. Rodney Pond has managed hunting, which decreases moose density (Messier 1994, Ferguson and Messier 1996, McLaren and Mercer 2005), without natural or anthropogenic disturbances to promote preferred early successional stands (Rempel et al. 1997, Collins and Schwartz 1998). In contrast to my hypothesis, balsam fir saplings located in the west coast sites (where there is higher moose density) have less browsing damage than east coast sites. MMA 02 and GMNP show more browsing damages of maple spp. and yew than sites on the east coast. The significantly higher browsing severity observed on balsam fir in the east coast in low moose density could be explained by the fact that this areas has gone through a peak and decline phase in moose density while high moose densities were peaking and slowly declining/stable in MMA 02 and Gros Morne. Thus, the vegetation reflects the legacy of previously high impact periods of moose browsing so the smallest amount of browsing may still be causing the observable vegetation damage (Ruzicka et al. 2010).

Sapling height reduction may be the result of impacts from multiple herbivores (Denyer et al. 2010), including moose and snowshoe hare (*Lepus americanus*; Dodds 1960). Browsing patterns may also be related to species availability on the landscape as the east coast areas are mostly dominated by black spruce (Damman 1983; Table A.1.2). Thus, there is less preferred browse available overall which may make impacts on balsam fir more discernible. Since balsam fir has a higher abundance on the west coast (Damman 1983; Table A.1.2), the impacts of moose browsing may appear lower than where there is less balsam fir available on the landscape (Brandner et al. 1990). Martin et al. (2010) suggest that overabundant large herbivore populations can alter the forest composition at different temporal scales due to species presence locally but that ultimately the result is the same, a reduction in forage species diversity and greater uniformity among habitat patches across the landscape.

On Newfoundland, moose foraged selectively, choosing more palatable deciduous over coniferous species. Moose used winter forage species in a greater proportion than what was available on the landscape. Percent browsing was only significantly higher in protected areas for wild raisin, while it did not differ with moose density or management designation for the other browse species. Even though the percent browsing was not significantly different for all species except wild raisin, overall the percentage of browsed stems was high. Few yew stems were found in the study areas during this study. Bergerud and Manual (1968) predicted that if moose browsing continued beyond the tolerance levels of the vegetation community, yew would decrease in abundance. I also observed severely browsed balsam fir saplings, as well as low numbers of white birch saplings across all study sites. This provides more evidence consistent with the hypothesis that moose may be contributing to a shift in the trajectory of forest regeneration (Pastor et al. 1988, McInnes et al. 1992, Pastor and Danell 2003, Côté et al. 2004, Ruzicka et al. 2010), since both balsam fir and white birch have historically been important components of the forest composition in Newfoundland (Pimlott 1953, Bergerud and Manual 1968). This shift may provide less preferred or browse tolerant species such as black or white spruce to become dominant within the canopy of mature stands where they would not have been prior to moose browsing disturbances (Pastor et al. 1988, Thompson et al. 1992, Thompson and Curran 1993, Connor et al. 2000).

Explaining Variation in Moose Browsing Patterns

Browsing patterns were not fully explained by top-down regulation of moose density or management designation as I had hypothesized. Model selection results suggested that the global model (which included management designation, moose density, stand type, forage species, and sapling height) was the most plausible model explaining the observed browsing patterns, however this model had poor fit (Table 2.5 & 2.6). Thus, the results of my thesis support the hypothesis that moose populations are regulated by a mix of landscape scale processes and factors that are top-down (i.e., management designation and moose density) and bottom-up (i.e., stand type, forage species, and sapling height). The low fit and non-normality of the best model may be a result of the complexity of the interactions at the landscape level, as well as not accounting for other potentially important processes and factors, such as soil composition. Denyer et al. (2010) showed that soil properties and grazing explained the majority of the plant community composition. On Isle Royale, bottom-up regulation explained more of the inter-annual variation in moose population dynamics than top-down processes from wolves, but together they only explained over half of the variation (Vucetich and Peterson 2004). McLaren and Peterson (1994) illustrated evidence of mainly top-down regulation of wolves on moose on Isle Royale but they also acknowledged the importance of some bottom-up process from disturbances on moose population dynamics. Schmitz et al. (2000) found that top-down regulation was weakened when plants contained defences against herbivory as well as when herbivore species diversity was high in carnivore-prey relationships within terrestrial ecosystems. Another herbivore of the boreal forest, the snowshoe hare, seems to have multiple regulation factors such as food, predation, and social interactions, which include both bottom-up and top-down regulation (Krebs et al 2001). There is some evidence from this study suggesting that there may be some bottom-up regulation from available species as balsam fir is being browsed at high densities as the preferred deciduous forages have been removed by browsing. In areas where the moose density exceeds 1.5 to 2 moose·km^{-2}, it seems that bottom-up regulation, where available forage becomes the limiting factor, controls the moose population because predation by wolves/bears or hunting cannot remove enough animals to influence the moose population (Messier 1994). The negative association between moose browsing and moose density may be explained by chemical defenses of forage as a response to browsing as moose density increase, acting as a limiting factor due to the lack of natural predation.

The variance in the analyses of the browsing patterns was high. This was not unexpected as this study was restricted in the number of sample sites that were be possible, due to the large distances between study areas and the distance between browse plot locations. The *a priori* power analysis showed that 5 browse plots would be sufficient to capture moose browsing patterns but that the variance would be high, or have low rigour. Nevertheless, such low rigour in an analysis conducted at a broad spatial extent is common in landscape ecology. In a review of spatial scaling in ecology, Wiens (1989) acknowledges that expanding the extent (study area) to study broad-scale processes carries a cost of higher variance due to the lower resolution of fine-scale details. Wiens (1989) goes on to explain how patterns may be more apparent at the broad-scale while biological mechanisms underlying the patterns may be better revealed at fine-scales. The main focus of my study was to examine the patterns of moose browsing at the extent of the management unit so as to be applicable to the extent at which moose are managed in Newfoundland. A fine-scale study would have carried higher rigour but would not have matched the spatial extent at which management practices are applied. Nevertheless, had time allowed, additional browse plots would have reduced variance and potentially yielded insights at finer-scales. Future work might consider increasing the number of browse plots while still maintaining focus at large spatial extent.

Management Implications

Removal of herbivores where they have been present in high numbers does not guarantee the forest will revert to the pre-high herbivore density state (Nugent et al. 2001, McLaren et al. 2009) and may demand the addition of restoration efforts (Royo et al. 2010, Ruzicka et al. 2010, Gosse et al. 2011). This is especially true if low balsam fir seedling density persists due to herbivory by other species (in Newfoundland these include red squirrels, insects, birds, rodents, hares, and slugs; McLaren et al. 2004, Gosse et al. 2011). Moose are foraging selectively and consequent browsing patterns appear to be changing the trajectory of forest regeneration on Newfoundland. Moose browsing patterns appear to be regulated by both top-down processes (i.e., moose density and management strategy) and bottom-up processes (i.e., stand type, forage species, and sapling height). Future research concerning moose browsing impacts in relation to density and management designation should explore the role of bottom-up regulation and plant biomass to better understand the effects of moose population dynamics upon forest regeneration.

Large herbivores at high densities can be also attributed to the lack of communication between wildlife managers and foresters in terms of management goals and it is believed that increased communication could help better manage large herbivores populations (Healy et al. 1997, Côté et al. 2004). An improved understanding of the complex interactions between top-down and bottom-up regulation of moose densities within Newfoundland's ecosystem is necessary for conservation or re-establishment of forest processes and to direct management actions to achieve sustainable ecosystems within management units.

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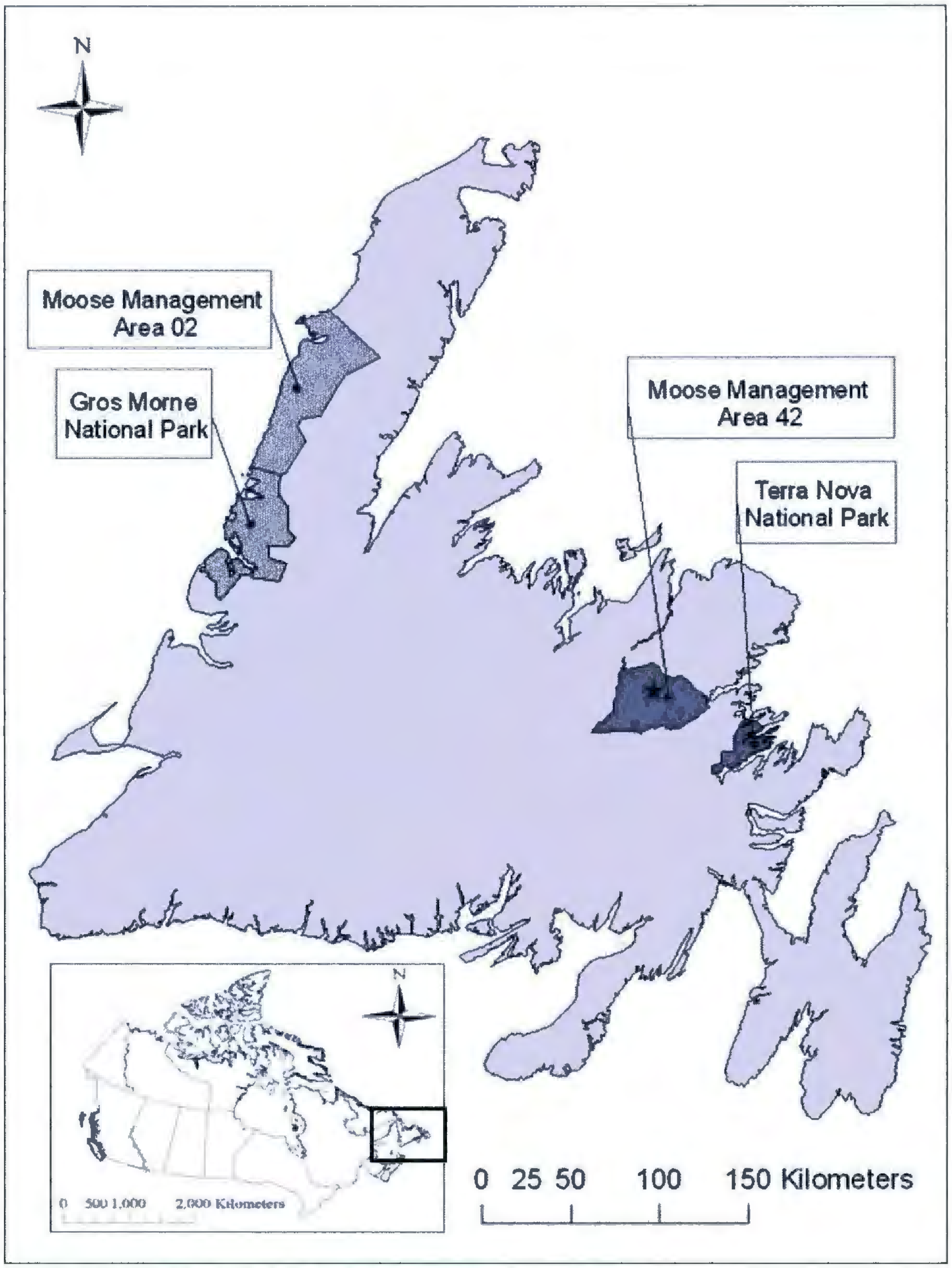

Figure 2.1 Study areas in Newfoundland, Canada including Moose Management Area 02, Gros Morne National Park, Moose Management Area 42, Terra Nova National Park, and Rodney Pond (within Moose Management Area 42 indicated by the star).

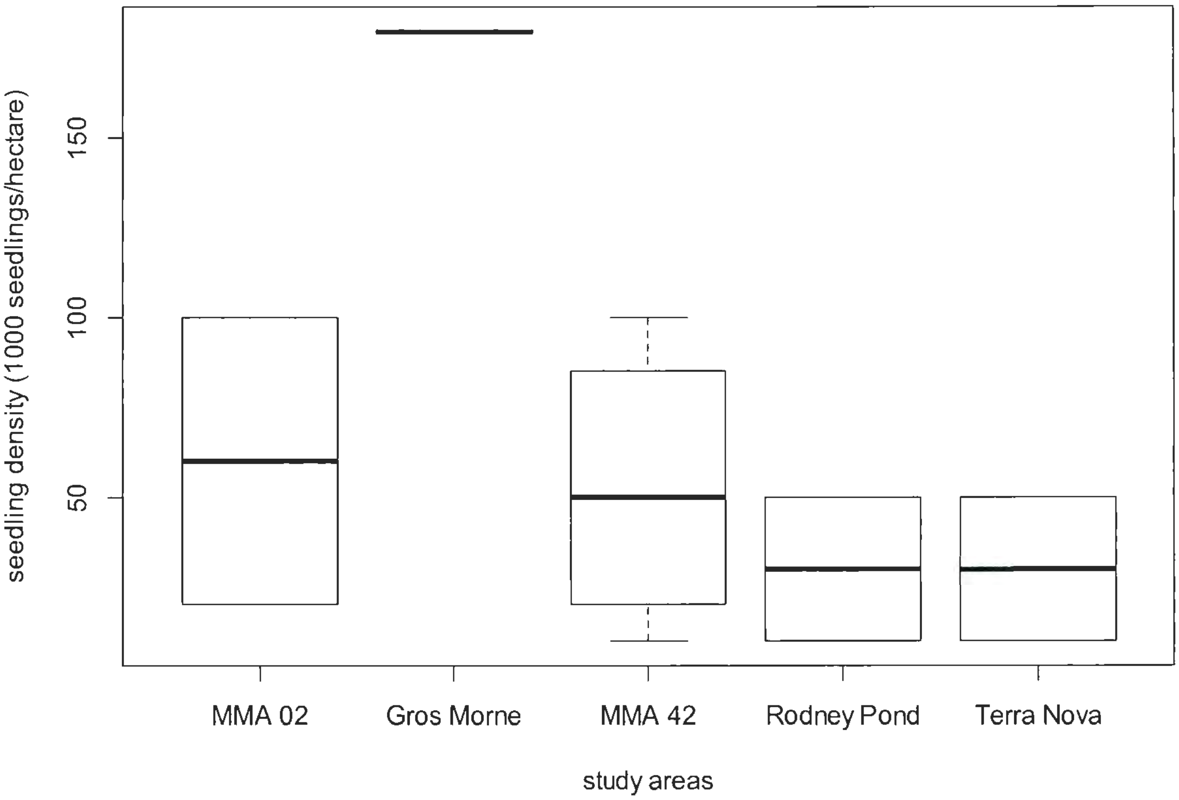

Figure 2.2 Balsam fir seedling (*Abies balsamea*) density (seedling per hectare) observed in western Newfoundland (Moose Management Area 02 and Gros Morne National Park) and eastern Newfoundland (Moose Management Area 42, Terra Nova National Park, and Rodney Pond).

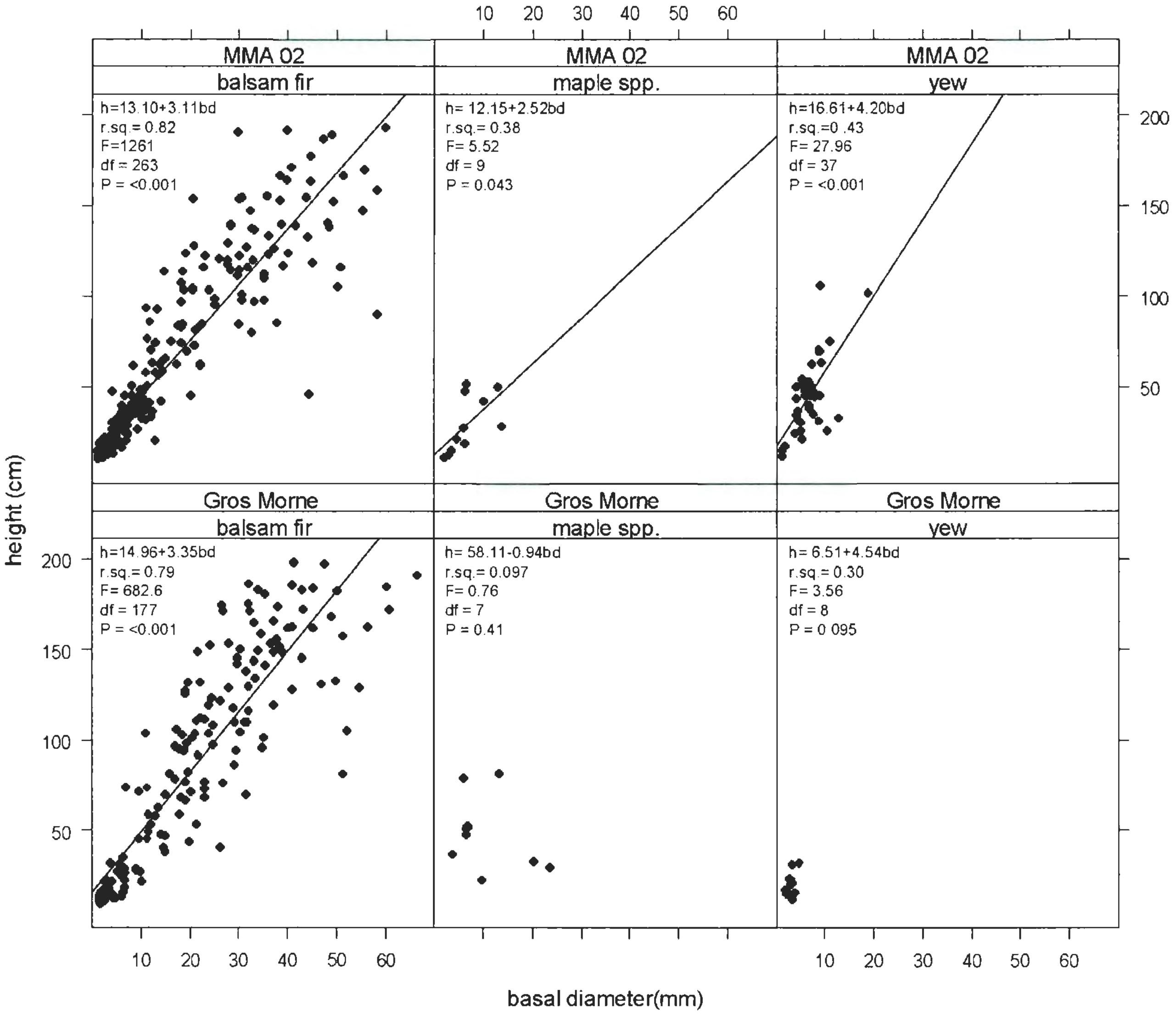

Figure 2.3 Sapling (10 cm – 200 cm) structure described by linear regressions of height (cm) and basal diameter (mm) of moose winter forage species (balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), and white birch (*Betula papyrifera*) found within western Newfoundland study sites, Moose Management Area 02 and Gros Morne National Park. Other species examined in the field (e.g., wild raisin) did not have sufficient samples to run linear regressions.

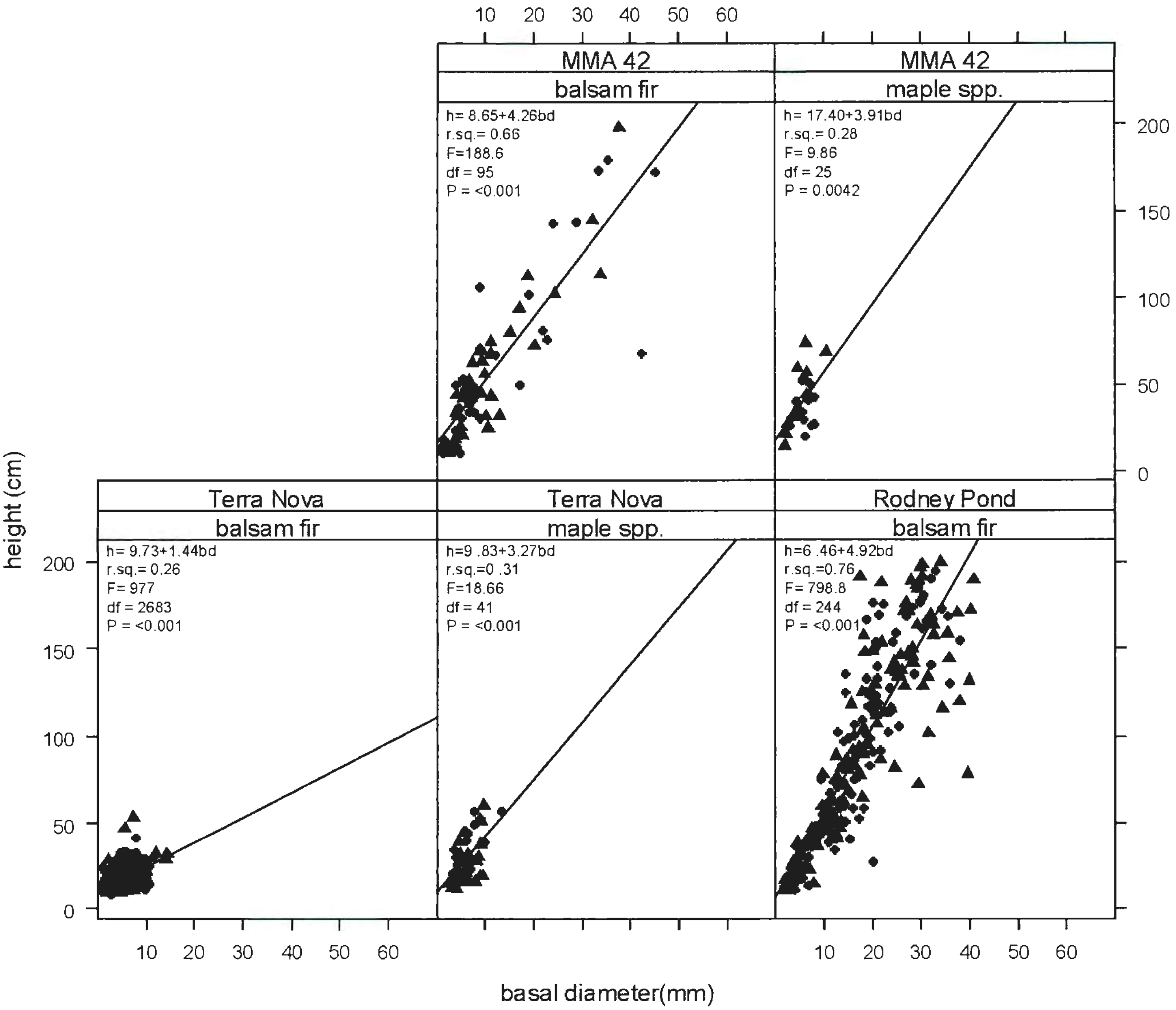

Figure 2.4 Sapling (10 cm - 200 cm) structure as described by linear regressions of height (cm) and basal diameter (mm) of moose winter forage saplings (balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), and white birch (*Betula papyrifera*) in eastern Newfoundland study sites. Data from 2009 (triangles) and 2010 (circles) did not differ (t-tests = p>0.05). Other species examined in the field (e.g., wild raisin) did not have sufficient samples to run linear regressions).

Table 2.1 The availability and use of moose foraging species (balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), and white birch (*Betula papyrifera*)) found in Moose Management Area 02, Gros Morne National Park, Moose Management 42, and Terra Nova National Park analyzed using a chi-square (χ^2) test.

Study Area	**Species**	**Percent Browsing (%)**	**Percent Cover (%)**	**Degrees of Freedom (df)**	χ^2	**p-value**
MMA 02	Balsam Fir Maple spp.	18.11 63.64	42.82 0.91	1	43.41	<0.0001*
Gros Morne	Balsam Fir Maple spp. White Birch	44.44 58.33 1.00	47.74 2.95 15.55	2	14.99	0.0005*
MMA 42	Balsam Fir Maple spp.	34.18 58.33	13.42 0.054	1	629.59	<0.0001*
Rodney Pond	Balsam Fir White Birch	12.60 25.00	8.17 9.98	1	0.25	0.62
Terra Nova	Balsam Fir Maple spp. White Birch	13.46 70.71 0.50	20.35 $3.9\ \mathrm{x}10^{-5}$ 8.14	2	12895.42	<0.0001*

* p-value that are significant within 95% confidence intervals ($\alpha = 0.05$).

Table 2.2 Stems of moose winter foraging species (balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), white birch (*Betula papyrifera*), and yew (*Taxus canadensis*)) availability, use, and palatability factor index (Dodds 1960) found in the dominant plot stand type within Moose Management Area 02, Gros Morne National Park, Moose Management Area 42, and Terra Nova National Park.

Study Area	Plot Stand Type	Species	Percent Availability	Percent Use	Palatability Factor Index
MMA 02	Hardwood	Balsam Fir	100	0	0
	Mixedwood	Balsam Fir	100	14	0.14
	Balsam Fir	Balsam Fir	100	35.29	0.35
	Black Spruce	Balsam Fir	92.96	0	0
		Yew	7.94	0.2	0.025
GMNP	Hardwood	Balsam Fir	75	33.33	0.33
		Maple spp.	25	100	4
	Mixedwood	Balsam Fir	42.42	0	0
		Maple spp.	24.24	50	2.06
		White Birch	3.03	100	33.00
		Yew	30.3	1	0.033
	Balsam Fir	Balsam Fir	99	35.29	0.35
		Wild Raisin	1	100	100
	Black Spruce	Balsam Fir	100	25.93	0.26
MMA 42	Mixedwood	Balsam Fir	81.08	26.67	0.33
		Maple spp.	10.81	25	2.31
		Yew	8.11	66.67	8.22
	Balsam Fir	Balsam Fir	100	0	0
Rodney Pond	Balsam Fir	Balsam Fir	100	0	0
	Black Spruce	Balsam Fir	100	0	0
TNNP	Hardwood	Balsam Fir	62.07	11.11	0.18
		Maple spp.	20.69	50	2.42
		Yew	17.24	60	3.48
	Mixedwood	Balsam Fir	91.18	0	0
		Maple spp.	8.82	0	0
	Balsam Fir	Balsam Fir	100	0	0

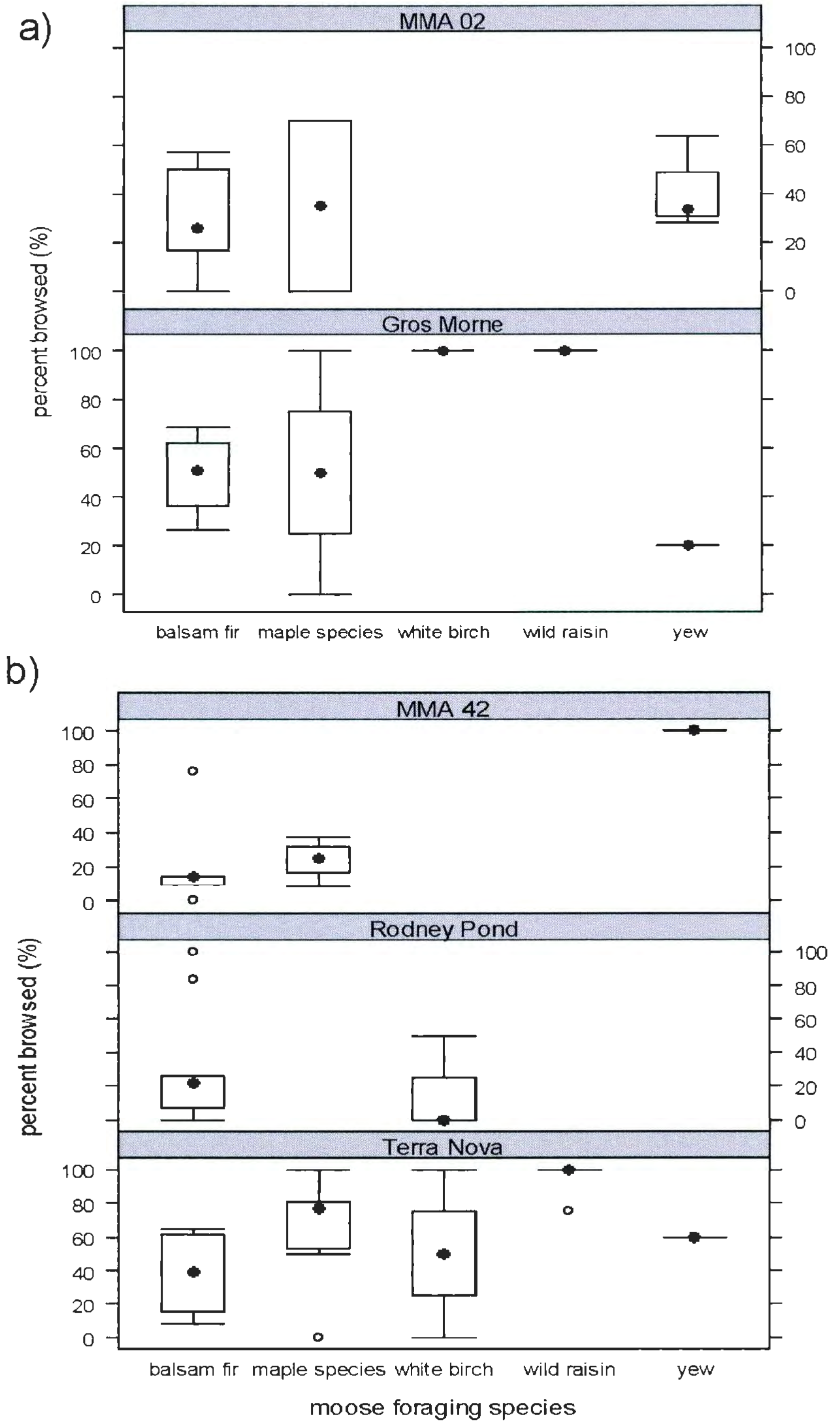

Figure 2.5 Moose browsing (percent) on winter forage species including balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), white birch (*Betula papyrifera*), wild raisin (*Viburnum nudum, var. cassinoides*), and yew (*Taxus canadensis*) in **a)** western Newfoundland and **b)** eastern Newfoundland.

Table 2.3 Odds (logistic regressions with binomial distributions) of moose browsing percentages of forage species (balsam fir (*Abies balsamea*), maple spp. (*Acer spp.*), white birch (*Betula papyrifera*), wild raisin (*Viburnum nudum var. cassinoides*), and yew (*Taxus canadensis*)) in: **a)** in low (<0.50 moose·km^{-2}) and high (>2 moose·km^{-2}) moose densities, **b)** western Newfoundland, and **c)** eastern Newfoundland.

a)

Moose Density	Species	Odds	Standard Error	Lower CI (95%)	Upper CI (95%)
Low	Balsam Fir	-1.62	0.076	-1.78	-1.48
	Maple spp.	2.25	0.31	1.64	2.90
	Yew	2.14	0.73	0.72	3.73
High	Balsam Fir	-0.93	0.10	-1.11	-0.70
	Maple spp.	1.46	0.45	0.59	2.40
	Yew	0.27	0.31	-0.37	0.88

b)

Management Designation	Species	Odds	Standard Error	Lower CI (95%)	Upper CI (95%)
Managed	Balsam Fir	-1.50	0.15	-1.83	-1.20
	Maple spp.	2.06	0.64	0.83	3.44
	Yew	1.03	0.36	0.30	1.74
Protected	Balsam Fir	-0.21	0.15	-0.50	0.080
	Maple spp.	0.77	0.64	-0.46	2.14
	Yew	-1.17	0.80	-3.08	0.24

c)

Management Designation	Species	Odds	Standard Error	Lower CI (95%)	Upper CI (95%)
Managed	Balsam Fir	-0.45	0.34	-1.14	0.20
	Maple spp.	0.25	0.56	-0.86	1.36
	Yew	1.14	1.27	-1.28	4.26
Protected	Balsam Fir	-1.67	0.078	-1.83	-1.52
	Maple spp.	3.11	0.50	2.20	4.22
	Yew	2.08	0.91	0.28	4.11

Table 2.4 a) Models derived to complete AIC_c for model selection of moose browsing **b)** Model selection for moose browsing on winter foraging species using AIC_c (n = 1897; Burnham and Anderson 2002) across all study areas.

a)

Global Model	browsing = management strategy + moose density + stand type + forage species + forage height
Model 2	browsing = moose density
Model 3	browsing = management strategy
Model 4	browsing = moose density + stand type
Model 5	browsing = management strategy + stand type
Model 6	browsing = moose density + forage species
Model 7	browsing = management strategy + forage species
Model 8	browsing = moose density + stand type + forage species
Model 9	browsing = management strategy + stand type + forage species
Model 10	browsing = stand type + forage species + forage height
Model 11	browsing = stand type + forage species

b)

Models	Log-likelihood	k	AIC_c	Delta AIC-i	Exponents	Weights
Global Model	-890.84	6	1793.73	0	1	0.96
Model 10	-896.21	4	1800.45	6.71	0.034	0.033
Model 8	-924.93	4	1875.88	64.14	$1.18e^{-14}$	$1.14e^{-14}$
Model 11	-926.39	3	1858.79	65.05	$7.47e^{-15}$	$7.22e^{-15}$
Model 9	-925.92	4	1859.87	66.13	$4.35\ e^{-15}$	$4.21e^{-15}$
Model 4	-933.37	3	1872.77	79.03	$6.88e^{-18}$	$6.65e^{-18}$
Model 5	-933.86	3	1873.73	80.00	$4.25e^{-18}$	$4.10e^{-18}$
Model 6	-969.40	3	1944.82	151.08	$1.55e^{-33}$	$1.50e^{-33}$
Model 7	-979.63	3	1965.28	171.54	$5.61e^{-38}$	$5.42e^{-38}$
Model 2	-1007.03	2	2018.07	224.33	$1.93e^{-49}$	$1.87e^{-49}$
Model 3	-1019.38	2	2042.77	249.03	$8.37e^{-55}$	$8.09e^{-55}$

Table 2.5 Parameter weights calculated for predictors of moose browsing from the sum of the Akaike weights (∑wi) (Burnham and Anderson 2002) from each of the plausible models as determined by the Akaike Information Criterion (AICc).

Parameters	Sum of Akaike weights ($\sum w_i$)
Management Designation	0.96
Moose Density	0.96
Forage Species	0.96
Stand Type	0.96
Forage Height	0.96

Table 2.6 Parameter estimates, adjusted r-squared, and normality (Shapiro-Wilk test) of the residuals for the plausible models as determined from the AICc (Burnham and Anderson 2002) while analyzing moose browsing.

Model	**Model Testing**						**Shapiro-Wilk test for Normailty**	
	Parameters	**Estimates**	**Standard Errors**	**t value**	**p-value**	R^2_{adj}**	**W**	**p-value ***
Global Model	**Intercept**	-3.59	0.46	-7.47	<0.0001*	0.0012	0.71	<0.0001*
	Management Designation	0.57	0.17	3.27	0.001			
	Moose Density	-0.11	0.16	-0.69	0.48			
	Forage Species	0.17	0.074	2.30	0.021			
	Stand Types	0.50	0.054	9.17	<0.0001*			
	Height	0.011	0.0014	7.93	<0.0001*			

*** p-value from the Shapiro-Wilk test had an $\alpha = 0.05$**

**** The adjusted r-squared takes into account the variance, resulting in lower values than r-squared.**

Chapter 3. The influences of landscape processes, factors, and pattern on moose (*Alces americanus*) density in Newfoundland.

3.1 Abstract

Overabundant large herbivore populations are becoming more common globally and their dynamics are proving to be a challenge to effectively manage. I examined the influence of landscape scale processes and patterns on a high density moose (*Alces americanus* syn. *Alces alces*) population on Newfoundland, which was introduced in the early 1900s. I used linear regression models to test whether landscape processes and factors (i.e., natural disturbances, cut blocks, hunter success, and hunter access) explained the variance observed in moose density and compared the models using the information theoretic approach. Further, I quantified landscape pattern (composition and configuration) using landscape indices in GIS in survey blocks where moose were present in low and high densities. Model selection indicated that all landscape scale processes are important in explaining observed moose densities. Higher moose densities were found in high diversity landscapes of young balsam fir and mixedwood as well as older black spruce. This study highlights the complexity of population regulating mechanisms influencing moose density which should be incorporated into hunting quotas to achieve more effective management.

3.2 Introduction

Moose (*Alces americanus*) inhabit the boreal forest, at densities between 0.5 to 1.5 moose·km^{-2} in North America (Karns 1998). Moose densities are generally considered top-down regulated by natural predation (McLaren and Petersen 1994). Predation is primarily from wolves (*Canis lupus*), but black bear (*Ursus americana*) may also prey on calves (Messier 1994, McLaren and Petersen 1994). However, bottom-up regulation has been shown to play a role on Isle Royale (McLaren and Petersen 1994). Both top-down and bottom-up regulation result in part from landscape scale processes and factors. Natural disturbances such as fire, windfall, and insect disturbance have been shown to result in increased moose density by providing preferred early successional habitats (Crête 1989). Forest harvesting also provides moose with preferred habitats and is generally followed by an increase in moose density (Potvin et al. 2005). Silviculture activities also modify moose habitat. Moose appear to select pre-commercially thinned stands over unthinned stands because stems that have been thinned have larger twigs containing higher protein levels despite the presence of secondary compounds (Thompson et al. 1989). McLaren et al. (2000) showed that moose densities can increase in areas that have been pre-commercially thinned, but if coupled with good hunter access, moose densities can be reduced along with their browsing impacts. Hunting can lower moose density (Fergusson and Messier 1996); however, hunters are often dependent on forest resource roads to access their hunting area (Brown et al. 2000). Hunting is often used by wildlife managers as the main tool to control large herbivores populations (Brown et al. 2000).

The manipulation of landscape scale processes and factors by either natural or anthropogenic disturbances have altered many landscapes in such a way that large herbivore populations have increased significantly with subsequent decoupling of ecosystem processes (Pastor et al. 1988, McShea et al. 1997, Pastor and Danell 2003). Overabundant large herbivores populations are also a result of the extirpation of large predators such as wolves (Crête and Daigle 1999, Côté et al. 2004) as well as the introduction of large herbivores populations to non-native ranges (Côté et al. 2004, Gosse et al. 2011).

Landscape scale processes and factors can alter moose carrying capacity (Crête 1989, Messier 1994). These processes shape the mosaic of patches that constitute a landscape (Forman and Godron 1986, Urban et al. 1987), where a patch is defined as a community which varies from its neighbouring communities in either structure or composition (Wiens 1976, Forman and Godron 1981). Moose occupy a subset of available patches, often ones that are highly diversified in forages associated with edge habitats (Dussault et al. 2005).

The available habitat patches from which moose can select are largely dependent on landscape composition and configuration (O`Neill et al.1988). Landscape composition and configuration can be described using landscape indices (McGarigal and Marks 1995, Haines-Young and Chopping 1996) that quantify the extent and spatial configuration of patches within a landscape (McGarigal & Marks, 1995). These indices have been used to compare landscapes, identify significant temporal changes, and relate patterns to function (Turner 1989).

The first objective of this study was to determine if the moose densities on Newfoundland could be explained by landscape scale (i.e., the extent of the moose management areas (MMAs)) patterns and processes including hunter success, hunter access, cut blocks, and natural disturbances. My second objective was to explore if variation in moose density could be predicted with landscape indices.

It is still unknown how introduced large herbivore densities are influenced by landscape scale processes and factors occurring within their recently established range. In Newfoundland, two moose introductions occurred in 1878 and 1904 (Pimlott 1953) and were followed by the extirpation of wolves (*Canis lupus beothucus*) in the early 1930s (Allen and Barbour 1937). After the introduction, the moose population steadily began to increase, reaching its first peak in the 1960s (Pimlott 1959, Mercer and Manual 1974) then peaking again in the 1980s at approximately 217 000 individuals (Newfoundland and Labrador Wildlife Division, unpublished data). The population declined again to reach estimates of 117 000 individual, where the 2010 population remains today (Newfoundland and Labrador Wildlife Division, unpublished data).

factors could be managed with methods such as hunting quotas. Bottom-up regulation of an overabundant large herbivore population would require landscape processes and factors to be incorporated for effective management, such as targeting hunter effort where forest cuts and natural disturbances have occurred or preferred moose habitat is available on the landscape.

3.3 Study Area

I selected Moose Management Areas (MMAs) on the west and east coasts of Newfoundland, Canada (Figure 3.1 & Table A.7.1) which had varying. The MMAs on the west coast are located within the Western Newfoundland Forest, Northern Peninsula Forest, and the Northern Long Range Barrens Ecoregions. The MMAs on the east coast are within the Central Newfoundland Forest, North Shore Forest and Eastern Hyper-Oceanic Barrens Ecoregions.

The Northern Peninsula and Western Newfoundland Ecoregions are balsam fir (*Abies balsamea*) dominated, except at higher elevations where black spruce (*Picea mariana*) is dominant (Damman 1983). The Western Newfoundland Ecoregion has abundance of mountain maple (*Acer spicatum*), with red maple (*A. rubrum*) and trembling aspen (*Populous tremuloides*) as sub-dominants. The Northern Peninsula Ecoregion has few deciduous species present because their northern limits approach the southern border of the Ecoregion. Nevertheless, yew (*Taxus canadensis*) is found to be present in higher abundance than anywhere else on Newfoundland. The Long Range Barrens are characterized by ericaceous shrubs with scattered balsam fir and black spruce stands (Damman 1983).

The Central Newfoundland Forest Ecoregion has historically been disturbed by fire resulting in forests dominated by black spruce interspersed with stands of white birch (*Betula papyrifera*) and trembling aspen, albeit in lesser amounts (Damman 1983). North Shore Forests are described as being similar to the Central Newfoundland Forest but with a higher occurrence of white spruce (*Picea glauca*) and trembling aspen (Damman 1983). The Eastern Hyper-

Oceanic Barrens Ecoregion is characterized by elevations lower than 200 m dominated by balsam fir krummholz (Damman 1983).

3.4 Methods

Moose Density & Landscape Processes and Factors

Moose aerial surveys were conducted in MMAs across 5 Ecoregions between 2000-2009 (Newfoundland and Labrador Wildlife Division, unpublished data). Moose density was classified as low and high within each 4 km^2 survey block of the aerial survey within each MMA (Newfoundland and Labrador Wildlife Division 2000-2009). I calculated moose density as the total number of moose counted during the aerial surveys (Newfoundland and Labrador Wildlife Division 2000-2009, unpublished data) divided by the total terrestrial area of each MMA (Figure A.6.2). I calculated the area (km^2) where landscape scale processes and factors (e.g. natural disturbances, cut blocks, and silviculture) occurred in the year of the aerial survey to match temporal extent to account for the spatial variation of the landscape as I did not have subsequent aerial surveys (moose surveys are typically carried out once every 10 years within each MMA in Newfoundland) and cannot account for variation in moose densities over several years.

I determined hunter success from the average success of the four licence types (male-only, female-only, either-sex, and non-resident) of the fall hunter surveys calculated by the Wildlife Division (Newfoundland and Labrador Wildlife Division, unpublished data) (Figure A.6.3). For my study purposes, licence type was not considered important to the analysis because I was interested in the number of individual moose removed from the MMAs.

I used a Geographic Information Systems (GIS, ArcGIS (ESRI v. 9.3) to quantify hunter access, forest cuts, and natural disturbances. I extracted the necessary data for these analyses from the 2006 Forest Resource Inventory Data (FRI) (Newfoundland and Labrador Forestry Division, unpublished data).

I quantified hunter access based on roads developed within the MMAs as follows. Roads were determined by merging main roads (the Trans-Canada Highway and small main roads in communities) from the topographic layers of CANVEC data available online through Natural Resources Canada with logging roads from FRI (Forestry Division 2006, Government of Newfoundland and Labrador). I buffered all of the roads by 2 km on each side as hunters have been shown to travel on average small distances to retrieve their kill (Courtois and Beaumont 1999; Mercer and McLaren 2002). I calculated the area covered by this buffer in km^2 and considered this area as accessible to hunters. I computed the total area for the MMAs in km^2 from their boundaries. I quantified the area covered by waterbodies as delimited by the FRI including all lakes, ponds, and rivers and then subtracted from the total area of the MMA to give the terrestrial area of each MMA. I then divided the hunter accessible area by the terrestrial area of each MMA to give the percentage of the MMA that had hunter access (Figure A.6.3-A.6.5).

I determined the cut blocks from forestry activities using the FRI (Forestry Division 2006, Government of Newfoundland and Labrador). I computed the total area cut (km^2) in each MMA for the year(s) concurring with the moose aerial survey. I divided the cut area by the terrestrial area of each MMA for the purposes of comparison between MMAs. Silviculture activities are categorized in the FRI as commercial thinning, plantation, pre-commercial thinning, and diameter limited thinning. I determined the total area of silviculture (km^2) in each MMA for each year concurring with the moose aerial survey. Silviculture activities have been shown to influence moose occupancy of an area because of the increase of available browse that results. However, the spatial extent of silviculture activities was too small to be captured at the scale of the MMA and it was dropped from the analysis.

Natural disturbances are described in the FRI (Forestry Division 2006, Government of Newfoundland and Labrador) and include: fire, wind, miscellaneous, vegetation, and insect mortality. The summed total area of all natural disturbances (km^2) in each MMA was determined for each year concurring with the moose aerial survey. I divided the area by the terrestrial area of each MMA for the purposes of comparison among MMAs.

To test the relationship between landscape processes and factors and moose density, I created generalized linear regression models (binomial distribution). Candidate models were derived using the landscape scale processes and factors (forest cuts, hunter access, hunter success, and natural disturbances) described in the introduction and hypothesized to influence moose browsing patterns (Table 3.1.a). To address my third hypothesis, I developed models (3 and 4) that include factors that are top-down regulators (i.e., hunter access and hunter success). I developed other models (2 and 5) that included bottom-up regulation factors (i.e., forest cuts and natural disturbances). Finally, models 6-11 are a combination of bottom-up and top-down regulation factors (i.e., forest cuts, hunter access, hunter success, and natural disturbances). Model selection was carried out to test these multiple competing hypothesis resulting from the complexity of the interactions of the landscape scale processes and factors (sensu Chamberlin 1965) using the information-theoretic (IT) approach (Burnham and Anderson 2002). I calculated log-likelihood, parameters (K), AICc values, Akaike weights (w_i), and delta AICc (Δ_i) according to the methods outlined in Burnham and Anderson (2002). I determined plausibility of the models using Δ_i values. Models with $\Delta_i < 2$ are considered highly plausible, models with Δ_i between 2- 4 are plausible and any model with Δ_i larger than 4 is not very plausible (Burnham and Anderson 2002). I computed parameter weights ($\sum w_i$) of the plausible models where each parameter was present) to determine the weight of each parameter across all plausible models. I calculated parameter estimates with standard errors for the plausible models to determine how these parameters and moose densities interact. The models were verified for normality using the Shapiro-Wilk Test (α=0.05) and were tested for fit using the adjusted r-squared which takes into account the variance resulting in lower values than r-squared (Crawley 1997).

Landscape Patterns in Areas of Low and High Moose Density

I classified patch type (described below) in the MMAs through the FRI (Forestry Division 2006, Government of Newfoundland and Labrador). I ran a script [written by C. Marks (NLWD) in Python (CWI (Guido) v. 2.4.1)] on the FRI to produce a data layer of dominant stand type classified by 20 year age groups for balsam fir, black spruce, hardwood, mixedwood as well as other classifications that included: Moose density was considered as high or low according to the North American density range of 0.5 to 1.5 moose·km^{-2} (Karns 1998). The median of this range, 1 moose·km^{-2}, was considered the mid-point so densities below 1 moose·km^{-2} was classified as low and densities higher than 1 moose·km^{-2} was classified as high. A frequency histogram of the moose densities (moose·km^{-2} of forest and scrub) in the 10 MMAs further support this mid-point break for the classification of low and high moose density (Figure A.6.1).

bogs and barrens, disturbed areas, not sufficiently stocked areas, scrub, water, and other (e.g. roads, transmission lines, etc.).

To determine if landscape pattern (i.e., composition and configuration) varied where moose were found in low and high moose density, I analyzed the landscape indices by low and high moose density for all available habitat types in the MMAs with a series one-way analysis of variance (ANOVAs) with an α = 0.05 in R (R base package v. 12.0; R Development Core Team 2012). Landscape indices were the response variables (patch area, contrast-weighted edge density, and Shannon's Diversity Index) and moose density was set as the explanatory variable. I quantified landscape composition and configuration within the each surveyed 4 km^2 blocks of each MMA using Fragstats (McGarigal et al. 2002; v. 3.3) with the 8-cell patch neighbour rule. Specifically, I used Fragstats to calculate patch area for each individual patch at the patch-level, as well as contrast-weighted edge density and Shannon's Diversity Index at the landscape level. Patch area calculates the area of each patch type in the landscape mosaic of each MMA (McGarigal and Marks 1994). Patch type is classified by 20 year age groups for balsam fir, black spruce, hardwood, mixedwood as well as other classifications that included: bogs and barrens, disturbed areas, not sufficiently stocked areas, scrub, water, and other (e.g. roads, transmission lines, etc.). I divided these values by the total area covered by all the survey blocks to standardize across MMAs. Contrasted-weighted edge density is the sum of the edge length between different patches that are adjacent divided by the landscape area (survey block area) (McGarigal and Marks 1994) and was selected over the edge density because not all edges are equally important to moose. Weighted values were developed reflecting moose habitat preferences (Table A.8.1). Shannon's Diversity Index is described as the sum of the proportion of patch area to total area multiplied by that proportion (McGarigal and Marks 1994).

3.5 Results

Explaining Moose Density

Model selection results suggest that all the models were plausible explanations of the moose density as the delta AICc (Δ_i) values were all between 2 - 4 (Table 3.1b). Natural disturbances had the highest parameter weight; but overall, the parameter weights were low (Table 3.2). Parameter estimates suggest a negative association between moose density and hunter success, hunter access, and natural disturbances, but a positive association with forest cuts (Table 3.3). All models fit a normal distribution (Table 3.3). The parameter estimates values were small and there were generally low Akaike and parameter weights suggesting that moose density is influenced by a large number of landscape scale processes and factors, including factors not in the candidate models, which reflects the complexity of the system.

Landscape Patterns in Areas of Low and High Moose Density

At the patch-level, moose densities varied within the survey blocks (Table 3.4; Figure 3.2). Overall higher moose densities were recorded in younger habitats (1-80 years) than older habitats (81-161$^+$ years). Also, higher moose densities occurred in balsam fir habitats across the five age classes, as well as older age classes of black spruce. High moose densities occurred in habitats of balsam fir age classes of 21-40 years, 41-60 years, and 81-161$^+$ years but moose density did not differ in habitats of balsam fir age classes of 1-20 years and 61-80 years. Moose were located in most age classes of black spruce habitats. In black spruce habitats of age classes of 1-20 years, 41-60 years, 61-80 years, and 81-161$^+$ years, there were high moose densities. There was no difference in moose density in black spruce habitats of 21-40 years. Overall, moose densities were low in hardwood habitats, but older habitats had higher moose density than younger habitats. There were no moose (1-20 years) or low densities (21-40 years) found in hardwood habitats less than 40 years old. This is most likely due to the very low abundance of this habitat at the landscape level rather than moose avoiding these habitats (Table A.1.2). Hardwood habitats of 41-60 years and 61-80 years did not differ in moose density. The oldest hardwood habitats (81-161+ years) had higher moose densities than other hardwood habitats. Moose densities increased with increasing ages of mixedwood habitats. Highest moose density was in mixedwood habitats of 41-60 years, 61-80 years, and 81-161$^+$ years. There was no difference in moose densities in mixedwood habitats of 1-40 years. There was no difference in moose densities in habitats of bog and barren. Overall there was a higher moose density in habitats of disturbed areas, not stocked areas, scrub, water, and other.

At the landscape level, high moose densities were found within landscapes of higher diversity ($F_{1,413}$=6.05; p=0.01) while moose density did not vary with the contrast-weighted edge density ($F_{1,413}$=2.98; p=0.08).

3.6 Discussion

A complex interaction of landscape scale processes and factors accounted for the variation observed in moose density in Newfoundland. In contrast to my first hypothesis, there were several factors that explained the observed moose density, including both top-down and bottom-up regulators, rather than either top-down or bottom-up regulation. My second hypothesis was supported in that moose appeared to prefer younger habitat of mixedwood, hardwood, balsam fir as well as older black spruce habitat. Further to my second hypothesis, moose occupying landscapes with higher diversity was supported, but I did not find support that high moose density would also occur with high contrast-weighed edge density.

Moose Density and Landscape Processes and Factors

Moose density was explained by all of the landscape scale processes and factors measured (i.e., forest cuts, natural disturbances, hunter access, and hunter success) suggesting that these could be used as predictors of moose densities at a larger spatial extent. However, there are likely other factors on the landscape influencing moose density that I did not include in my study (e.g., soil composition and snowfall), since the parameter estimates and weights in this analysis were low. Forest cuts had a positive association with moose density. There was a negative association between moose density, natural disturbances, hunter success, and hunter access. The negative association between moose density and natural disturbances was not expected. This may be a result of the recent nature of these disturbances, as they occurred the same year as the moose aerial survey, such that the patches had not yet reached the preferred age for good moose habitat. Natural disturbances also may have occurred at a finer scale than my study's landscape scale. Forest cuts have been shown to influence large herbivore densities, increasing their presence and densities across their North American range by leading to preferred early successional stands (Collins and Schwartz 1998, Eason 1989, Sinclair 1997, Fuller and Gill 2001, Potvin et al. 2005). Forest cuts can further influence large herbivore densities by providing hunters with access to hunting sites.

Hunter access, which is associated with the presence of forestry roads, was shown to a have negative association to the observed variance in moose density. Hunter success had a negative or a low positive association with moose density. Hunter access and hunter success are most likely correlated in terms of their influence on moose density. Elsewhere, hunter success has been attributed to higher hunter access which in turn results in lower moose densities (e.g., Newfoundland (Fergusson et al. 1989, McLaren and Mercer 2005); Québec (Courtois and Beaumont 1999); and Ontario (Eason 1989)).

Models which included the predictors of hunting activities, forest harvest activities and natural disturbances explained the variance of moose density on the landscape. In particular, hunting success and natural disturbances as well as hunter success and forest cuts explained some of the observed variation in moose density. This implies that the occurrence (or lack of) a natural disturbance or forest harvest can affect hunter success and its impact on moose density. Other studies have shown similar interactions. Moose harvest rate was highest in recent cut blocks in Québec (Courtois and Beaumont 1999) and Ontario (Eason 1989). Moose density varied in areas in Ontario where both hunter access and landscape disturbances occurred (Rempel et al. 1997). Rempel et al. (1997) also found that moose density did not necessarily always increase in forest cuts as there is high hunter access attributed to forestry resource roads.

McLaren and Mercer (2005) found that hunter kill density can result in lower moose densities but is highly dependent on hunter access on Newfoundland.

There is evidence that populations of large herbivores can be influenced by a combination of landscape processes and factors that are regulated by both top-down and bottom-up factors. This seems to be especially true of low diversity ecosystem such as boreal forests (Sinclair 2003). For example, Vucetich and Peterson (2004) found that the variation in moose population growth was attributed mostly to bottom-up and abiotic factors rather than top-down factors on Isle Royale. In other cases, large mammalian herbivores have grown more numerous than their predators (i.e., overabundance) and have become regulated by resources (i.e., bottom-up regulation; Sinclair 2003). In Québec, the overabundant white-tailed deer (*Odocoileus virginianus*) population have no predators and showed bottom-up regulation in a non-linear relationship between their population densities with forest regeneration and forest cuts (Tremblay et al. 2007). Some large herbivores, such as caribou (*Rangifer tarandus*) in North America and Eurasia, Wildebeest (*Connochaetes taurinus*) in Africa, and American Bison (*Bison bison*), escape top-down regulation from predation by migration, leading to bottom-up regulation via food availability (Fryxell and Sinclair 1988). The regulation, either top-down, bottom-up, or a combination of both, may vary with the characteristic of the ecosystem and the species in question (Sinclair 2003).

Landscape Patterns in Areas of Low and High Moose Density

It is apparent that moose densities vary with landscape composition and configuration at both the patch and landscape levels. As expected, moose densities are generally higher in habitats with a relatively higher abundance of preferred forage species (Telfer 1978, Senft et al. 1987, Schiwart et al. 2003). There were high moose densities in older black spruce habitats.

Although moose do not forage on black spruce, they have been shown to select older black spruce and other coniferous habitats as these provide thermal cover during the winter (Renecker and Hudson 1986); however, moose dependency on these black spruce stands for winter survival still remains to be validated (Balsom et al. 1996). Moose on Newfoundland also selected landscapes with higher habitat diversity. Maier et al. (2005) also found higher moose densities in diverse habitats in interior Alaska. Other studies have shown that edge habitat provides a higher selection of forage and influenced moose habitat selection (Crête 1989, Courtois and Beaumont 2002). My results suggested that moose density did not vary with edge density. This non-significant result could be explained by Newfoundland's landscape configuration which is naturally very patchy. Therefore, edge density could be high in all the MMAs and hence not influence moose habitat selection.

Management implications

To achieve better management of large herbivore populations, McShea et al. (1997) and Côté et al. (2004) suggest enhanced communication between wildlife and forest managers. Wildlife and forests have often been managed as separate entities but they are linked and influence each other within the ecosystem (Côté et al. 2004). Fergusson et al. (1989) and more recently McLaren and Mercer (2005) acknowledge that hunting quotas have the potential to influence moose densities in Newfoundland but other factors (e.g. habitat composition and snowfall) besides hunter return data should be included in quota setting to enhance efficiency of moose population management. Habitat composition as defined by landscape patterns (composition and configuration) could be used to predict higher moose density areas and targeted during the determination of management area quotas. Fryxell et al. (2010) stress the importance of re-assessing and monitoring harvest effort and quotas regularly for long-term management of resources. This study highlights the complexity of population regulating mechanisms, influencing moose density which should be incorporated into hunting quotas to achieve more effective management. Landscape scale processes and factors such as forest cuts, natural disturbances, hunter access, hunter success, and available habitats could be incorporated by wildlife managers when determining management area quotas.

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Figure 3.1 Moose Management Areas on Newfoundland, Canada (shown in inset map) where the influences of landscape scale processes and factors, composition, and configuration on moose density was analyzed.

Table 3.1 a) Competing models to explain landscape scale processes and factors influences on moose density. These were run via a General Linear Model in R (v. 2.12.0) and examined via an AIC$_c$ **b)** Model selection for landscape scale processes and factors, and moose density using AICc (n = 10; Burnham and Anderson 2002).

a)

Global Model	**Moose Density = forest cuts + hunter access +hunter success + natural disturbances**
Model 2	moose density = forest cuts
Model 3	moose density = hunter access
Model 4	moose density = hunter success
Model 5	moose density = natural disturbances
Model 6	moose density = hunter success + forest cuts
Model 7	moose density = hunter success + hunter access
Model 8	moose density = hunter success + hunter access + hunter success*hunter access
Model 9	moose density = hunter success + forest cuts + hunter success*forest cuts
Model 10	moose density = hunter success + natural disturbances
Model 11	moose density = forest cuts + natural disturbances

b)

Models	**Log-Likelihood**	**K**	**AICc**	Δ_i	**exp**	**weights**
Model 5	-1.176	2	2.353	0	1	0.1046
Model 10	-1.180	3	2.360	0.00758	0.9962	0.10426
Model 8	-1.180	4	2.361	0.00794	0.9960	0. 10424
Model 2	-1.182	2	2.364	0.0109	0.9945	0. 10409
Model 11	-1.182	3	2.365	0.0118	0.9941	0. 10404
Model 6	-1.189	3	2.379	0.0256	0.9872	0. 1033
Model 9	-1.199	4	2.399	0.0460	0.9772	0. 1022
Global Model	-1.218	5	2.437	0.0843	0.9587	0. 1003
Model 3	-1.755	2	3.511	1.158	0.5604	0.0586
Model 4	-1.783	2	3.567	1.213	0.5450	0.0570
Model 7	-1.783	3	3.567	1.213	0.5450	0.0570

Table 3.2 Parameter weights calculated for predictors of moose density from the sum of the Akaike weights (∑wi) (Burnham and Anderson 2002) from each of the models as determined by the Akaike Information Criterion (AIC$_c$).

Parameters	**Sum of Akaike weights (∑w$_i$)**
Forest cuts	0.51
Hunter access	0.32
Hunter success	0.62
Natural disturbances	1.45

Table 3.3 Parameter estimates, adjusted r-squared, and normality (Shapiro-Wilk test) of the residuals for the plausible models as determined from the AIC$_c$ (Burnham and Anderson 2002) while analyzing moose density.

Model	**Model Testing**						**Shapiro-Wilk Test for Normailty**	
	Parameters	**Estimates**	**Standard Error**	**t value**	**p-value**	**R^2_{adj} ****	**W**	**p-value ***
5	Intercept	-2.01	0.30	-6.69	<0.0001	-0.12	0.98	0.97
	Natural Disturbances	-0.025	0.048	-0.51	0.61			
10	Intercept	-3.44	1.64	-2.09	0.074	-0.28	0.97	0.90
	Hunter Success	0.020	0.023	0.90	0.39			
	Natural Disturbances	-0.030	0.045	-0.66	0.52			
8	Intercept	0.53	6.13	0.087	0.93	-0.49	0.97	0.94
	Hunter Success	-0.043	0.099	-0.44	0.67			
	Hunter Access	-0.053	0.080	-0.66	0.52			
	Interaction Term	0.00085	0.00012	0.66	0.53			
2	Intercept	-2.36	0.36	-6.45	<0.0001	-0.12	0.95	0.75
	Forest Cuts	0.04	0.035	1.25	0.24			
11	Intercept	-2.30	0.42	-5.38	<0.0001	-0.28	0.95	0.73
	Forest Cuts	0.041	0.038	1.07	0.31			
	Natural Disturbances	-0.014	0.049	-0.29	0.78			
6	Intercept	-4.10	1.59	-2.57	0.036	-0.27	0.97	0.92
	Hunter Success	0.024	0.021	1.13	0.29			
	Forest Cuts	0.051	0.033	1.53	0.16			
9	Intercept	-1.37	2.45	-0.56	0.59	-0.47	0.90	0.22
	Hunter Success	-0.012	0.033	-0.36	0.73			
	Forest Cuts	-0.025	0.24	-1.05	0.33			
	Interaction Term	0.0041	0.0031	1.28	0.24			

Global Model	Intercept	-3.89	1.82	-2.13	0.08	-0.78	0.96	0.80
	Hunter Success	0.027	0.025	1.08	0.32			
	Hunter Access	-0.00056	0.014	-0.39	0.70			
	Natural Disturbances	-0.012	0.053	-0.22	0.82			
	Forest Cuts	0.054	0.042	1.27	0.26			
3	Intercept	-2.20	0.87	-2.52	0.035	-0.12	0.96	0.85
	Hunter Access	0.00018	0.011	0.15	0.88			
4	Intercept	-3.39	1.66	-2.04	0.075	-0.12	0.98	0.99
	Hunter Success	0.018	0.023	0.81	0.43			
7	Intercept	-3.36	1.82	-1.85	0.10	-0.28	0.98	0.99
	Hunter Success	0.0018	0.025	0.74	0.48			
	Hunter Access	-0.000043	0.011	-0.004	0.99			

*** p-value from the Shapiro-Wilk test had an $\alpha = 0.05$**

**** The adjusted r-squared takes into account the variance, resulting in lower values than r-squared.**

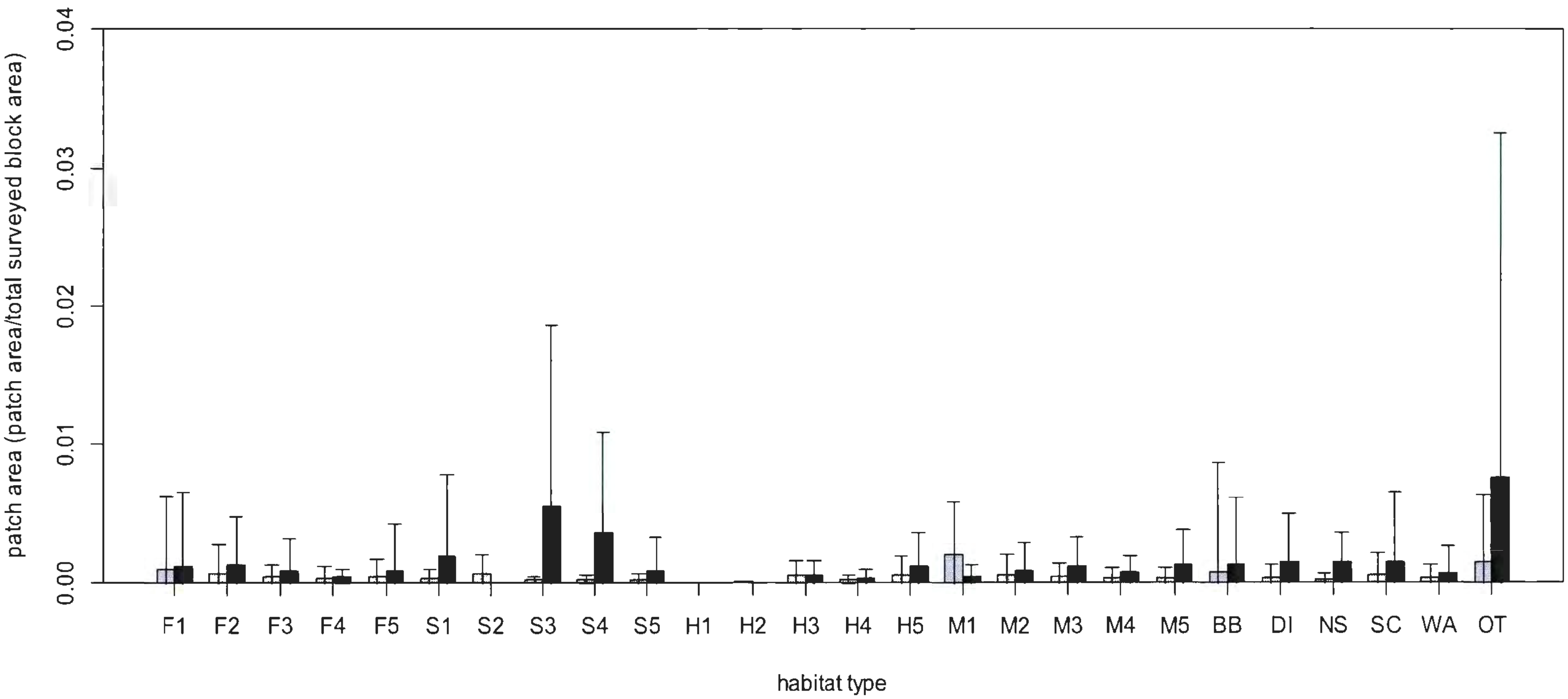

Figure 3.2 Mean and standard deviations of patch area at low (grey bars) and high (black bars) moose densities (low: < 0.5moose·km^{-2}; high: >1.5moose·km^{-2}) across the landscape. Forest patch areas are indicated by a combination of letter (F: balsam fir; S: black spruce; H: hardwood; M: mixedwood; BB: bog and barren; DI: disturbed; NS: not stocked; SC: scrub; WA: water; OT: other) and number (1: age class 1-20 years; 2: age class 21-40 years; 3: age class 41-60 years; 4: age class 61-80 years; 5: age class 81-161^{+} years).

Table 3.4 ANOVA analysis of moose density (low: <1 moose·km^{-2}; high:>1 moose·km^{-2}) in available patches (ha) at the patch-level within aerial survey blocks.

Patch Area (Dominant Stand Type by Age Class in 2006)	Factor/ Residuals	Df	Sum of Squares	Mean Sum of Squares	F-value	P-value
Balsam Fir 1-20	Moose Density Residuals	1 378	0.0000053 0.010	$5.29\ e^{-6}$ $2.85\ e^{-5}$	0.18	0.66
Balsam Fir 21-40	Moose Density Residuals	1 421	$4.09\ e^{-5}$ $2.85\ e^{-3}$	$4.09\ e^{-5}$ $6.77\ e^{-6}$	6.04	0.014*
Balsam Fir 41-60	Moose Density Residuals	1 584	0.000027 0.0012	$2.69e^{-5}$ $2.092\ e^{-6}$	12.90	0.00035*
Balsam Fir 61-80	Moose Density Residuals	1 426	$6.18\ e^{-7}$ $2.41\ e^{-4}$	$6.18\ e^{-7}$ $5.67\ e^{-7}$	1.088	0.29
Balsam Fir 81-161^{+}	Moose Density Residuals	1 3259	0.00011 0.016	$1.13\ e^{-4}$ $4.99\ e^{-6}$	22.60	<0.0001*
Black Spruce 1-20	Moose Density Residuals	1 365	0.00017 0.0032	0.00017 0.0000089	20.162	<0.0001*
Black Spruce 21-40	Moose Density Residuals	1 153	$1.98\ e^{-6}$ $2.96\ e^{-4}$	$1.98\ e^{-6}$ $1.94\ e^{-6}$	1.024	0.31
Black Spruce 41-60	Moose Density Residuals	1 188	0.00044 0.0027	0.00044 0.000014	30.23	<0.0001*
Black Spruce 61-80	Moose Density Residuals	1 224	0.00049 0.0029	0.00049 0.000013	36.9	<0.0001*
Black Spruce 81-161^{+}	Moose Density Residuals	1 1614	0.000080 0.0020	$8.098\ e^{-5}$ $1.24\ e^{-6}$	64.86	<0.0001*
Hardwood 1-20	Moose Density Residuals	N/A	N/A	N/A	N/A	N/A
Hardwood 21-40	Moose Density Residuals	1 18	$7.35\ e^{-9}$ $2.17\ e^{-8}$	$7.35\ e^{-9}$ $1.21\ e^{-9}$	6.079	0.023*
Hardwood 41-60	Moose Density Residuals	1 42	$1.10\ e^{-8}$ $4.86\ e^{-5}$	$1.09\ e^{-9}$ $1.15\ e^{-6}$	0.0095	0.923
Hardwood 61-80	Moose Density Residuals	1 35	$1.44\ e^{-7}$ $7.27\ e^{-6}$	$1.44\ e^{-7}$ $2.07\ e^{-7}$	0.69	0.40
Hardwood 81-161^{+}	Moose Density Residuals	1 165	0.0000099 0.00040	$9.98\ e^{-6}$ $2.44\ e^{-6}$	4.085	0.044*
Mixedwood 1-20	Moose Density Residuals	1 29	$1.74\ e^{-5}$ $2.77\ e^{-4}$	$1.74\ e^{-5}$ $9.58\ e^{-6}$	1.81	0.18
Mixedwood 21-40	Moose Density Residuals	1 225	$4.93\ e^{-6}$ $6.33\ e^{-4}$	$4.92\ e^{-6}$ $2.81\ e^{-6}$	1.74	0.18
Mixedwood 41-60	Moose Density Residuals	1 491	0.000048 0.00086	$4.83\ e^{-5}$ $1.77\ e^{-6}$	27.32	<0.0001*

Mixedwood 61-80	Moose Density	1	$5.31\ e^{-6}$	$5.13\ e^{-6}$	6.01	0.015
	Residuals	155	$1.36\ e^{-4}$	$8.83\ e^{-7}$		
Mixedwood 81-161^{+}	Moose Density	1	0.00011	$1.14\ e^{-4}$	54.26	<0.0001*
	Residuals	674	0.0014	$2.11\ e^{-6}$		
Bog and Barren	Moose Density	1	0.00015	$1.56\ e^{-4}$	3.00	0.08
	Residuals	3048	0.15	$5.19\ e^{-5}$		
Disturbed	Moose Density	1	0.00020	$2.077\ e^{-4}$	51.64	<0.0001*
	Residuals	902	0.0036	$4.022\ e^{-6}$		
Not Stocked	Moose Density	1	$6.65\ e^{-5}$	$6.65\ e^{-5}$	66.55	<0.0001*
	Residuals	261	$2.60\ e^{-4}$	$9.99\ e^{-7}$		
Scrub	Moose Density	1	0.00065	$6.53\ e^{-4}$	81.47	<0.0001*
	Residuals	4379	0.035	$8.020\ e^{-6}$		
Water	Moose Density	1	0.000048	$4.82\ e^{-5}$	27.89	<0.0001*
	Residuals	2902	0.0050	$173\ e^{-6}$		
Other	Moose Density	1	0.0021	0.0021	11.36	0.00086*
	Residuals	283	0.054	0.00019		

[*] p-value that are significant within 95% confidence intervals ($\alpha = 0.05$).

[**] N/A there were no moose found in these habitat patches

Chapter 4. Summary and Conclusions

4.1 Moose Browsing Patterns and Forest Regeneration

Moose (*Alces americanus*) forage according to relative abundance of browse (Telfer 1978, Osko et al. 2004) and habitat availability (Poole and Stuart-Smith 2006, Lundmark and Ball 2008), a common behaviour observed for most large herbivores (Senft et al. 1987). This behaviour can lead to altered forest composition and regeneration when large herbivores such as moose are abundant or overabundant (Brandner et al. 1990, McInnes et al. 1992). I evaluated the browsing patterns of a high density moose population on Newfoundland, Canada. The results validate the widely held belief that introduced moose have the potential to alter forest regeneration (Chapter 2). I observed low balsam fir seedling density across moose management areas and national parks, but this did not differ in areas with different moose densities (low and high) or management strategies (protected areas and moose management areas). On Newfoundland, moose preferred deciduous browse over coniferous browse, consistent with previous findings in other locations (Peterson 1955, Chamberlin 1972, Dodds 1960, Krefting 1974, Wiens 1976, Hundertmarkt et al. 1990). This exemplifies the potential of moose to alter forest regeneration in areas across Newfoundland, regardless of different moose density and management designation. These results agree with prior studies on Newfoundland (Bergerud and Manuel 1968, Thompson and Curran 1993, Connor et al. 2000, McLaren et al. 2009, Gosse et al. 2011), other areas experiencing high moose densities (Pastor et al. 1988, Risenhoover and Maass 1987, Brandner et al. 1990, McInnes et al. 1992), and observations of other large herbivores at high densities such as white-tailed deer (*Odocoileus virginianus*; Tremblay et al. 2007, Ruzicka et al. 2010, Tanentzap et al. 2011), black-tailed deer (*Odocoileus hemionus*; Martin et al. 2010), and elk (*Cervus elaphus*; Bee et al. 2010, Kamler et al. 2010, Mysterud et al. 2010). However, past browsing events across Newfoundland during the two peaks and declines of the moose population may have helped shape current browsing patterns (McLaren et al. 2009). Reduced heights and abundance of balsam fir (*Abies balsamea*) and deciduous saplings as a result of moose browsing were still noticeable nearly fifteen years later (McLaren et al. 2009). On Newfoundland, it appears that the regenerating balsam fir stands may shift dominance to non-preferred species such as black spruce (*Picea mariana*) (Thompson and Curran 1993, Connor et al. 2000). Questions remain on how this sustained browsing on forest regeneration will influence future forest succession as well as whether forest regeneration can be returned to its pre-moose state without restoration efforts (Kamler et al. 2010, Gosse et al. 2011).

Moose browsing on Newfoundland appears to be influenced by interactions between a number of landscape scale processes and factors. My thesis suggests that a combination of interactions between management designation (protected and moose management areas), moose density (low and high), available habitats, forage species, and forage sapling height explained the observed variance in moose browsing. Interactions between these various landscape processes and factors may help explain why there is more browsing damage in the eastern national parks and moose management areas where moose have always been at lower densities compared to the western national park and moose management area. Available habitats for moose may also play a role as the east coast of the island is mainly black spruce dominated (except for coastal areas in TNNP which are balsam fir dominated), but where the west coast is balsam fir dominated (Damman 1988). Thus, taking into consideration browsing pressure and forest composition, it would take a lower moose browsing pressure to observe damages or influences in the east compared to the west coast.

4.2 Moose Density and Landscape Patterns

Moose are known to be mainly top-down regulated with some bottom-up regulation (McLaren and Petersen 1994). My findings suggest that a combination of landscape scale processes and factors that are top-down and bottom-up regulators influence moose densities on Newfoundland (Chapter 3). At a landscape extent, available habitats vary in their potential to attract moose (Telfer 1978, Osko et al. 2004, Poole and Stuart-Smith 2006, Lundmark and Ball 2008). Moose densities varied at both the patch and landscape levels. Higher moose densities were found in habitats of young balsam fir, mixedwood, and disturbed patches and older black spruce. There was higher moose density in diverse landscapes compared to more homogenous landscapes. However, moose density did not vary with edge density. This selectivity may lead to some habitats being subjected to higher densities that will result in relatively greater browsing pressure, leading to a decrease in the abundance of preferred browse (Risenhoover and Maass 1987, Thompson and Curran 1993, Connor 2000).

4.3 Implications for Moose Management

On Newfoundland, moose browsing and densities, along with their influences from landscape processes and factors, are linked and share a dynamic relationship simply described as complicated. Bergerud and Manuel (1968, p. 744) stated that "it is doubtful that an equilibrium can be maintained between a moderate moose density and a quantity of highly palatable diversified winter moose foods in Newfoundland". This is supported with the continued evidence of alterations to forest composition on Newfoundland (Bergerud and Manuel 1968, Thompson and Curran 1993, Connor 2000, McLaren et al. 2004). The target density for Newfoundland as a whole of 2 moose·km^2 has been reached through hunting; but a wide range of densities of are present within MMAs. This large variation (0.25-14 moose·km^{-2}; NLWD, unpublished data) in moose density appears to be problematic when observing impacts on the landscape. Moose densities on Newfoundland are consistently above the 1.3-1.4 moose·km^{-2} threshold, especially in the west, where hunters cannot regulate the population in a top-down manner (Messier 1994). There are no epidemic diseases to cause a population decline to a density where hunters can influence the moose population (Ferguson et al.1989, Ferguson and Messier 1996), so one would assume that moose are currently regulated mainly via available forage (Messier 1994, Osko et al. 2004). The altered forest regeneration patterns due to moose browsing I observed are similar to those observed by others (Bergerud and Manuel 1968, Thompson and Curran 1993, Connor 2000, and McLaren et al. 2004). Interestingly, moose density still remains fairly high despite evidence of decreased abundance of browse and habitat degradation (Thompson and Curran 1993, Connor 2000).

When organisms exert pressure on resources it can lead to regime shifts in the ecosystem (Scheffer and Carpenter 2003). Hobbs (1996) suggests that large herbivores can influence regime shifts between alternate stable states which vary according to browsing intensity, evolutionary history of the ecosystem, and the likelihood of re-growth. Is Newfoundland, or portions of it, in an alternate stable state initiated by moose? If it is, it may remain in this state until some environmental impact on the ecosystem is large enough to shift back to equilibrium or another stable state depending on the ecosystem dynamics (Scheffer et al. 2001). For example, a study on an introduced overabundant population of white-tailed deer on Anticosti Island, Québec, Canada showed that if this high population was maintained for only a few years following a disturbance, it has the potential to shift forest regeneration cycles of balsam fir stands (Tremblay et al. 2007). New Zealand`s introduced herbivore populations of Australian Brushtail possums (*Trichosurus vulpecula*), red deer (*C. e. scoticus*), and goats (*Capra hircus*) have exerted browsing pressures resulting in areas susceptible to disturbances with low plant biomass and diversity which are headed towards alternate stable states (Nugent et al. 2001). The alternate stable state in New Zealand does not show evidence of an irreversible stable state. If herbivore removal is to occur where an ecosystem has been changed from browsing pressures, there will be a transitional plant community of browse resistant species in the short-term but the removed browsing species are believed to be able to gradually return to former levels of abundance (Nugent et al. 2001).

Alterations to forest regeneration may result from moose as well as influences from a combination of other species. Studies in Gros Morne and Terra Nova National Parks (Gosse et al. 2011) demonstrated that balsam fir is affected by herbivory at all growth stages. For example, red squirrels predated female cones, seedlings were exposed to slug and rodent predation once emerged, and moose browsed saplings during growth to reach the canopy (Gosse et al. 2011). If alterations in the trajectory of forest regeneration persist, the consequences could be far reaching in terms of future forest succession within the island ecosystem. The altered forest state could impact a number of organisms including passerines, epiphytic lichens, and beavers (McLaren et al. 2004). The threatened Newfoundland Marten (*Martes americana atrata*) which depends on mature forests could also be influenced as moose reduce forests to an earlier successional state (Thompson and Curran 1995, Hearn et al. 2010). If moose can influence several other organisms directly or indirectly through changes to landscape scale processes and factors, it would follow that moose could also be influenced by a number of landscape scale processes and factors. My findings support this as factors which were both top-down and bottom-up regulators helped explain the observed variance of moose browsing and density on Newfoundland. However, the overall explained variance for moose density was low; thus, there are more factors that need to be accounted for. Soil composition could be examined to see if past browsing trends have led to changes, as has been observed elsewhere (Pastor et al. 1988, McInnes et al. 1992). With the sustained overabundant population in a nearly predator free system and adverse browsing impacts on forest regeneration in Newfoundland, it may be important to determine the possibility of a non-linear relationship between herbivore densities and forest regeneration dynamics. Other herbivore populations that have persisted in being overabundant despite habitat degradation from browsing such as white-tailed deer have shown non-linear relationships between herbivore density, forest regeneration dynamics, and forest harvests (Tremblay et al. 2007). It may also be important to monitor snowfall trends. If climate continues to change as predicted and becomes warmer, it may result in lower snowfall which would give moose access to browse normally covered during winter (Telfer and Kelsall 1984, Ballard et al. 1991, McCracken & al. 1997, Poole and Stuart-Smith 2006, Stephenson et al. 2006) leading to increase moose browsing pressure and impacts on forest regeneration dynamics.

My findings also suggest that moose browsing has the potential to influence forest regeneration on Newfoundland. Areas experiencing heavy moose browsing should be targeted for a reduction of moose on the landscape, especially in areas where hunter access is limited. These areas will likely need restoration efforts such as planting native seeds of the decreased forage species to replenish the seed banks accompanying moose population reduction to achieve expected forest dynamics (Gosse et al. 2011).

A holistic approach to moose management may be more appropriate. Incorporating factors that influence moose browsing and density could help managers on Newfoundland deal with the known time-lag in management response to population declines and peaks (Fryxell et al. 1991, Fryxell et al. 2010). Describing these factors could help to understand and potentially determine the carrying capacity which changes temporally and spatially with environmental conditions (Crête 1989, McLaren and Mercer 2002). McShea et al. (1997) and Côté et al. (2004) argue that managers need to approach large herbivore management in a more holistic approach because large herbivore populations and their environments are managed as separate entities despite the fact that both interact and influence each other within the ecosystem. A holistic approach could be addressed by applying a similar philosophy as Aldo Leopold`s land ethic (1949) which he describes as: “simply enlarges the boundaries of the community to include soils, waters, plants, and animals, or collectively: the land” where “a thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community”.

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Appendix 1. Study Area Description

Study areas description including location, management designation, moose densities, Ecoregion, and landscape composition in Chapter 2.

Table A.1.1 Study area description including area (km2), latitude/longitude, and Newfoundland Ecoregions.

Study Area	Area (km^2)	Latitude	Longitude	Ecoregion	Management Designation
MMA 02 (Portland Creek)	3125	50°14′N	57°27′W	Northern Peninsula Forest; Long Range Barren Forest	*Managed*: Hunting & Forest Harvest
Gros Morne National Park	1805	49°38′N	57°46′W	Northern Peninsula Forest; Long Range Barren Forest; Western Newfoundland Forest	*Protected*: No Hunting or Forest Harvest
MMA 42 (Gambo)	2180	48°50′N	54°44′W	Central Newfoundland Forest	*Managed*: Hunting & Forest
Rodney Pond	110	50°14′N	57°27′W	Central Newfoundland Forest	*Protected*: Hunting & No Forest Harvest
Terra Nova National Park	400	48°33′N	53°52′W	Central Newfoundland Forest	*Protected*: No Hunting or Forest Harvest

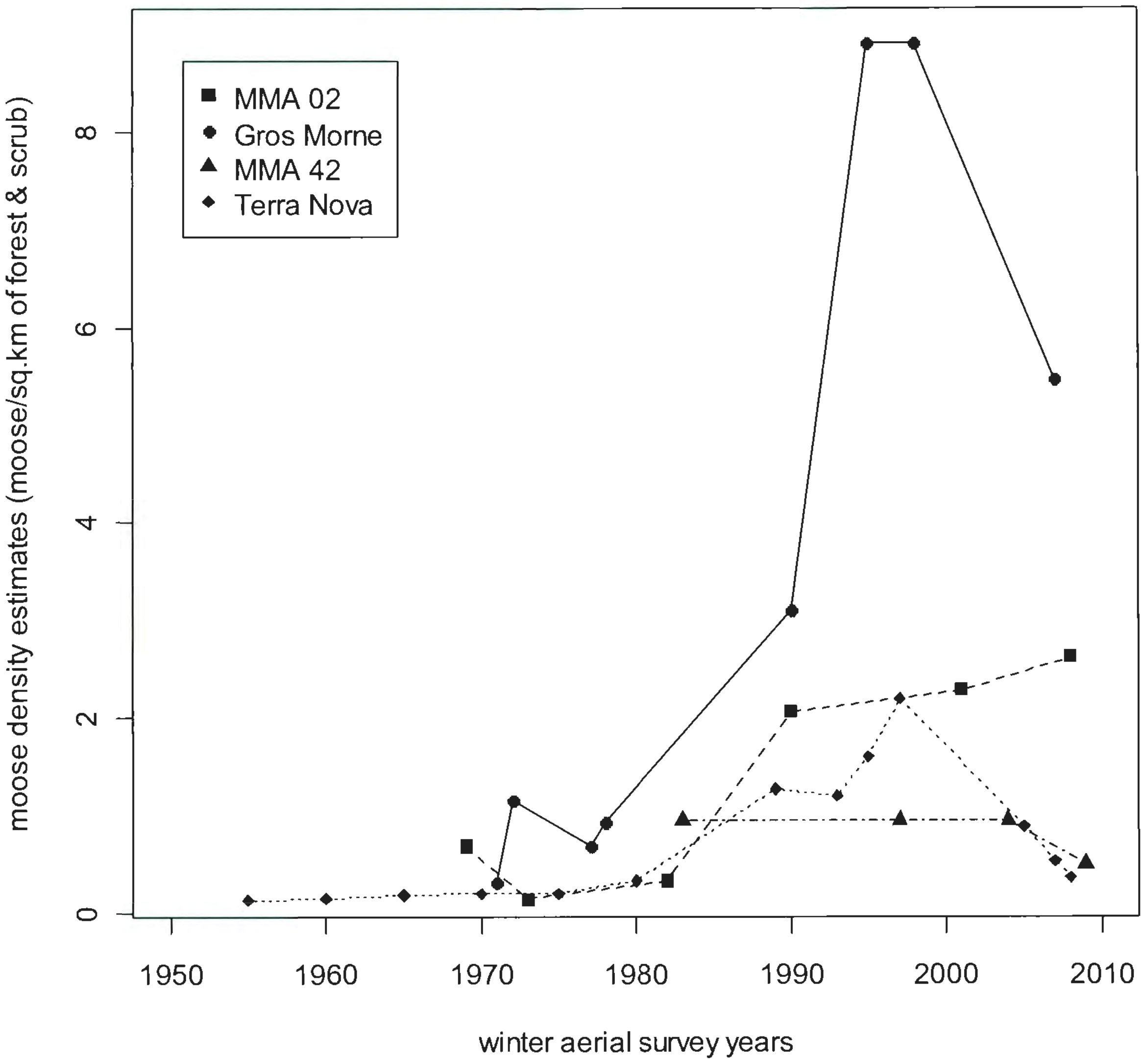

Figure A.1.1 Moose population estimates (number of moose) determined during moose winter aerial surveys (1955-2009) in Moose Management Areas 02 &42 (Wildlife Division, unpublished data) and Gros Morne & Terra Nova National Parks (Parks Canada, unpublished data).

Table A.1.2 Species composition of the landscape within Moose Management Area 02, Gros Morne National Park, Moose Management Area 42, and Terra Nova National Park. The percent cover represents the proportion of the stand cover of that species over total forested area including scrub and treed bog. Non-forested area represents the proportion of the total study area that is non-forested which includes waterbodies, barrens, bogs, and not sufficiently restocked stands from the Forest Resource Inventory Data (FRI) (Newfoundland and Labrador Forestry Division, unpublished data).

Study Area	Species	Composition (Percent Cover)
Moose Management Area 02	balsam fir	42.81
	black spruce	7.49
	hardwood stands	0.91
	tamarack	0.32
	white birch	4.44
	white spruce	0.53
	total non-forested area	43.49
Gros Morne National Park	balsam fir	47.74
	black spruce	2.25
	hardwood stands	2.95
	Tamarack	0.38
	trembling aspen	0.041
	white birch	15.55
	white spruce	0.64
	total non-forested area	30.44
Moose Management Area 42	balsam fir	13.41
	black spruce	41.12
	european larch	0.00012
	japanese larch	0.00016
	jack pine	0.018
	lodgepole pine	0.0012
	red maple	0.054
	red pine	0.00071
	scots pine	0.00056
	sitka spruce	0.0069
	tamarack	0.087
	trembling aspen	0.51
	white birch	4.17
	white pine	0.0083
	white spruce	0.35
	total non-forested area	40.26

Study Area	Species	Composition (Percent Cover)
Terra Nova National Park	balsam fir	20.35
	black spruce	37.49
	red maple	0.0039
	tamarack	2.65
	trembling aspen	0.86
	white birch	8.14
	white pine	0.0071
	total non-forested area	32.88
Rodney Pond	balsam fir	8.17
	black spruce	54.82
	trembling aspen	0.97
	tamarack	0.10
	white birch	9.98
	total non-forested area	25.96

Appendix 2: Browse plot study design and locations across study areas.

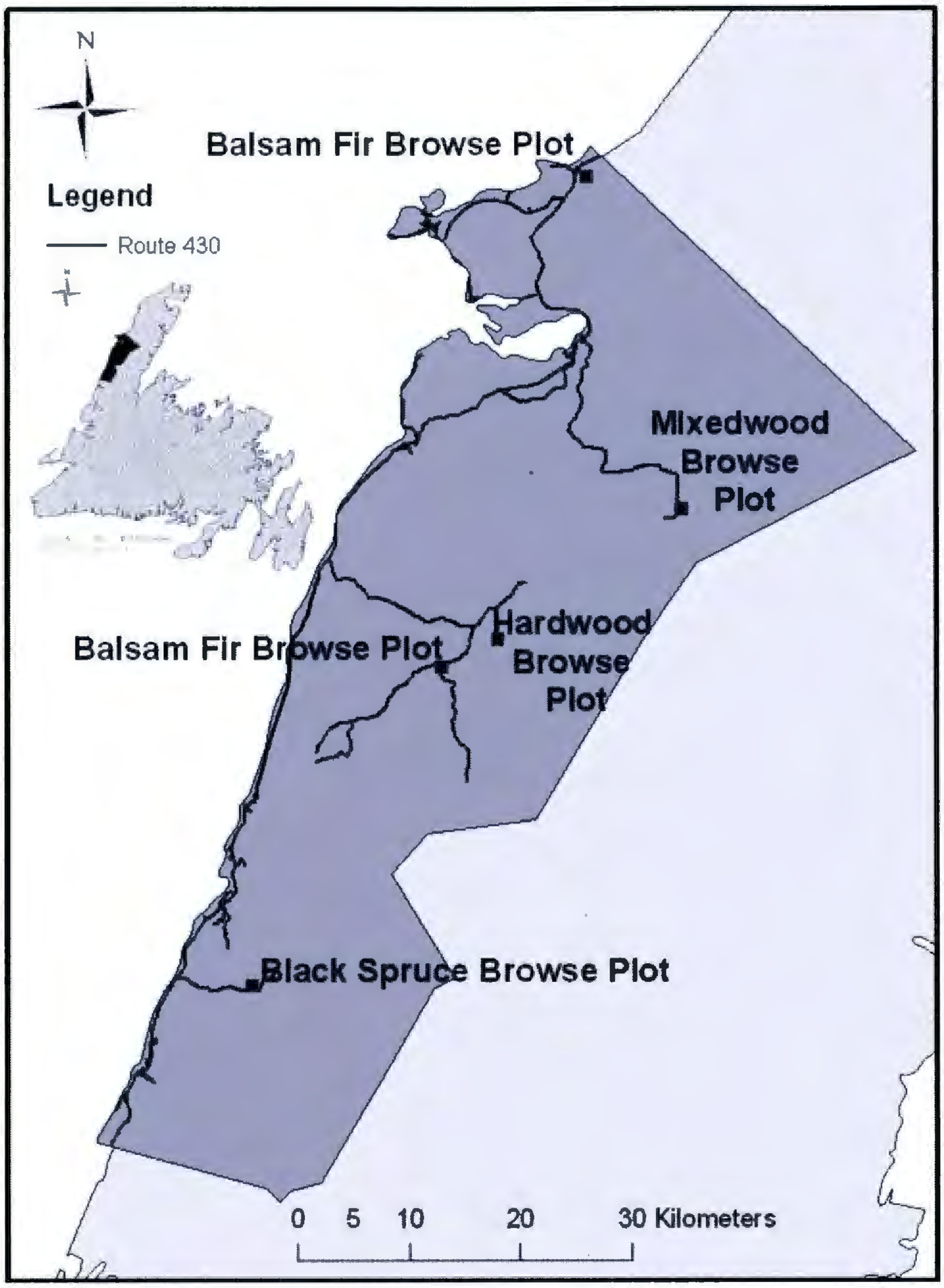

Figure A.2.1 Browse plot locations randomly chosen in Moose Management Area 02, NL.

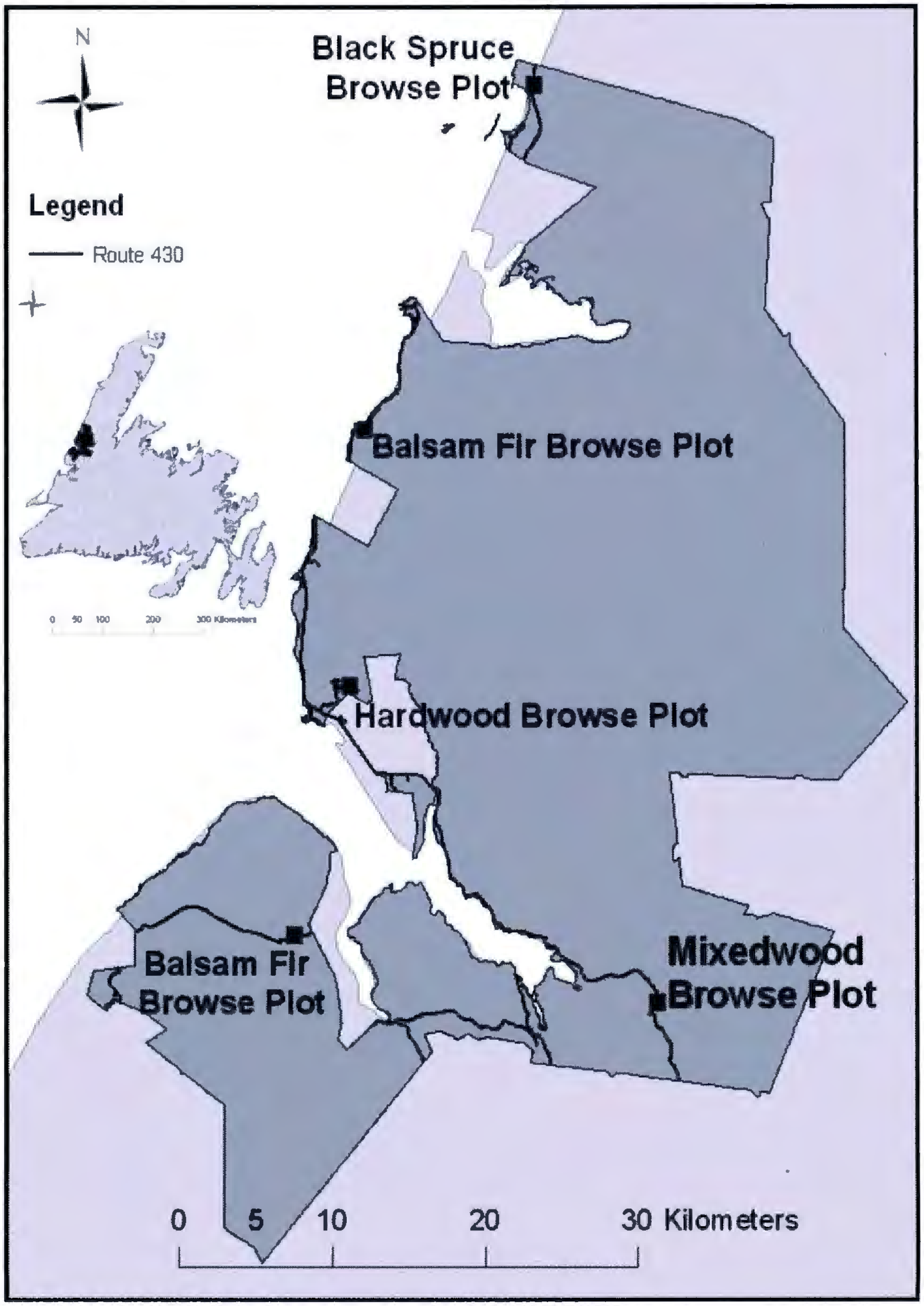

Figure A.2.2 Browse plot locations randomly chosen in Gros Morne National Park, NL.

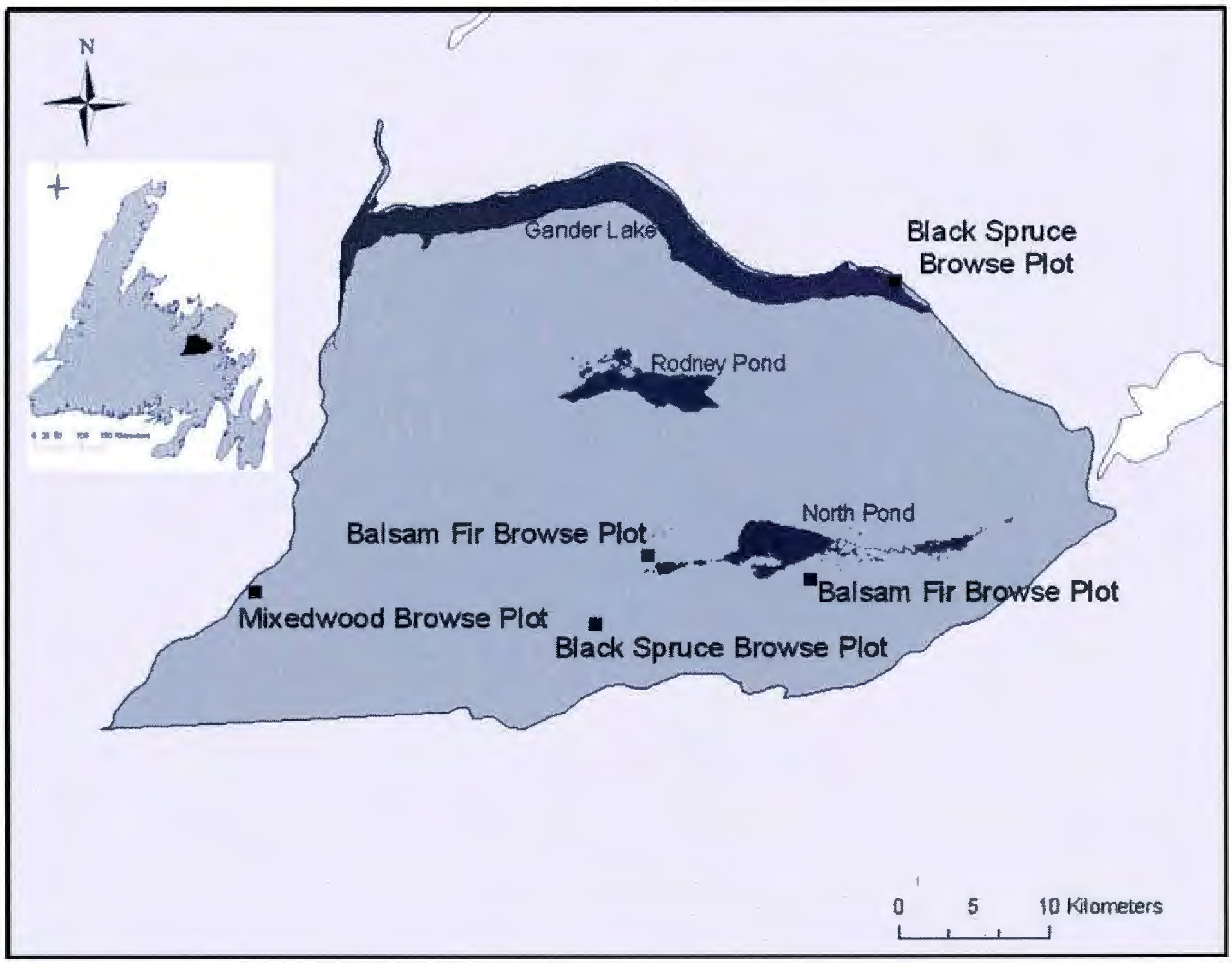

Figure A.2.3 Browse plot locations randomly chosen in Moose Management 42, NL.

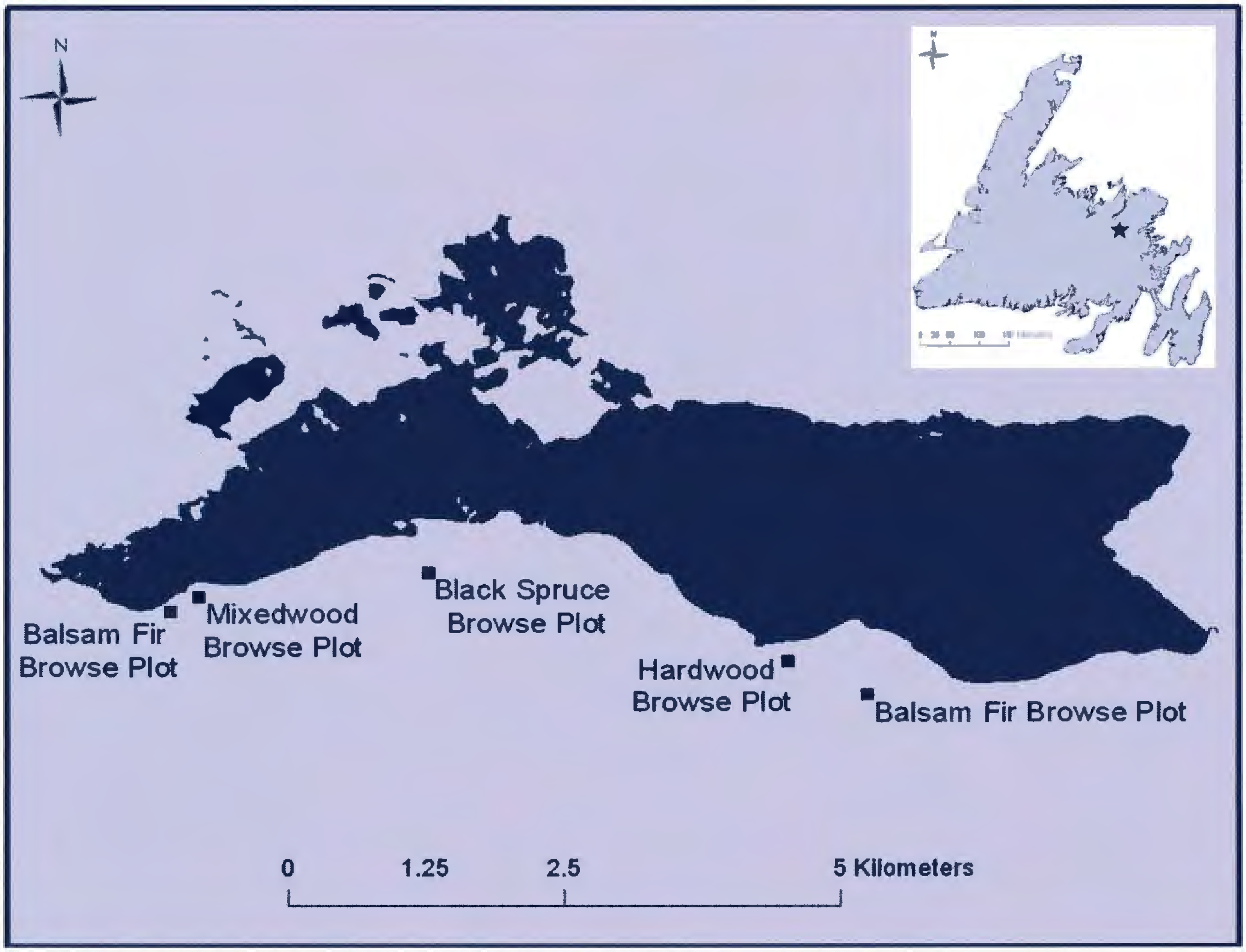

Figure A.2.4 Browse plot locations randomly chosen in Rodney Pond within Moose Management 42, NL

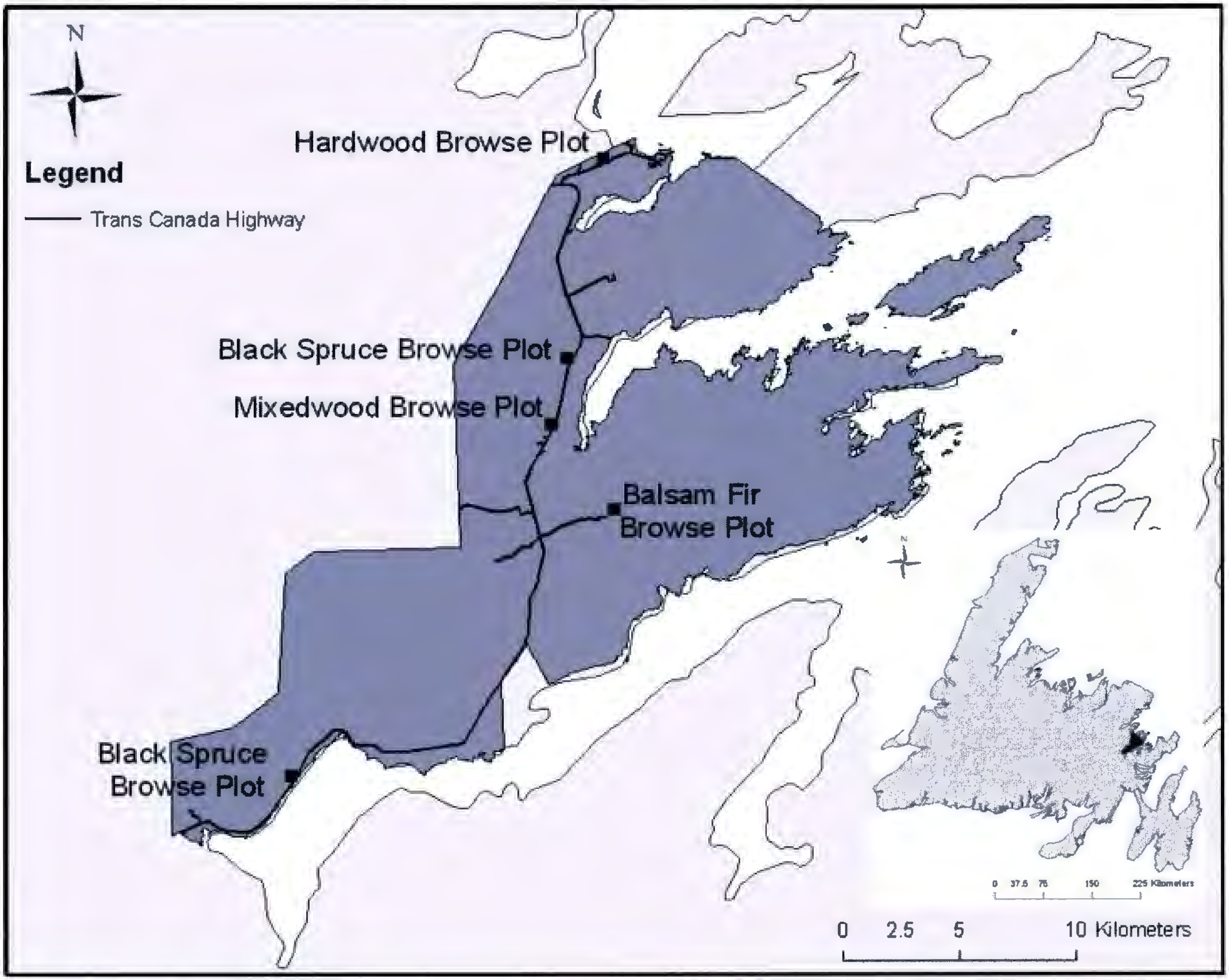

Figure A.2.5 Browse plot locations randomly chosen in Terra Nova National Park, NL.

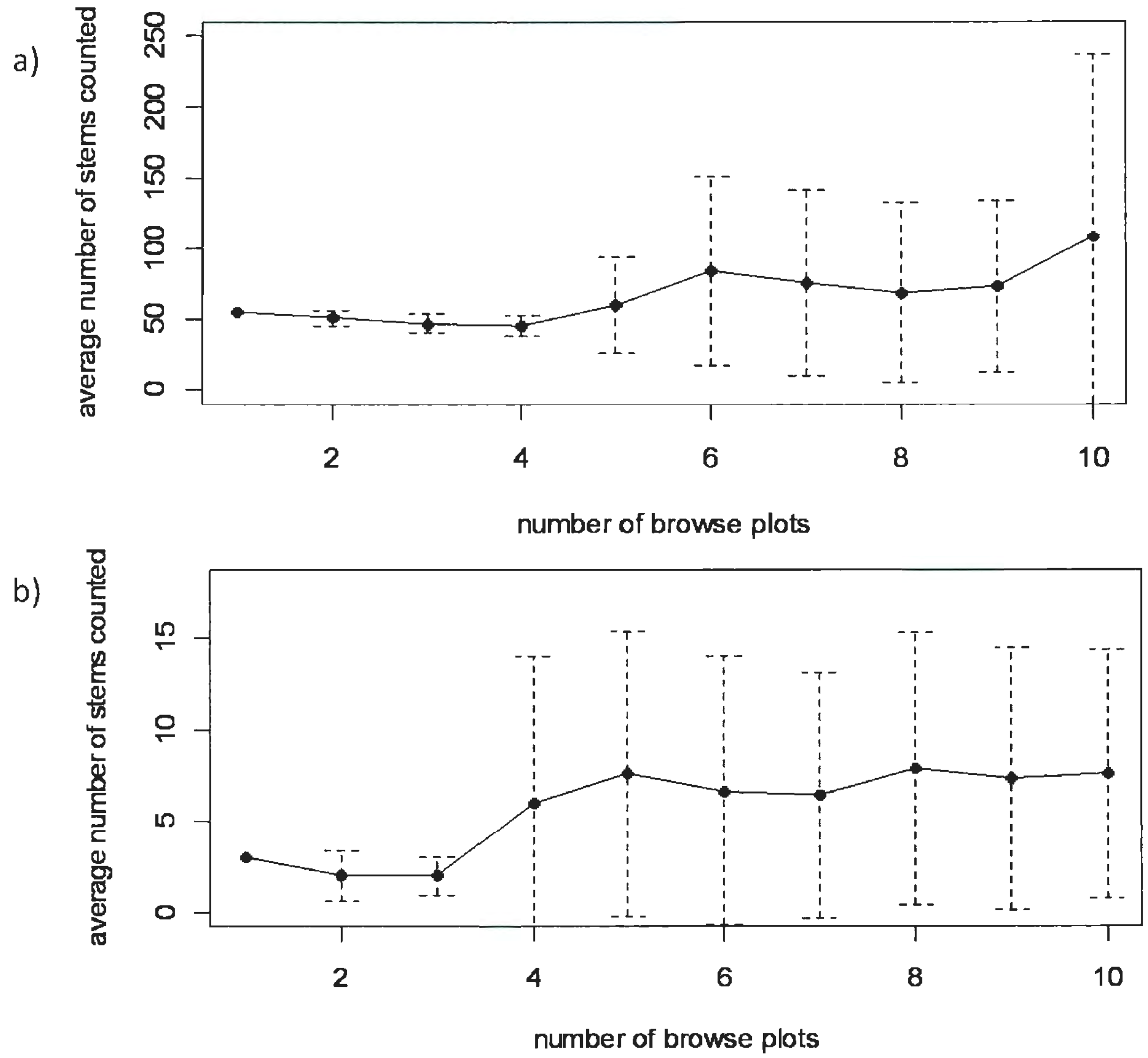

Figure A.2.6 Power analysis to determine the number of browse plots necessary to capture moose browsing patterns from the average number of stems counted (± Standard Deviation) in browse plots for a) Balsam Fir (*Abies balsamea*) and b) White Birch (*Betula papyrifera*). Analysis is based on data on moose browsing analysis in Terra Nova National Park (Parks Canada, Unpublished data).

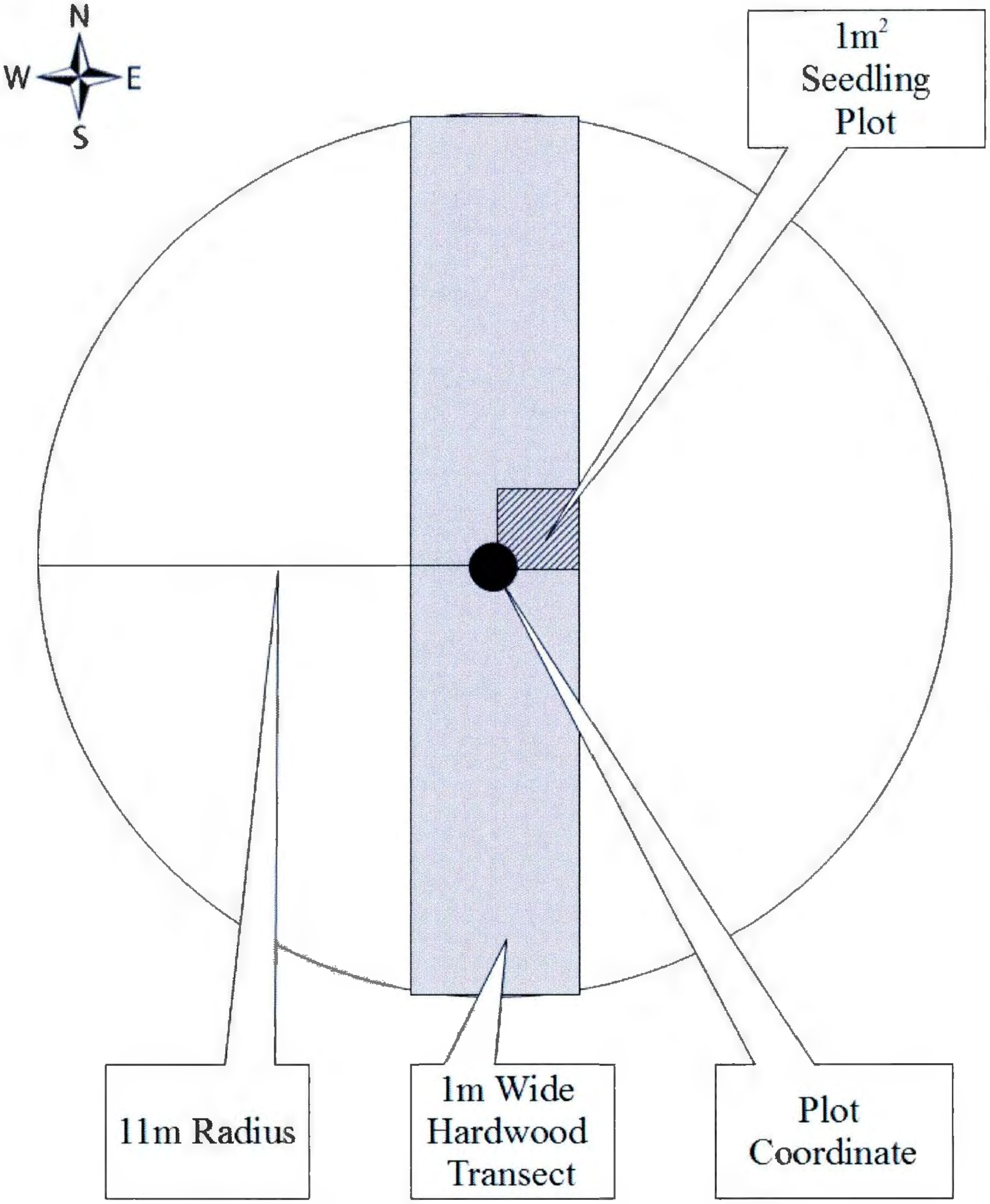

Figure A.2.7 Browse plot design (J. Gosse, Parks Canada Unpublished Data)

Appendix 3: Mean point at diameter of browse by species across all study areas.

These results can be used to see the range of diameter that moose are foraging. If moose are in an area of poor browse quality, they will select larger stem diameters that are more costly due to higher digestion demands. Moose in western Newfoundland foraged on stems with a larger range in diameter at point of browse compared to eastern Newfoundland.

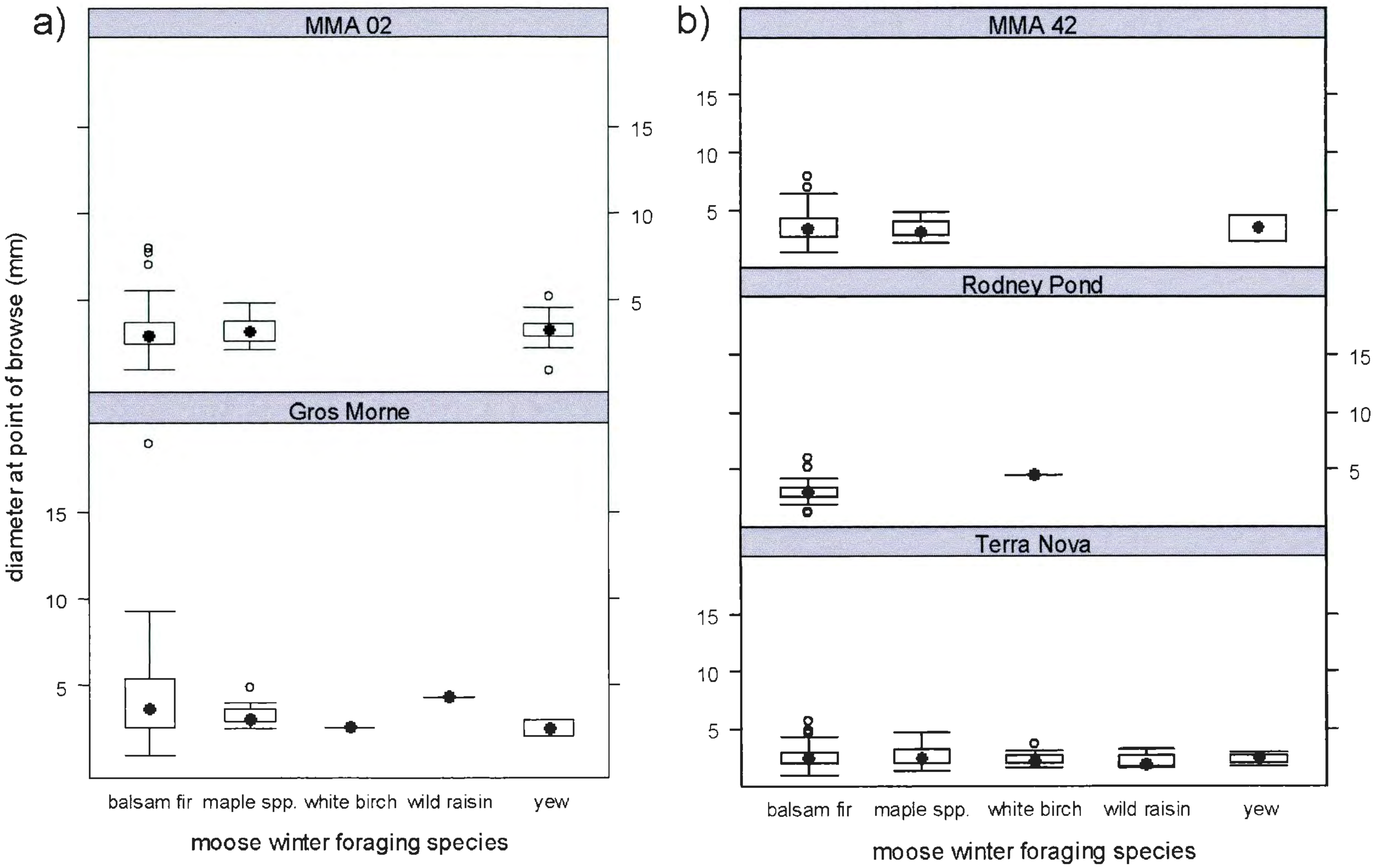

Figure A.3.1 Diameter of stem at point of browse for each species sample: balsam fir, maple spp., white birch, wild raisin, and yew in a) western Newfoundland and b) eastern Newfoundland.

Appendix 4. T-test results for 2009 and 2010 moose browsing data from eastern Newfoundland study areas (Moose Management Area 42, Rodney Pond, and Terra Nova National Park).

This test was conducted to see if it is possible to combine 2009 and 2010 data in the analysis since there was two years of data for the eastern Newfoundland sites but only one year of data for the western Newfoundland sites. There was no significant difference between the 2009 and 2010 data for eastern Newfoundland sites so they were combine during the analysis for Chapter 2.

Table A.4.1 T-test results for 2009 and 2010 for a general linear model of height and basal diameter of each browse species saplings in eastern Newfoundland study areas (Moose Management Area 42, Rodney Pond, and Terra Nova National Park).

Study Areas	Species	Height Coefficients	Basal Diameter Coefficients	t	Df	p-value
Moose Management Area 42	balsam fir 2009	5.02	4.76	-0.65	1	0.63
	balsam fir 2010	9.44	3.83			
	mountain maple 2009	16.72	3.32	-1.42	1	0.38
	mountain maple 2009	20.03	3.90			
Rodney Pond	balsam fir 2009	5.60	4.97	0.83	1	0.53
	balsam fir 2010	8.75	4.80			
Terra Nova National Park	balsam fir 2009	9.93	1.33	0.26	1	0.83
	balsam fir 2010	9.64	1.49			
	mountain maple 2009	25.01	0.28	0.93	1	0.52
	mountain maple 2010	14.44	0.65			
	red maple 2009	2.03	5.31	-0.72	1	0.60
	red maple 2010	16.65	2.98			

[*] p-value that are significant within 95% confidence intervals ($\alpha = 0.05$).

Appendix 5: Analysis of variance table for balsam fir seedling density in relation to management designation (protected and managed) and moose density (low density = < 0.50 moose/km^{-2} and high density => 2 moose/km^{-2}).

Seedling density did not differ with management designation or moose density. Analysis of variance table for percent browsing on winter foraging species in different management designation (protected and managed) and moose density (low density = < 0.50 moose/km^2 and high density => 2 moose/km^2). Percent browsing was significantly higher in protected areas than managed areas for wild raisin, but did not differ with moose density. Percent browsing did not differ with management designation or moose density for balsam fir, maple spp., white birch, and yew.

Table A.5.1 Analysis of variance (ANOVA) for balsam fir seedling density in different management designation (protected and managed), and moose densities (low density = < 0.50 moose/km^{-2} and high density = > 2 moose/km^{-2}).

Factor/Residual	**Df**	**Sum of Squares**	**Mean Sum of Squares**	**F-Value**	**P-value**
Management Designation	1	50.70	50.70	1.11	0.36
Residuals	3	136.50	45.50		
Moose Density	1	19.20	19.20	0.34	0.59
Residuals	3	168.00	56.00		

* p-value that are significant within 95% confidence intervals ($\alpha = 0.05$).

Table A.5.2 Analysis of variance (ANOVA) of percent moose browsing on winter foraging species in different management designation (protected and managed) and moose density (low density = < 0.50 moose/km^{-2} and high density = > 2 moose/km^{-2}).

Species	Factors/Residuals	Df	Sum of Squares	Mean Sum of Squares	F-value	P-value
Balsam Fir	Management Designation	1	721.20	721.24	0.91	0.34
	Residuals	27	21180.70	784.47		
	Moose Density	1	377.70	377.67	0.47	0.49
	Residuals	27	21524.30	797.20		
Maple spp.	Management Designation	1	3594.30	3594.30	3.54	0.079
	Residuals	15	15199.50	1013.30		
	Moose Density	1	300.50	300.52	0.24	0.62
	Residuals	15	18493.30	1232.88		
White Birch	Management Designation	1	1607.10	1607.10	0.79	0.40
	Residuals	6	12142.90	2023.80		
	Moose Density	1	3809.50	3809.50	2.28	0.19
	Residuals	5	8333.30	1666.70		
Wild Raisin	Management Designation	1	7872.00	7872.00	75.5	<0.0001*
	Residuals	5	520.80	104.20		
	Moose Density	1	20.83	20.833	0.16	0.70
	Residuals	4	500.00	125.00		
Yew	Management Designation	1	351.80	351.76	0.34	0.58
	Residuals	4	4091.90	1022.96		
	Moose Density	1	2553.00	2552.97	5.40	0.080
	Residuals	4	1890.60	472.66		

* p-value that are significant within 95% confidence intervals ($\alpha = 0.05$).

Appendix 6: Moose density, hunter success, and hunter access within 10 Moose Management Areas in Newfoundland.

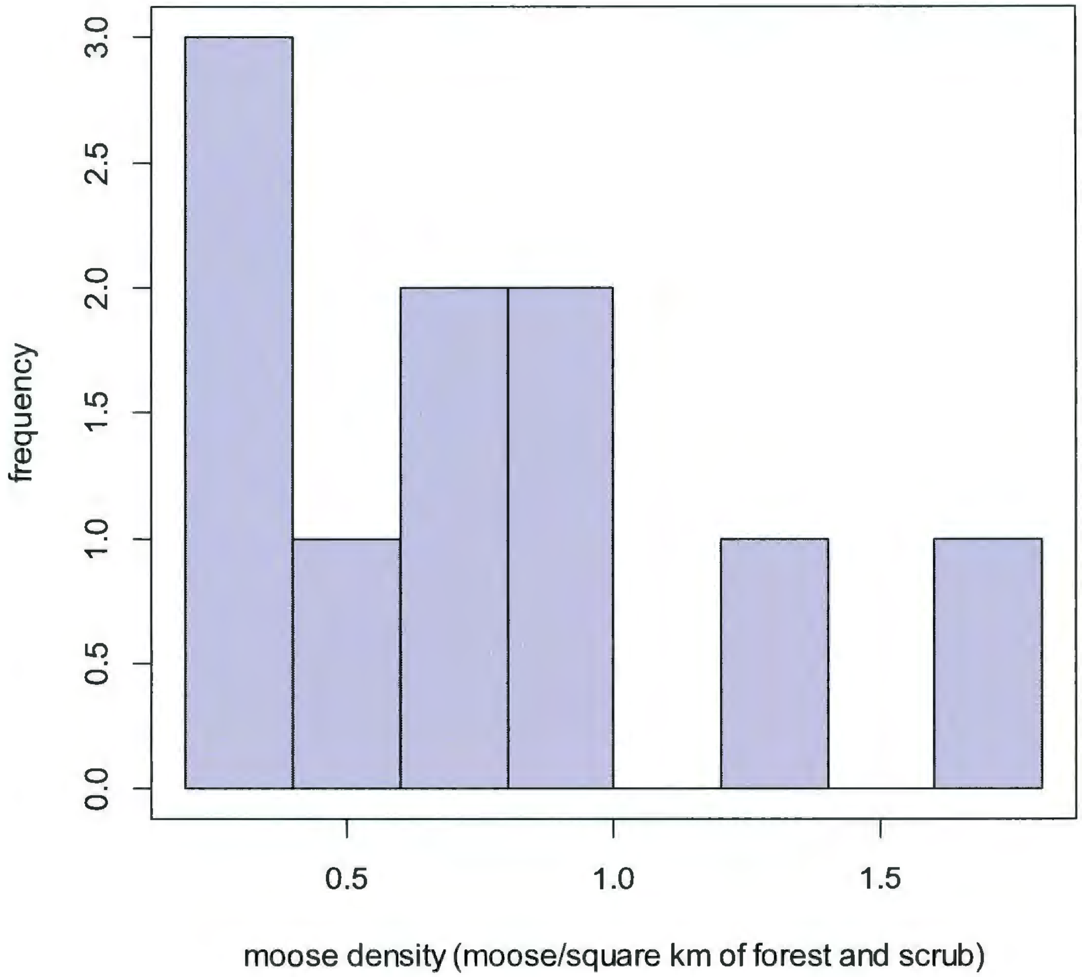

Figure A.6.1 The frequency of moose density (moose·km^{-2} of forest and scrub) for the 10 Moose Management Areas (MMAs) of this study demonstrates that moose density below 1 moose·km^{-2} can be classified as low, and higher than 1 moose·km^{-2} as high.

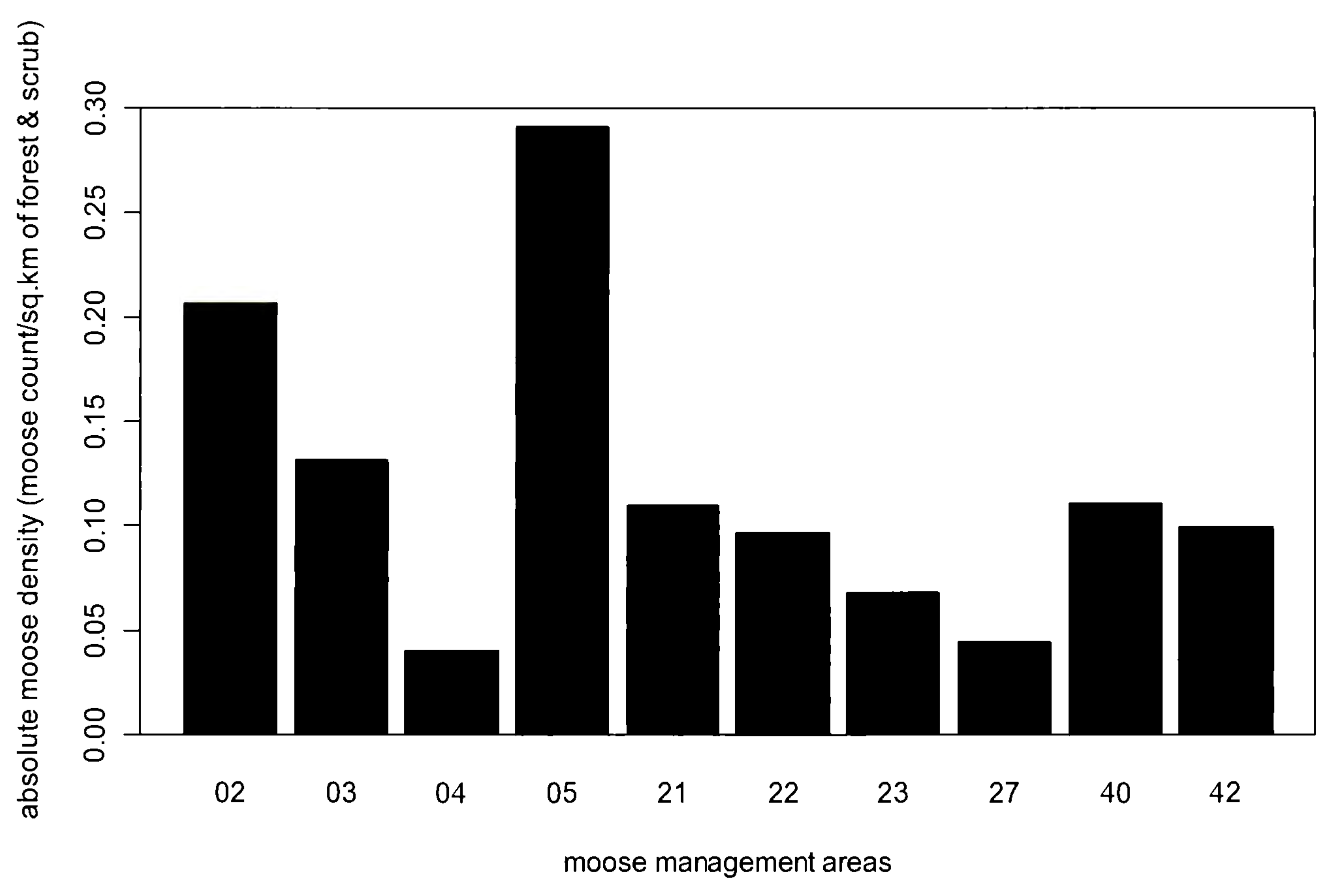

Figure A.6.2 Absolute moose density (moose counted during aerial surveys·km^{-2} of forest and scrub) in moose management areas: 02 (Survey Year: 2008), 03 (Survey Year: 2009), 04 (Survey Year: 2004), 05 (Survey Year: 2005), 21 (Survey Year: 2004), 22 (Survey Year: 2004), 23 (Survey Year: 2003), 27 (Survey Year: 2009), 40 (Survey Year: 2004), and 42 (Survey Year: 2009) (Wildlife Division, Government of Newfoundland and Labrador, 2004-2009).

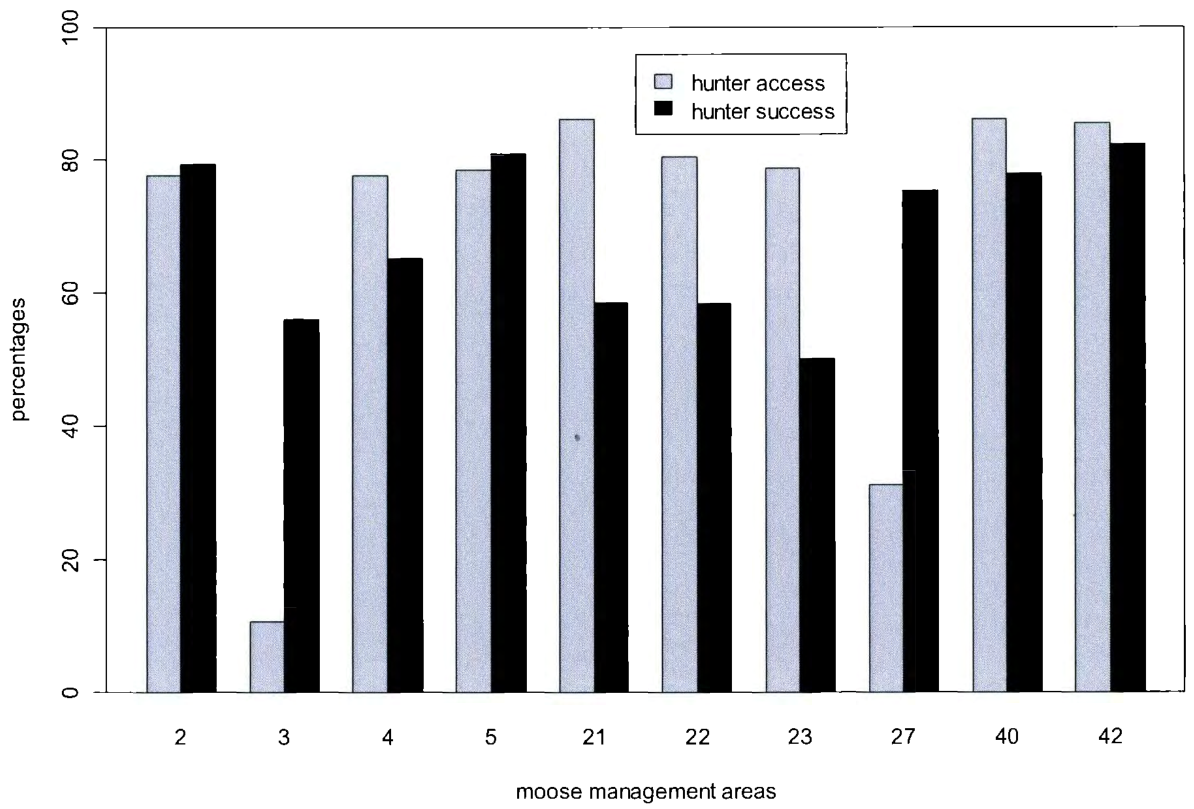

Figure A.6.3 Hunter access (percentage) and hunter success (percentage (kills/licenses); average of all four license types: male only, either sex, female only, and non-resident in each Moose Management Area) in Moose Management Areas: 02 (Survey Year: 2008), 03 (Survey Year: 2009), 04 (Survey Year: 2004), 05 (Survey Year: 2005), 21 (Survey Year: 2004), 22 (Survey Year: 2004), 23 (Survey Year: 2003), 27 (Survey Year: 2009), 40 (Survey Year: 2004), and 42 (Survey Year: 2009) (Wildlife Division, Government of Newfoundland and Labrador, 2004-2009).

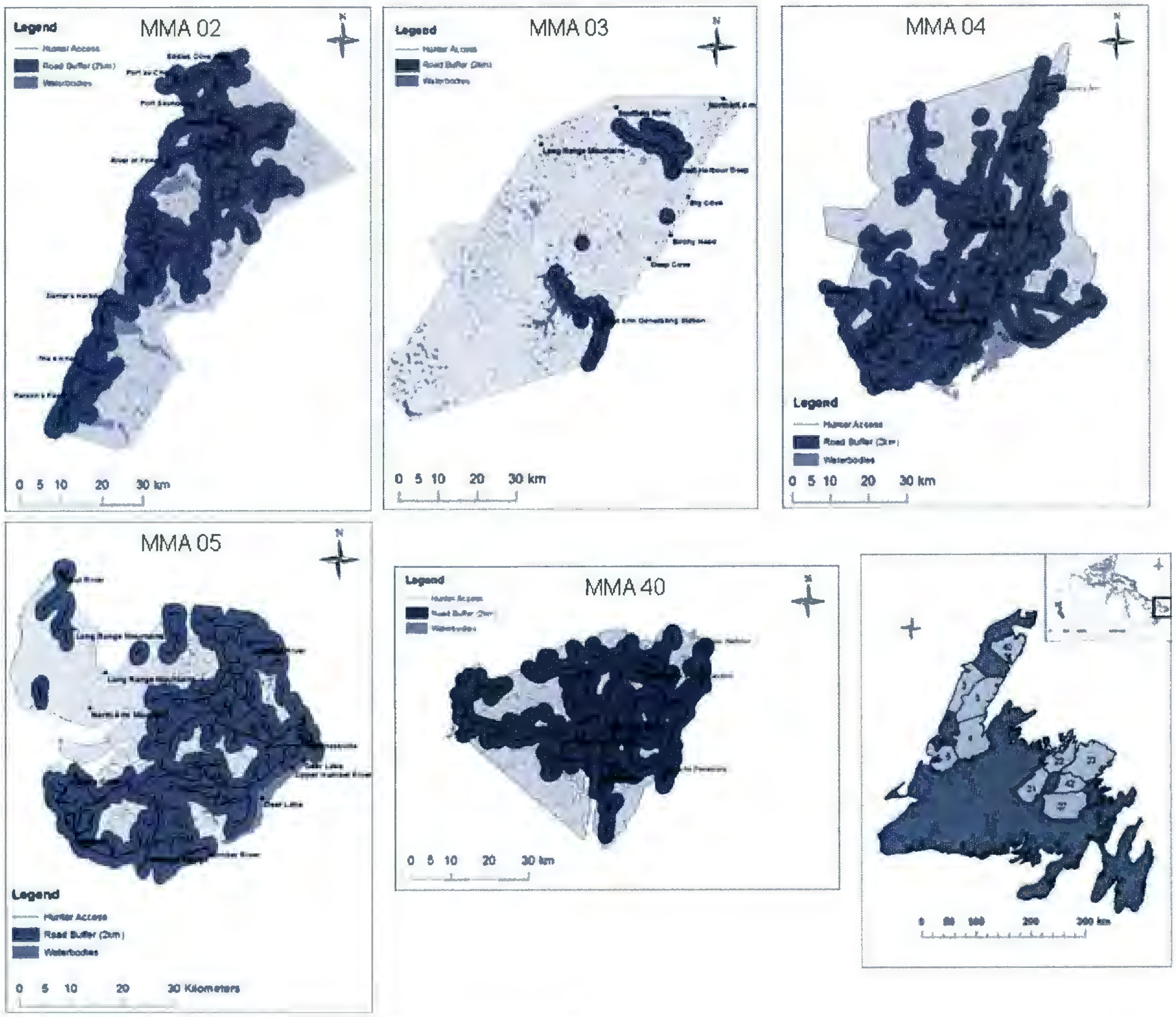

Figure A.6.4 Hunter access (area of 2km buffer/total terrestrial area of Moose Management Area) with a 2km road buffer in Moose Management Areas 02,03,04,05, and 40 in western Newfoundland, Canada.

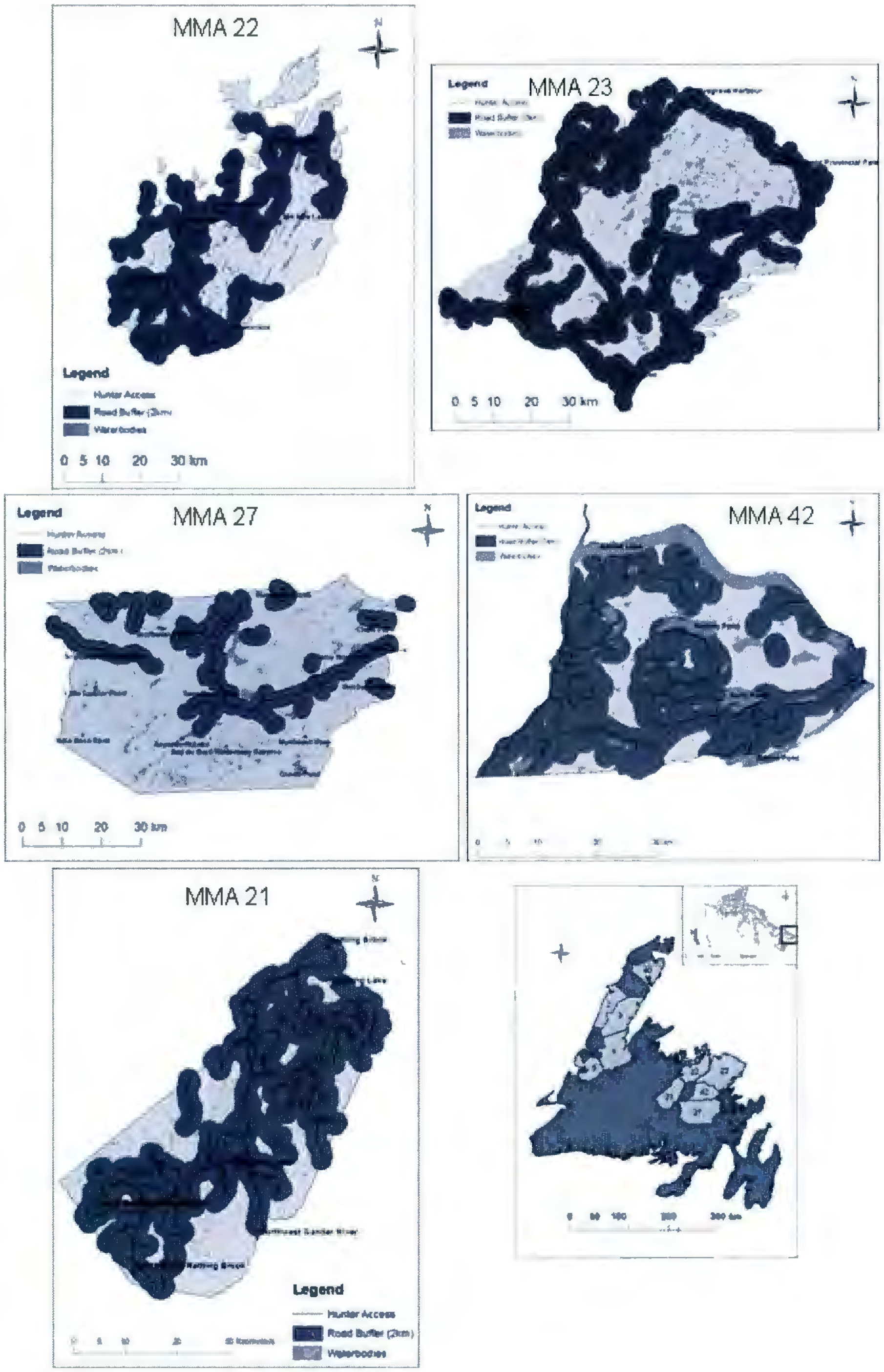

Figure A.6.5 Hunter access (area of 2km buffer on each side of a road/total terrestrial area of the Moose Management Area) with a 2km road buffer in Moose Management Areas 21, 22, 23, 27, and 42 in eastern Newfoundland, Canada

Appendix 7: Study areas description including location and Ecoregion for the 10 Moose Management Areas in Chapter 3.

Table A.7.1 Study area descriptions of area (km2), latitude/longitude, and Newfoundland Ecoregions.

Moose Management Area	Area (km^2)	Latitude	Longitude	Ecoregion
02 (Portland Creek)	2490.37	50°14′N	57°27′W	Northern Peninsula Forest; Long Range Barren Forest
03 (Harbour Deep)	3743.93	50°21′N	56°37′W	Northern Peninsula Forest; Long Range Barren Forest
04 (Taylor`s Brook)	3921.89	49°40′N	57°11′W	Northern Peninsula Forest; Long Range Barren Forest;Central Newfoundland
05 (Trout River)	2046.23	49°08′N	57°46′W	Western Newfoundland Forest
21 (Rattling Brook)	2079.32	48°40′N	55°36′W	Central Newfoundland Forest
22 (Lewisport)	2389.41	49°13′N	54°51′W	Central Newfoundland Forest; North Shore Forest
23 (Bonavista North)	4250.96	49°06′N	54°10′W	Central Newfoundland Forest; North Shore Forest; Eastern Hyper-Oceanic Barren
27 (Terra Nova)	3659.91	48°45′N	54°35′W	Central Newfoundland Forest
40 (Conche)	2165.44	51°00′N	56°03′W	Northern Peninsula Forest; Long Range Barren Forest
42 (Gambo)	2165.44	48°50′N	54°44′W	Central Newfoundland Forest

Appendix 8: Weighted values for the contrast-weighted edge density at landscape level analysis.

Contrasted-weighted edge density is the sum of the edge length between different patches that are adjacent divided by the landscape area (survey block area) and was selected over the edge density because not all edges are equally important to moose. The contrast-weighted values were developed reflecting moose habitat preferences.

Table A.8.1 Weighted values (between 0-1, with 1 having the highest weight and 0 having the lowest weight) for the contrast-weighted edge density at landscape level analysis.

Combination of patch types with adjacent edges	Weighted value
mixedwood with hardwood	1.0
balsam fir with either mixedwood or hardwood	0.9
black spruce with either mixedwood or hardwood	0.8
mixedwood or hardwood with bog & barren or scrub	0.6
balsam fir with bog & barren or scrub	0.5
black spruce with bog & barren or scrub	0.4
disturbed with either mixedwood, hardwood, balsam fir, or black spruce	0.3
other with either mixedwood, hardwood, balsam fir, or black spruce	0.2
not sufficiently stocked with either mixedwood, hardwood, balsam fir, or black spruce	0.1
same patch types or a combination of either of these patches together: water, bog & barren, scrub, other, not stocked, or disturbed	0

Appendix 9 Testing for multi-collinearity

In the AIC analysis, the global model was the only plausible model. Thus, the coefficients of the parameters in the logistic regression were tested for multicollinearity.

Table A.9.1: Testing for multi-collinearity of the explanatory variables using relative odds ratios in the logistic regressions used in the AIC analysis to identify the relationship between moose browsing and landscape processes and factors.

	Multivariate		**Univariate**	
Variable	**Odds Ratio**	**Confidence Intervals (Lower; Upper)**	**Odds Ratio**	**Confidence Intervals (Lower; Upper)**
Management Designation2 (Categorical; 2 factors)	1.75	(1.22; 2.15)	0.84	(0.64; 1.09)
Moose Density2 (Categorical; 2 factors)	1.09	(0.77; 1.54)	1.83	(1.45; 2.30)
Forage Species2 (Categorical; 5 factors)	2.99	(1.64; 5.54)	7.13	(4.32; 12.05)
Forage Species3 (Categorical; 5 factors)	2.85	(0.32; 24.75)	3.89	(0.46; 32.52)
Forage Species4 (Categorical; 5 factors)	7.60	(1.22;146.73)	23.35	(3.97; 441.72)
Forage Species (Categorical; 5 factors)	1.60	(0.84; 3.01)	2.44	(1.39; 4.19)
Stand Type2 (Categorical;4 factors)	0.95	(0.58;1.53)	2.49	(1.68; 3.64)
Stand Type3 (Categorical; 4 factors)	8.08	(4.92; 13.47)	11.09	(7.03; 17.86)
Stand Type4 (Categorical; 4 factors)	2.73	(1.90; 3.92)	3.73	(2.78; 4.99)
Height (Continuous)	1.01	(1.00; 1.01)	1.01	(1.00; 1.01)