Habitat Selection by the Slate Island Boreal Woodland Caribou (*Rangifer tarandus caribou*).

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ABSTRACT

The Slate Islands caribou (*Rangifer tarandis caribou*) is an insular population which has experienced several population crashes and has been described as likely to succumb to extirpation. While a great deal of research has been conducted on mainland woodland caribou, factors which influence caribou distributions may differ between island and main land populations. In this thesis, I investigate relationships between habitat, landscape, anthropogenic features, population size, predation and spatial distribution of woodland caribou across the Slate Islands Provincial Park (Ontario) at the forest-patch spatial scale. Generalized linear models were used to compare observed caribou locations to available locations across the park, based on data from 1978 to 1995. Results indicated that the Slate Islands caribou selected deciduous cover, larger forest patches, areas further to water, flatter areas, lower elevations and areas closer to anthropogenic features. Population size had a limited effect on caribou distributions.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

1.1 Background

Boreal woodland caribou (*Rangifer tarandus caribou*) is an ecotype of woodland caribou (Thomas and Grey 2002) and listed as a threatened species both federally (COSEWIC 2002) and provincially in Ontario (Ontario Endangered Species Act 2007). The listing of boreal woodland caribou as a threatened species has spurred intensive study of their populations, with great emphasis being placed on quantifying caribou habitat use and population demographics in order to contribute to management plans.

One woodland caribou population that has been intensively studied is the Slate Islands caribou (Slate Islands Provincial Park, Lake Superior, Ontario).The Slate Islands caribou population is an insular caribou population located approximately thirteen kilometers south of the northern shores of Lake Superior (Bergerud *et al.* 2007; Carr *et al.* 2012). This population is the most southerly woodland caribou population remaining in Canada (Environment Canada 2011) and has been the focus of annual monitoring and research projects since 1974 (Bergerud *et al.* 2007). Studies of this population have contributed greatly to how we understand woodland caribou and their interactions with predators (Bergerud *et al.* 1974; 2007). Additionally, this population has also become an economic driver in the small town of Terrace Bay in northern Ontario, with several ecotourism operations providing tours of the archipelago allowing tourists to view caribou and learn more about the area.

Although extensive research has been conducted on the Slate Islands caribou population, there are aspects of this population that are have not been well explored. For example, there have been studies conducted on the forage preferences and fine scale habitat selection of the Slate Islands caribou (Bergerud *et al.* 2007). While these finer-scale surveys provide a great deal of

information, they require a large time commitment and travelling out to isolated areas to conduct the survey (Carr *et al.* 2012). Alternatively, geospatial studies using broader-scale variables (such as forest cover type, elevation, and slope) have become common in modelling caribou distributions because they allow researchers to characterize and understand animal movement while requiring less time in the field. These types of broader-scale habitat preferences have yet to be characterized for the Slate Islands caribou population. Additionally, while population densities and rates of predation have been documented on the Slate Islands (Bergerud *et al.* 2007), the influence of these variables on habitat selection has yet to be explored.

1.2 Problem Statement

The Slate Islands caribou population have experienced several population crashes (documented in 1984-85, 1989-90 and 2007-08), and have been described as a population likely to succumb to extirpation (Bergerud *et al.* 2007; Carr *et al.* 2012). If this population is to be maintained, fully understanding the dynamics and influencing factors of the Slate Islands population caribou will be required.

To date, there has been over four decades of annual monitoring and research conducted on the Slate Islands caribou population (Bergerud *et al.* 2007). The majority of this research has focused on the caribou's fine scale forage selection (i.e. preferred plant species). Broader-scale factors that can influence caribou distributions, such as influence of habitat types, landscape features, predation, population size, and presence of anthropogenic features on the Slate Islands have not been incorporated as part of an analysis of habitat selection by Slate Islands' caribou. Creation of such statistical models could provide sights to habitat use that would be useful in future management and maintenance of this population.

1.3 Objectives

The purpose of this project was to determine how habitat, population size and predation influence woodland caribou distribution across the Slate Islands Provincial Park at the forest-patch spatial scale. Specific objectives of this thesis were to:

1. Investigate caribou preferences for forest and landscape features available on the Slate Islands;

2. Investigate caribou preferences for anthropogenic and natural features (i.e. mineral licks) available on the Slate Islands;

3. Investigate the potential role of density dependence on habitat selection; and

4. Explore the potential influence of predation on habitat selection.

1.4 Research Hypotheses

To meet my objectives, I generated four working hypotheses to examine the Slate Island woodland caribou distribution. (1) If the caribou are selecting habitat based on availability of forage, then they will select deciduous forest stands, which are more likely to contain forbs, sedges and grasses preferred by caribou (i.e. deciduous overstory) during the summer months. (2) If the caribou are selecting habitat to avoid human presence, I predict that they will prefer areas of the park further away from camp sites and human lodgings (i.e. anthropogenic features). (3) If resource constraints increase intraspecific competition for food or predator free spaces as the population increases, caribou should become less selective of foraging habitat at high population densities and will be present in less desirable foraging habitat (if selecting for foraging habitat) or predator-free spaces (i.e. areas away from ambush habitat and closer to escape routes). Finally, (4) if the caribou are selecting habitat for predator avoidance (even when predators are not present), I predict that they will; i) use areas closer to shorelines or water bodies

to stay close to potential escape routes, and ii) space themselves out (be negatively autocorrelated) in an attempt to maintain a lower prey density, thereby reducing the number of predators which can be supported on the landscape and lower their predation risk. I also predict that (iii) when predators inhabit the archipelago, caribou will shift their habitat use away from deciduous foraging areas and use areas that may provide a lower predation risk (higher elevations and/or shorelines), in addition to spacing themselves out on the landscape.

CHAPTER 2: LITERATURE REVIEW

Forage availability and quality, intraspecific competition for habitat, and predation can all affect boreal woodland caribou populations (Environment Canada 2011). In this review, I examined the influence of these variables on caribou behaviour and population dynamics. I also reviewed the status of woodland caribou populations, their ecology and behaviour, and the specific circumstances of the Slate Islands caribou population.

2.1 Background on Woodland Caribou

2.1.1 Status of Rangifer tarandus

Caribou (*Rangifer tarandus)* have a circumglobal distribution (Kelsall 1984). They occur as three subspecies in Europe, two of which (*R. t. tarandus* and *R. t. fennicus*) are wild or semi-domesticated populations commonly referred to as reindeer. The third European variety is Svalbard's caribou (*R. t. platyrhynchus*). There are four extant subspecies of caribou in North America: woodland caribou; Grant's caribou (*R. t. granti*); Greenland or tundra (barren ground) caribou (*R. t. groenlandicus*); and Peary caribou (*R. t. pearyi*; Environment Canada, 2011). A fifth North American subspecies, Dawson's caribou (*R. t. dawsoni*), is extinct (Thomas and Grey 2002).

Within Canada, there are eight caribou designatable units (DUs) which have been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; COSEWIC 2011). These DUs were distinguished based on caribou biogeography (i.e. ranges), taxonomy, genetics, morphology, life history and behaviour of the species. Each designatable unit generally consists of multiple local populations (colloquially referred to as "herds"; Thomas

and Grey 2002) across the various subspecies in Canada. A summary of assessed designatable units and their status is provided in Table 1.

Table 1. Designatable units, species types and COSEWIC statuses for *Rangifer* species in North America (COSEWIC 2011).

Designatable Unit	Subspecies Type(s)	Population	COSEWIC Status
DU2	Peary caribou	Arctic Archipelago	Endangered
DU3	Barren-ground and Peary caribou	Dolphin and Union caribou	Species Concern
DU5	Woodland caribou	Newfoundland	Not at Risk
DU6	Woodland caribou	British Columbia to Northwest Territories to Labrador (Boreal population)	Threatened
DU7	Woodland caribou	Northern Mountain caribou	Species Concern
DU9	Woodland caribou	Southern Mountain population	Threatened
DU11	Woodland caribou	Atlantic-Gaspésie caribou	Endangered
DU12	Dawson's caribou	N/A	Extinct

Caribou in North American are broadly described as three ecotypes: migratory forest-tundra, montane and sedentary forest-dwelling (Figure 1; Bergerud 2000; Thomas and Grey 2002; Courtois 2003). The migratory, forest-tundra caribou ecotype reach over 300,000 individuals and undertake long-distance migrations of hundreds of kilometers between their summer range in the tundra and winter range in the boreal forest (Environment Canada 2008).

The montane caribou ecotype are located in western Canada (Alberta and British Columbia) and form smaller groups than migratory populations, with few local populations exceeding more than five hundred individuals (Thomas and Grey 2002). Finally, populations of forest dwelling caribou form groups typically comprising fewer than one thousand individuals (Thomas and Grey 2002; Environment Canada 2011).

Forest-dwelling woodland caribou are widely distributed within their ranges, with a national average local population density of 3.3 caribou per 100 km^2 (ranging from 1.8 to 13.1 caribou per 100 km^2; Thomas and Grey 2002). Interactions between individuals within a local population vary seasonally. Caribou tend to be solitary during the spring and summer months (calving season) and form small groups for the purposes of mating and migration during the fall and winter. Overall, this ecotype travels less than one hundred kilometers between summer and winter ranges (Thomas and Grey 2002).

2.1.2 Woodland caribou biology

Woodland caribou are dark brown members of the Cervidae family. Their average shoulder height is between 1.0 and 1.2 meters; the average weight of females ranges from 110 to 150 kg, while males range from 160 to 210 kg. Both sexes grow antlers annually, though less-dominant females may lack antlers or grow only one (Thomas and Grey 2002). A distinctive characteristic of woodland caribou is their large hooves with slightly webbed toes. These large webbed hooves reduce sinking when walking in snow, act as shovels when cratering for lichen under snow and aid in propulsion when swimming (Banfield 1974; Kelsall 1984). Caribou also have hollow hairs that aid in thermo-insulation and buoyancy for swimming. Finally, caribou have characteristic dew claws set on the posterior side of each hoof. This increases the weight-

bearing area for the caribou through their hooves and improves stabilization while walking through snow (Banfield 1974; Kelsall 1984; Thomas and Grey 2002).

2.2 Habitat Use

There are three terms most often associated with habitat use studies: 1) use; 2) selection and; 3) preference. Manly (2002) defines the use of a habitat or resource as the quantity of the habitat or resource used by an individual or population during a fixed period of time. Habitat selection is defined as the process by which an animal chooses a habitat or resource, and preference is defined as the likelihood of a habitat or resource being selected if all habitats or resources are equally available (Johnson 1980; Manly 2002). When the proportional use of a habitat by an animal exceeds its proportional availability in the landscape, the habitat is said to be selected (Manly 2002). For the purposes of this thesis, landscape is defined as " a mix of local ecosystem or land use types is repeated over the land forming a landscape, which is the basic element in a region at the next broader scale," (Forman 1995, pg 134).

In general, individuals or groups make "decisions" about what resource or habitat patch (a landscape element defined by its size, form or nature; Burel and Baudry 2003) to use and how to use it (Orians and Wittenberger 1991). Habitat selection theory proposes that individuals will select resources that improve their chances of survival or reproductive success (Levins 1968; Orians and Wittenberger 1991). Conversely, individuals that use less beneficial resources experience reduced chances for survival or reproductive success. Resources that are regularly evaluated in habitat studies include habitat variables associated with foraging or hunting, reproduction (e.g. migration areas, rutting or denning), those related to protection from environmental hazards and weather, and those that provide shelter from predators (Smith and Smith 2000).

2.2.1 Resource selection functions

Habitat use and selection are often quantified using resource selection functions (RSFs; Manly 2002). Resource selection functions are models that compare a species' habitat use with habitat availability (Manly 2002; Environment Canada 2011). This can be achieved by statistically comparing an individual's or population's known habitat use to a series of random points (representing available habitat locations) within a defined area. A key assumption of RSF models is that resource selection occurs in a hierarchical fashion (Manly 2002). Resource selection functions can also incorporate other variables such as population density, interspecific competition, the characteristics of available forage, and predation pressure, to help account for factors that may influence behaviour beyond habitat preference alone (Peek 1986; Manly 2002).

There are many statistical methods that can be used to create an RSF. The most common methods for computing RSFs include logistic regression (Manly *et al.* 2002), generalized linear models (GLMs), and generalized estimating equations (GEEs; Mcloughlin *et al.* 2010; Koper and Manseau 2012). Generalized linear models are one of the more common methods for creating an RSF. They are an extension of linear models that generalize to data that allows for use of dataset with non-normal error structures (Venables and Ripley 1999). This is accomplished through use of a link function (Quinn and Keough 2002; Koper and Manseau 2009, 2012). Generalized linear models can also handle categorical, continuous and binary data within a single model (Quinn and Keough 2002; Koper and Manseau 2009, 2012). Generalized linear models consist of three components: the random component, the systematic component and a link function. The random component of the GLM consists of the model response variable (*Y*) and a probability distribution (such as a normal, binomial, Poisson, or negative binomial

distribution; Quinn and Keough 2002). The systematic component identifies the explanatory variables that make up the parameters (β) of the model.

The link function of the GLM connects or "links' the random error or residual and systematic components of the model. There are several types of link functions, varying based on the type of model or type of data within a model. Identity link functions are used for data with a normal distribution, log link functions are used for count data, and logit link functions are used for binary data and logistic regressions (Quinn and Keough 2002). In a GLM, all levels within a categorical variable are compared with one other level, the reference level. Therefore, it is important that the reference level be biologically meaningful. Thus a common, abundant or representative category type is selected to be the reference level to allow for comparison to a common feature across the model.

Resource selection functions are a popular tool in species management, particularly with boreal woodland caribou. Environment Canada (2011) developed RSF-based models to describe habitat use by local populations of woodland caribou. Results of these RSFs indicated that the measurement of total disturbance (natural and anthropogenic) within a caribou range was the best predictor of cow-calf ratios (recruitment level) in boreal woodland caribou populations. Other authors have developed RSFs at multiple spatial and temporal scales to evaluate habitat use of woodland caribou to inform management decisions. Polfus *et al.* (2011) determined that northern mountain woodland caribou showed hierarchical and seasonal avoidance of human presence on the landscape, avoiding town sites more in the winter and avoiding cabins, camps and mines during the summer. Brown *et al.* (2007) found that caribou in northern Ontario preferred areas with large patches of mature black spruce forests. Johnson *et al.* (2004) used

RSFs to describe caribou habitat selection across multiple scales finding that at the habitat-patch and landscape scales, caribou preferred areas with pine species, lakes, rivers and grasses.

2.2.2 Foraging theory

Foraging theory is concerned with an animal's or species' acquisition of food (i.e. where to search for food, when to feed, which foods to consume, and feeding duration; Schoener 1971; Pyke *et al.* 1977; Stephens & Krebs 1986; Owen-Smith *et al.* 2010). These decisions take place at multiple spatial and temporal scales, from food patches to home ranges and seconds to decades (Owen-Smith *et al.* 2010).

Foraging is best described as an area-restricted search for food (Owen-Smith *et al.* 2010). The act of foraging is normally interspersed with periods of rest or activities such as migration or predation avoidance (Owen-Smith *et al.* 2010). If predators are present in an area and can influence a forager's fitness (i.e. ability to survive and pass on genetic material) or behaviour, the forager will often avoid habitats with higher predation risks to maximize its potential fitness (Pyke 1984; Belovsky 1991).

Optimal foraging theory was developed by MacArthur and Pianka (1966) and Emlen (1966) as an attempt to link forage or prey choices with a population's carrying capacity (Belovsky 1991). The core message of optimal foraging theory is that regardless of origin, foraging behaviours develop to minimize feeding and processing time while maximizing nutrient intake (Belovsky 1986; Stephens and Krebs 1986; Belovsky 1991). Under optimal foraging theory, these two goals tend to lead to foragers selecting the habitat that provides the greatest energetic returns (MacArthur and Pianka 1966; Belovsky 1991).

2.2.3 Caribou foraging behaviour and habitat use

Woodland caribou habitat use has been studied at a number of different scales. Most commonly, woodland caribou habitat is described at either a fine or broad spatial scale. Fine scale habitat use describes forage species or habitat patch use, while broad scale refers to a range or landscape-level scope of study (Wiens and Milne 1989). At the habitat patch scale, woodland caribou select individual patches that efficiently provide food (Stuart-Smith *et al.*1997; Rettie and Messier 2000).

At the seasonal or home range scales, caribou select large continuous tracts of forest, preferably old growth (Thomas and Grey 2002). During the winter months, woodland caribou primarily forage in mature to old-growth coniferous forest, primarily consisting of spruce (*Picea* spp.), pine (*Pinus* spp.), balsam fir (*Abies balsamea* L. Mill) or tamarack (*Larix laricina* Koch) abundant with lichen (Rettie and Messier 2000; Courtois 2003; Environment Canada 2008). During non-snowpack months, woodland caribou use peatland forest types intermixed with uplands dominated by mature to old-growth forest (Stuart-Smith *et al.* 1997; Rettie and Messier 2000; Courtois 2003). At this time of year, caribou prefer forbs, sedges, grasses and other vascular plants (Thomas and Gray 2002). It has also been noted by Bryany *et al.* (1985) that deciduous browse is more nutritious and palatable than most coniferous species for ungulates in general. Breeding female caribou in particular have been noted to eat *Equisetum* spp. and graminoids during the spring, which contain important nutrients to support lactation (Helle 1980 *in* Rettie and Messier 2000). The Slate Islands caribou population has a similar summer diet to that of other woodland caribou populations, with the difference being that the Slate Islands caribou can deplete all accessible preferred forage due to their confined habitat (Bergerud *et al.* 2007).

All caribou spend a large portion of their day browsing, with the amount of ground covered and plant species browsed varying based on geographic area and forage availability. The foraging activities also overlap with other activities, including seasonal migrations, predator avoidance and reproductive activities. Thus, foraging activities are not only driven by a caribou's selection of available forage but are also influenced by factors such as seasonality, predation, human presence, disturbance on the landscape and the availability of forage (Kelsall 1984).

Predator avoidance can also play a role in caribou habitat use and selection; Miller (1982) suggested that woodland caribou are cautious when using habitats with a dense understory, fearing ambush by predators that may be hiding within vegetation (Belovsky 1991). Crisler (1956) and Kelsall (1968) also support this, suggesting that caribou are vulnerable to ambush by wolves in areas containing dense understory (Belovsky 1991). Similarly, Belovsky (1991) suggested that caribou may prefer foraging in areas close to shorelines during summer months, allowing them to flee from potential predators by escaping into the water (Belovsky 1991). This use of shoreline and lakeside environments has also been also observed in other aspects of caribou behaviour. Woodland caribou populations in Ontario have been noted to use islands and shorelines particularly during calving periods (Bergerud 1985; Bergerud and Page 1987; Bergerud *et al.* 1990; Environmental Canada 2011). This use of islands and shorelines is thought to allow the cow/calf pair to be inaccessible to predators and provide an avenue for escape (into the water; Bergerud and Page 1987; Environmental Canada 2011).

2.2.4 Caribou and anthropogenic features

Numerous studies have noted that woodland caribou distributions are influenced by alterations to their landscape. Both natural (i.e fire) and anthropogenic disturbances can negatively influence boreal woodland caribou populations both behaviourally and

demographically. Negative effects on caribou populations growth associated with anthropogenic disturbance include habitat removal (i.e. deforestation via anthropogenic activities; Environment Canada 2008), avoidance of industrial developments due to sensory disturbance (Dyer *et al.* 2001, Schaefer and Mahoney 2007), roads acting as barriers (Dyer *et al.* 2002), enhanced predator movement along roads and trails (James and Stuart-Smith 2000), and enhanced alternative prey leading to increased predation levels (Seip and Cichowski 1996).

In a national evaluation of caribou demography and range disturbance in Canada, Environment Canada (2008) concluded that that there was a correlation between disturbances on the landscape and reduced caribou recruitment. Analysis provided through this report found that caribou ranges overlapping with high rates and areas of disturbance (i.e. fire and human development) results in low calf recruitment rates due to increased predation on calves and adults (Environment Canada 2008; 2011).

The presence of humans on foot also affects caribou behaviour (Duchesne *et al.* 2000). For example, caribou spend more time being vigilant and less time foraging when ecotourists are present within their range (Duchesne *et al.* 2000) but this effect appears to dissipate with time (i.e. with continued exposure to ecotourists). Similarly, wild reindeer in Svalbard were shown to become habituated to humans on foot (though it is important to note that there are no natural predators on Svalbard; Coleman *et al.* 2001). These observations suggest that while *Rangifer* species generally avoid area with anthropogenic disturbances ((Mahoney and Schaefer 2001; Environment Canada 2011), they may have a tolerance for human presence occurring at a smaller scale and lower level of intensity (Duchesne *et al.* 2000).

2.3 Population Structure and Dynamics

2.3.1 Population growth rates

Understanding the variables that affect population growth and reproduction is fundamental to understanding population dynamics. Recruitment (i.e. annual number of new individuals that survive to adulthood), predation rates, inter and intraspecific competition, sex and age ratios, availability and quality of habitat, weather and other environmental variables, disease, parasitism, and anthropogenic disturbance all interact to affect population growth (Gaillard *et al.* 1998; Ballard *et al.* 2001).

Ungulate survival rates and population growth are also influenced by age structure (Gaillard *et al.* 2000; Gaillard and Cote 2003; Wittmer *et al.* 2007). Populations with a high proportion of reproductive-aged females may contribute to higher recruitment rates, and as a result, higher rates of population growth, whereas populations with fewer reproductive-aged females experience a lower population growth rate (Wittmer *et al.* 2007). Predation is also regularly cited as a variable that restricts ungulate population growth (Gaillard *et al.* 1998; Ballard *et al.* 2001), including moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus),* woodland caribou, and other ungulate populations (Bergerud 1974; Connolly 1978; Bergerud *et al.* 1983; Bergerud and Snider 1988; Seip 1991; Van Ballenberghe and Ballard 1994; Gese and Knowlton 2001; Stuart-Smith *et al.* 1997; Rettie and Messier 1998; Wittmer *et al.* 2005).

2.3.2 Population regulation

Bottom-up control and *top-down control* are terms that are commonly used to describe population regulation include (Smith and Smith 2001). Bottom-up control refers to species at lower levels of a food chain regulating species at higher trophic levels. Bottom-up control can

move through a food chain to influence even top predators (Smith and Smith 2001). This type of population regulation is observed in mule deer (*Odocoileus hemionus;* Pierce *et al.* 2012). It has been documented that the availability of preferred mule deer forage (bitterbrush; *Purshia tridentata L*) regulates the deer population and size, ultimately affecting the number of predators that can be supported in the area (i.e. mountain lion, *Puma concolor;* Pierce *et al.* 2012).

Conversely, top-down regulation refers to processes where the species at a higher trophic level regulate species at a lower trophic level (i.e. prey species or plants; Smith and Smith 2001). Under top-down control, as predator numbers decrease, the number of herbivores increases. For example, wolf-elk-aspen interactions in Yellowstone National Park are a well-documented example of top-down regulation. Between 1914 and 1926, wolves (the main predator of elk in the park; *Cervus elaphus*) were extirpated from the park (Ripple *et al.* 2001). With no wolf predation, elk populations quickly grew and began to suppress growth of trembling aspen (*Populus tremuloides* Michx). With wolf re-introductions in 1995, elk populations declined within the park. Elk also began to use more open habitat outside the protected area to improve vigilance against predation. The decline in herbivore presence resulted in the improved vegetative growth of aspen within the park boundaries (Ripple *et al.* 2001).

Top-down regulation is also well documented in woodland caribou populations in Canada. In the majority of populations, the key determinant of caribou population dynamics is predation from grey wolves, grizzly bears (*Ursus arctos*) or black bears (*Ursus americanus*) (Bergerud 1974; Seip 1991; Stuart-Smith *et al.* 1997; Rettie and Messier 1998; Whittmer *et al.* 2005). However, under certain circumstances, bottom-up regulation might also limit caribou populations. Examples include the Slate Islands and George's Island caribou (located in Labrador), which are restricted in movement and do not experience regular predation (Bergerud

et al. 2007; Jeffery *et al.* 2007). Similarly, the George River and the Central Arctic barren ground caribou populations may be limited by summer forage through bottom-up regulation (Cameron and Smith 1992; Crete and Hout 1993). During periods of low summer forage these caribou populations are regulated through decreased survival and recruitment rates as a result of decreased fat reserves in females (Cameron and Smith 1992; Crete and Hout 1993).

Carrying capacity

The term carrying capacity (*K*) describes the relative maximum population size an environment can support for a specific species (Smith and Smith 2001; Hui 2006). The carrying capacity for a species varies based on forage availability and the pressures of competition. The effects of each of these factors may vary from season to season, year to year, or with the availability of resources (Smith and Smith 2001).

Other variables can also prevent a population from reaching its carrying capacity. Diseases and parasites can contribute to high mortality levels in ungulates. For example, the winter tick (*Dermacentor albipictus*) is a common parasite within moose populations in winter months which causes severe itching, hair and weight loss on affected moose (Samuel 2007). This parasite can lead to population-wide die-offs (Samuel 2007) and is hypothesized to have contributed to moose population declines in western Manitoba during the winter of 2002 (CCWHC 2002).

Inbreeding depression can also prevent populations from reaching their carrying capacity through reducing population health and depressing recruitment rates (Stephens and Sutherland 1999; Wittmer *et al.* 2005). Populations that fluctuate and have inconsistent patterns in growth can also become more susceptible to the Allee effect. The Allee effect is defined as the decline in individual fitness as a population declines, making the population more vulnerable to extirpation

at lower densities (Courchamp *et al.* 1999; Stephens and Sutherland 1999; Courchamp *et al.* 2008). Inbreeding depression and Allee effects are most common in small isolated populations, such as the Slate Islands caribou population. These effects can be counter-acted through reintroduction programs; however, these programs have had limited success in caribou populations (Bergerud *et al.* 2007; Gorden 2012).

Boom-Bust cycles

As populations approach or exceed carrying capacity, they begin to over-use and degrade their available resources (Ballard *et al.* 2001). With increased competition for forage, the physical condition of individuals begins to decline, resulting in lower birth rates and increased mortality (Ballard *et al.* 2001). This decline in individual health results in a decline in population size and can contribute to a higher chance of extirpation. These patterns of decline are referred to as "Boom-Bust" events (Ballard *et al.* 2001; Carr *et al.* 2012). Resources may recover after a population decline but they may subsequently support a lower carrying capacity of herbivores than in previous years due to damage incurred during high use periods (Ballard and Van Ballenberghe 1997).

Moose and grey wolf population crashes have been well documented on Isle Royale (Lake Superior) over the course of a series of long-term monitoring projects. Historically, moose population estimates ranged from 600 (1.1/km^2) to 1500 (2.8/km^2) moose within the 544 km^2 park, while the wolf population stayed around 24 individuals (Peterson 1999). From 1980 to 1996, canine parvovirus (CPV) was documented in the wolf population and was the suspected in a wolf population crash that resulted in a decline from a historic high of 50 animals to 14 animals (Peterson 1999). After the wolf population crash, the moose population grew to approximately 2,412 individuals, and subsequently crashed to approximately 500 individuals in 1996 due to

26

starvation (Peterson 1999). It has been hypothesized that the poor reproduction now seen in the wolf population is a result of inbreeding depression associated within the genetic bottle-neck resulting from the wolf population crash (Peterson 1999). This low level of genetic diversity and low level of population growth is thought to leave the Isle Royale wolf population at risk of being extirpated within the park (Peterson 1999).

2.3.3. Distribution

Spatial distribution of individual animals may depend on i) level of competition within a given area, ii) habitat preference, iii) resource availability and iv) threat of predation (Smith and Smith 2001). Three classic spatial distributions tested in ecological studies are random (individuals are distributed randomly and independently from one another; Smith and Smith 2001), uniform (individuals are evenly spaced) and clumped or aggregated distributions (individuals are grouped together; Blackith 1958; Brown and Orians 1970). Of these three distribution patterns, "clumped" is generally considered to be the most common spatial pattern (Brown and Orians 1970). Clumping of individuals can be seen across many different species and behaviours, and is particularly noted in species that form social and/or mating groups (i.e. green frog [*Rana clamnitan*]; Brown and Orians 1970).

In addition to random, uniform and clumped distributions, the ideal free distribution (IFD) is a theoretical distribution type that is regularly examined in ecological studies (Fretwell and Lucas 1970; Pyke 1984; Belovsky 1991). The primary hypothesis of IFD predicts that competing species or individuals will distribute themselves across a given area based on the proportion of high-quality habitat available within that given area (Fretwell and Lucas 1970). When this occurs, the habitat with the next-best quality will begin to be used once the highest quality habitat has been depleted or as habitat becomes saturated with territories (Pyke 1984;

27

Belovsky 1991). While the IFD is commonly considered a theoretical distribution, there are some examples of the IFD existing in "wild" populations. For example, the red knot (*Calidris canutus*) has a distribution that is best described as an ideal free distribution (Quaintenne *et al.* 2011). In addition to postulating the IFD, Fretwell and Lucas (1970) also provide two alternative hypotheses; the territorial hypothesis and the spacing hypothesis. The territorial hypothesis predicts individuals (most commonly dominant males) will be distributed across habitats in a territorial manner, pushing subordinates out of the higher quality habitat and resulting in an ideal dominance distribution or ideal despotic distribution (IDD). This hypothesis also predicts that individuals in the highest quality habitat will exist at higher densities and enjoy greater fitness than those in lower quality habitats. Ideal despotic distribution has numerous examples found in wild populations and has been noted particularly in avian populations (Eckert and Weatherhead 1986).

A third and final hypothesis outlined by Fretwell and Lucas (1970) is the spacing hypothesis; this hypothesis essentially serves as an alternative hypothesis for ideal free or ideal despotic distributions, predicting that territorial behaviour has evolved to space individuals away from one another as much as possible. This type of distribution has been documented in species that have strong social dominance structures, such as chimpanzees (*Pan troglodytes*; Murray *et al.* 2006)

2.3.4 Competition

Competition is defined as an interaction between individuals that is detrimental to one or both of the parties involved (Smith and Smith 2001). This interaction normally occurs between individuals that share limited resources, such as food, habitat or mating opportunities (Smith and Smith 2001). Common themes of competition include competing for access to forage or prey,

refuges from predators, refuge from the weather, access to breeding opportunities, or denning
sites.

Intra and interspecific competition

Intraspecific competition (i.e. competition among members of the same species; Birch *et al.* 1950) is common for forage in ungulate populations. One of many examples of intraspecific ungulate competition is the study of red deer (*Cervus elaphus* L.) on the Isle of Rhum, Scotland (Thouless 1990). Female red deer reduced the amount they ate when more dominant females approached a feeding site. Thouless (1990) concluded that red deer compete for forage in a passive manner, through subordinates avoiding dominant individuals. Competition can also be studied remotely (i.e. through use of GPS or satellite collars); for example, a project in Norway captured and collared female moose to monitor their use of diversionary feeding station use and habitat-selection (Beest *et al.* 2010). Moose maintained a high population density around the feeding stations, regardless of level of competition. Beest *et al.* concluded that intraspecific resource competition was not an influencing factor for this study population.

While intraspecific competition is more commonly studied in ungulate populations, there are also examples of interspecific ungulate competition (i.e. competition between individuals of different species; Schoener 1971). In a study examining cervid competition and habitat use in Montana, Jenkins and Wright (1998) found that although prime habitat was located in both the southern and northern portions of the study area, moose were only observed using habitat in the northern study area. The authors suspected that competition for winter browse from white-tailed deer and elk populations in the southern study area may have competitively limited moose from exploiting the southern study area.

Interspecific competition for forage is not regularly studied in woodland caribou

populations because they distance themselves from other ungulate populations through selecting

habitats that differ from habitats selected by sympatric ungulate species, presumably to avoid

interspecific competition (Seip 1991; Wittmer *et al.* 2005; Dussault *et al.* 2012). However,

interspecific competition for predator-free or "enemy-free" spaces (i.e. a way of living or an area

that reduces a species vulnerability to predators; Jeffries and Lawton 1983) is common

occurrence between caribou populations another ungulate species. This type of indirect

interaction between prey populations is called apparent competition (Holt 1977; Jeffries and

Lawton 1983; Holt 1984). In systems with a predator species and two or more prey populations

(i.e. moose-wolf-caribou predator-prey systems), a change in the population of the dominant

prey species can lead to the decline or the extinction of the other prey population (Jeffries and

Lawton 1983; Wittmer *et al.* 2005). In this circumstance, predators can begin to

disproportionally reduce the population of the least competitive or slowest reproducing prey

species. Competing prey species are thought to co-exist over the long term only in areas where

they are spatially separated, or where they have access to refuges during higher levels of

predation (Holt and Lawton 1994; Wittmer *et al.* 2005).

2.4 Predation

2.4.1 Predator-prey relationships

Predation can have either lethal or non-lethal effects on prey populations. While the term

lethal effect is self-evident, a non-lethal effect is best described as the "costs that arise from

behaviours that enhance short term survival in the presence of a predator but that decrease long

term fitness, such as body condition or reproductive potential" (Cresswell 2011, pg 5). Prey

behaviours associated with non-lethal effects of predation include activities such as avoidance of

preferred habitat in favour of predation-reducing habitats, increased vigilance behaviours and reduction of mating displays (Lima 1998; Cresswell 2008; Cresswell 2011). Variables that influence how predation risk affects prey include prey-habitat heterogeneity, availability of secure cover, synchrony of prey birthing season, prey size, vulnerability by age class, and the ratio between the different prey species within a given area (Skogland 1991; Gese and Knowlton 2001).

Predators may be specialists or generalists (also referred to as obligate or facultative; Gese and Knowlton 2001). A specialist predator is a species that focuses on one primary prey species, whereas a generalist predator switches among prey species based on prey availability (behaviour referred to as prey switching; Gese and Knowlton 2001).The population size of specialist predators fluctuates with the availability of their primary prey species. A well-known example of population fluctuation under predation by a specialist species is the cyclical population fluctuations of lynx and snowshoe hare (*Lepus americanus*) populations (Elton and Nicholson 1942). Elton and Nicholson (1942) demonstrated that lynx population size varied with the rise and fall of hare populations. Conversely, an example of a generalist predator that exhibits prey switching behaviour is grey wolves interacting with moose and woodland caribou. In areas where moose and woodland caribou populations overlap, woodland caribou experience more predation than they do in areas without moose (Seip 1991, 1992). In these areas, wolves hunt both caribou and moose populations, ultimately reducing the population size of the more vulnerable woodland caribou.

Under certain circumstances, predation completely suppresses prey population growth. This type of interaction is commonly seen in ungulate-predator populations (Ballard *et al.* 2001). This scenario is referred to as a predator pit, where the prey population cannot increase due to

density-dependent predation, resulting in a perpetually low population density (Bergerud 1980; Peterson 1988; Ballard *et al.* 2001; Figure 1). A prey population can escape a predator pit if the predator population decreases or the prey population increases (Messier 1994).
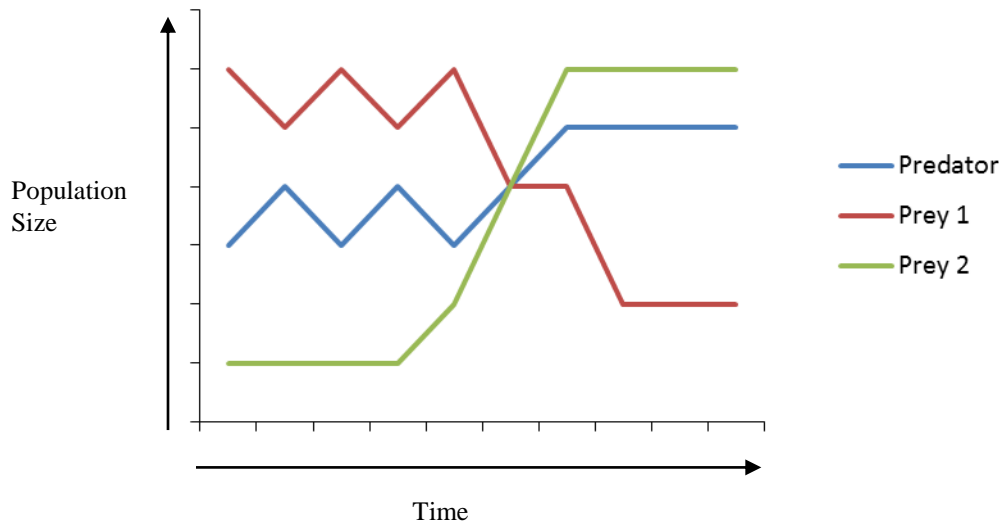
Figure 1: Graphical representation of a simple predator pit scenario in a two prey – one predator system. In this scenario, prey 1 and predator co-exist at sustainable levels until prey 2 enters the system. Prey 2 increases the capacity for the predator populations, which ultimately begins to suppress the less competitive prey 1 population. Adapted from Ballard *et al.* 2001.

Situations where prey switching occurs can also result in a predator pit. In a study examining grey seal (*Halichoerus grypus*) diet in the North Sea, Smout *et al.* (2013) demonstrated that seals are generalists and exhibit prey switching behaviour. A high abundance of available prey species maintains high seal populations and may result in depression of cod (*Gadus morhua*) populations. A similar scenario has also been observed between moose-caribou-wolf interactions (Seip 1991, 1992). High moose populations work to support a high wolf presence within given an area, resulting in a suppression of caribou populations.

2.4.2 Caribou predator-prey interactions

Predation is the most limiting factor for the majority of woodland caribou populations in Canada (Rettie and Messier 1998; Thomas and Grey 2002; Wittmer *et al.* 2005). While wolves are the main predator of woodland caribou (James and Stuart-Smith 2000), other predators of woodland caribou include black bear (Ballard 1994), coyotes (*Canis latrans*), wolverine (*Gulo gulo)* and eagles (*Aquila chrysaetos* and *Haliaeetus leucocephalus*; Crete 1995). Bergerud (1988) found that wolf densities greater than $6.5/1,000 \text{ km}^2$ may lead to a decline in woodland caribou populations. Studies examining predator removal in woodland caribou areas also support the contention that predators are the primary cause of caribou declines. A study conducted on woodland caribou populations in British Columbia documented an 11% increase in caribou recruitment rates upon two years effort of wolf removal within the area of the Horseranch population, resulting in population growth for this group (Bergerud and Elliott 1998).

In circumstances where apex predators (i.e. wolves) are removed from an ecosystem, it is important to be aware of mesopredators (intermediate or "middle ranked" carnivores) and their potential effects on prey species. In the absence of large carnivores, mesopredators can then become the top predators, leading to cascading effects and suppression/extirpation of preferred mesopredator prey species in some circumstances (Prugh *et al.* 2009). For example, coyotes (*Canis latrans*) function as top predators in many areas of the United States where wolves have been extirpated (Crooks and Soute 1999) but in Yellowstone National Park where wolves have been reintroduced, they function as a mesopredators (Berger *et al.* 1998). Relative to caribou, mesopredators generally do not affect recruitment or survival rates at the population level but it is important to recognize their potential role in the food web relative to wolves and bears.

Wolves exhibit prey-switching behaviour, allowing their populations to remain high even if rates of predation upon a particular species are low (Seip 1991). Prey-switching increases the probability that caribou populations will be suppressed by a high predator population. Seip (1991) proposed that woodland caribou reduce their susceptibility to wolf predation by being widely dispersed and living at low densities. Woodland caribou also avoid other ungulate species, thereby avoiding areas with higher prey densities that support larger predator populations. Woodland caribou have been documented to use enemy-free spaces with poor quality forage (i.e. mature conifer stands) during summer months, presumably in an attempt to distance themselves from other prey species (Courtois 2003). Mountain caribou have also been documented to use areas with higher elevations in attempt to distance themselves from alternative prey and predator populations (LeReache and Linderman 1975; Terry *et al.* 1994).

From a physiological standpoint, caribou are considered relatively more vulnerable to predation that moose and deer. Caribou are small and are unable to fight off predators as effectively as larger and more aggressive species, such as moose (Seip 1991). Caribou also have a low reproductive rate compared to other ungulate species. Moose and deer regularly produce twins, while caribou never produce twin calves (Seip 1991). Although caribou pregnancy rates can range from 80% - 90% of females in a population (Rettie *et al.* 2000; James *et al.* 2004; Wittmer *et al.* 2005), calf mortality within the first year of life is consistently high (30 to 50% ; Thomas and Gray 2002). This high level of calf mortality is often attributed to predation (Bergerud *et al.* 2000; Thomas and Gray 2002; Environment Canada 2011) and results in a low recruitment rate, reducing replacement rates. Combined, these factors make caribou less more vulnerable to depredation than other ungulate (Seip 1991).

Predation, in combination with forage availability, influences caribou distributions (Wittmer *et al.* 2005). In Ontario, caribou have been noted to space themselves across their home range and away from areas containing high wolf populations (Bergerud *et al.* 1992). In areas where they cannot space themselves away from wolves, caribou forage along shorelines, allowing them to browse for forage while staying near an escape route from predators during the summer months (Bergerud and Page 1987). Bergerud (1985) purposed that this preference for islands and shorelines lead to woodland caribou inhabiting the Slate Islands, Michipiocten Islands and Pic Islands in Ontario. Additionally, woodland caribou have been documented to distance themselves away from linear corridors, dense understories (Young and McCabe 1998) and areas which support higher ungulate densities (Siep 1992; Cumming 1996; Boan *et al.* 2014) in attempt at reducing predator interactions.

In the absence of predators, caribou populations can grow to a higher density than populations that are suppressed by predation. For example, the average caribou density on the Slate Islands is 7.3 - 8.4 individuals/ km^2 in the absence of predation (Bergerud *et al.* 2007). By comparison, the national average woodland caribou density is 3.3 caribou per km^2 including populations that interact with predators (Environment Canada 2008). The barren-ground caribou populations of the Coat and Southampton Islands (located in the north end of Hudson's Bay) also have no known predators (Ouellet *et al.* 1997). Like the Slate Islands caribou, the Southampton Islands caribou are regulated by forage availability, though this population is thought to be more influenced by winter than summer forage (Ouellet *et al.* 1997). Another example of a predator-free caribou population is the George's Island woodland caribou population. Like the Slate Islands population, the relatively high population density of the George's Island population (22.5

- 26.5 caribou km^2) is attributed to a high recruitment and female survivorship in absence of predation (Jeffery *et al.* 2007).

2.5 Summary of Literature Review

Predation and forage availability are the most influential variables affecting woodland caribou distributions in Canada (Environment Canada 2011). Of these, predation is the most limiting variable to caribou population growth (Seip 1992). In areas containing alternative prey species, predator pits potentially keep caribou populations from rebounding through maintaining low recruitment rates within the population (Bergerud *et al.* 2000; Thomas and Gray 2002; Environment Canada 2011). Predation also influences caribou habitat use and selection through forcing caribou to spread themselves away from high quality forage habitat in preference of habitat with lower predation risk (Siep 1991; Rettie and Messier 1998; Courtois 2003).

Interspecific and intraspecific competition for forage is unlikely to limit caribou distributions because woodland caribou generally live at a low population density and distance themselves from other ungulate populations (Rettie and Messier 2000). As habitat specialists, caribou select for older growth habitat containing lichen accessible during snow-pack months (Rettie and Messier 2000; Courtois 2003) and palatable plant species during the summer (Thomas and Gray 2002).

The Slate Islands caribou hypothesized to have different limitations to than mainland caribou populations because the Slate Islands are 1) normally predator-free and 2) a closed system (an isolated archipelago in Lake Superior). Previously, Bergerud *et al.* (2007) found that availability of summer forage and body weight heading into the winter months was negatively correlated with winter survival rates; thus, Bergerud concluded that summer forage is considered to be the most limiting factor for the Slate Islands caribou (Bergerud *et al.* 2007). Despite what is

known about the Slate Islands population, the main drivers for the caribou's habitat selection and

spatial distribution beyond fine-scale patch selection have yet to be described.

CHAPTER 3: METHODS

3.1 Site Description: Slate Islands Provincial Park

Slate Islands Provincial Park is situated near the northern shore of Lake Superior, approximately 13 km offshore from Terrace Bay, Ontario. The archipelago covers approximately 37.2 km^2 and consists of seven major islands (Carr *et al.* 2010; Figure 2). Elevation of the archipelago ranges from 600 meters above sea level (masl) to over 1,000 masl. The climate is maritime due to the Slate Islands remote location in Lake Superior. The park is monitored via a seasonal weather buoy by Environment Canada (Environment Canada n.d.a). There was a federal weather station located on the islands from 1967 to 1988; however, this station was closed in 1989 (Bergerud *et al.* 2007) Historical daily average temperature (as produced by the near-by Terrace Bay weather station) ranges from -14.7 degrees Celsius in the winter to 14.5 degrees in the summer, with historical temperature extremes ranging from -45.0 to 30.0 ºC (Table 2).
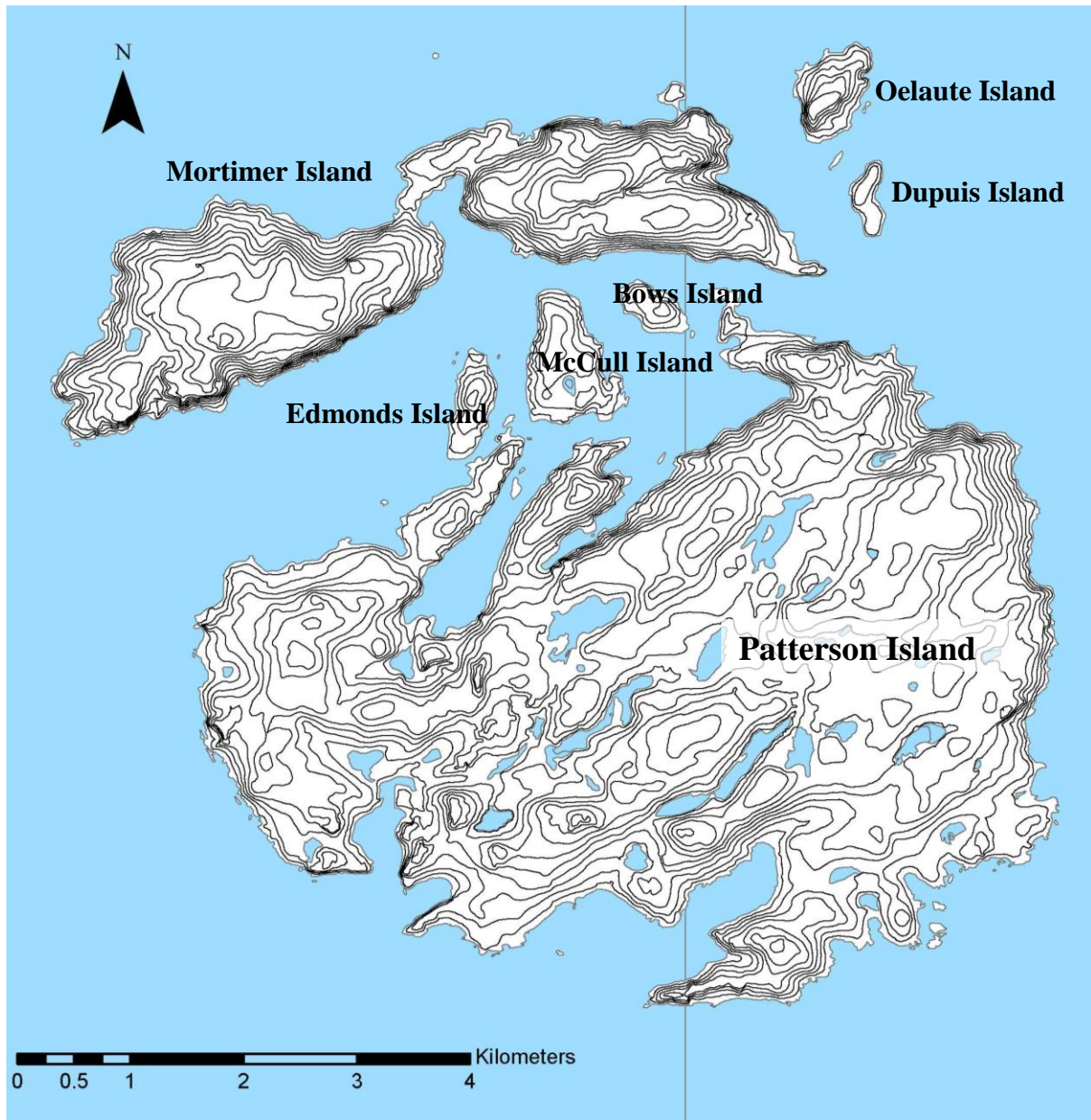
Figure 2. A topographic map of the Slate Islands Provincial Park (Ontario, Canada). Map created in ArcMap GIS with data provided by Ontario Ministry of Natural Resource.

Table 2: Historical climate data (1971 to 2000) for Slate Islands Provincial Park provided by the all season weather station in Terrace Bay, Ontario. Data from Environment Canada n.d.a.

Month	Climate Variable	Statistic
January	Daily Maximum/Minimum temperature (°C)	-8.9/-20.5
	Extreme Maximum/Minimum temperature (°C)	5.0/-45.0
	Average Snowfall (cm)	53.6
July	Daily average temperature for July (°C)	14.5
	Daily Maximum/Minimum temperature (°C)	19.7/9.3
	Extreme Maximum/Minimum temperature (°C)	30.0/-0.5
	Average Rainfall (cm)	80.5

The Slate Islands landscape has been strongly influenced by past human activities. The islands were extensively harvested for white pine (*Pinus strobus* L.) during the late 19th century and again during the 1930's (OMNR 2011; Bergerud unpublished data). Evidence of these activities includes abandoned cabins and camps (Figure 3), old logging roads and remains of an old horse barn (Bergerud unpublished data). There is also evidence of mining throughout the archipelago, with two entrances of mine shafts remaining on the islands today.

Figure 3. The Come 'n Rest cabins, originally built in the 1930's during logging of the park. Located on McCull Island, Slate Islands Provincial Park, Lake Superior, Ontario.

The most recent habitat classification of the Slate Islands was obtained from a set of 1974 aerial photographs (Table 3). Arboreal lichens are present on most trees, with lichen species and quantity varying by tree age and species. Tree species, including white birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides* L.), have established in logged and burnt areas of the archipelago (Given and Soper 1981). The Slate Islands also contain a number of arctic-alpine plant species. The majority of the archipelago has experienced fires, the most recent of which occurred in 1902 (Bergerud unpublished data). The oldest forest stands of the islands have been dated to between 110 and 300-years old (Bergerud unpublished data).

Today, the Slate Islands are designated as a provincial park. Human activities are restricted to recreational boating, kayaking, camping, fishing, and research. Several tourism

outfitters based out of Terrace Bay provide non-invasive eco-tourism opportunities for caribou-watching along the shorelines of the Slate Islands. These recreational activities occur along the shoreline of the islands, with visitors rarely venturing into the interior of the islands.

Table 3. The classifications of the Slate Islands Provincial Park landmass and vegetation from 1979 aerial photography (Bergerud *et al.* 2007*).*

Landmass or Vegetation Type	Percentage of Provincial Park Comprised of Landmass	Total area* (km^2)
Meadows and sedge covered areas	<1%	<0.1
Lichen covered bedrock	1.4%	0.5
Alder (*Alnus viridis* Chaix. DC.)	1.9%	0.7
Lakes and ponds (total of 30)	3.3%	1.2
Conifer-sphagnum forest	3.9 %	1.5
Conifer-feathermoss forest	5.8 %	2.2
White birch forest (birch only)	14.0 %	5.2
Fir-birch forest (fir dominant)	21.1 %	7.8
Birch-fir forest (birch dominant)	48.5 %	18.0

* based on a total park area of 37.2 km^2

3.2 The Slate Islands Caribou

3.2.1   Description of the Slate Islands caribou

The first recorded evidence of woodland caribou on the Slate Islands was in 1907, when tracks were observed along the ice bridge connecting the Slate Islands to mainland at Terrace Bay (Middleton 1960 *in* McGregor 1974). Intensive study of the Slate Islands caribou began in 1972. They were monitored on an annual basis by A. T. Bergerud and co-workers in conjunction with the Ontario Ministry of Natural Resources (OMNR) from 1974 to 2003. Other research initiatives continued to periodically/occasionally monitor caribou populations from 2004 to

present, (Bergerud *et al.* 2007; Carr *et al.* 2012). Recent initiatives used radio collaring projects to collect data on a small subset of the population (Bergerud *et al.* 2007) and study of genetic variation of the Slate Islands caribou in relation to other populations (Rood *et al.* 1991).

The Slate Islands caribou have some characteristics that have not been observed in other woodland caribou populations (Figure 4). Unlike mainland caribou, many adult males (referred to as hummels) do not grow antlers until the age of 3 or 4, while relatively few females of this population grow antlers at all (Bergerud *et al.* 2007). This population has a smaller body than mainland caribou populations and contains a relatively high number of albino individuals (Bergerud unpublished data). Given that this population became isolated from mainland populations over 100 year ago, it is highly probable that these physical features are due to a high level of inbreeding and genetic drift (i.e. changes in the gene frequency and consequent relatedness in members of a small population due to restricted mating opportunities; Campbell *et al.* 1999).

Figure 4. Picture of mature adult male Slate Islands caribou. Picture taken mid-July 2008 on McCull Island, Slate Islands Provincial Park. Photo credit Jeff Renton (used with written permission).

3.2.2   Research on the Slate Islands caribou

The annual monitoring of the Slate Islands caribou has been facilitated by their restriction to the isolated archipelago. Decades of data have been collected on recruitment rates, foraging behaviour, forage competition, population density, and the influence of predation on population dynamics. The majority of the caribou data has been collected from the results of King census strip transects (adapted from Leopold 1953). The King census was originally developed in 1931

by A. Leopold as a method of surveying for ruffed grouse (*Bonasa umbellus*; Leopold 1933), and has subsequently been used to survey caribou on Slate Islands and other areas (Bergerud *et al.* 2007). The King census involves a solo observer walking straight-line transects, recording visual and auditory observations of the study species to provide an estimate of the population size within a given area (Leopold 1953; Bergerud *et al.* 2007).

In the Slate Islands Provincial Park, solo observers walked straight-line transects throughout the park, recording total distance walked, location and number of observed caribou and providing an estimate of distance to each caribou observation (Bergerud *et al.* 2007; Carr *et al.* 2012). A caribou observation was recorded upon sighting or hearing a caribou flush in the brush; a natural behaviour seen in almost all caribou when startled or approached in the forest(Bergerud *et al.* 2007). The total number of kilometers surveyed during leaf-out (primarily May/June) ranged between 25 and 158 km annually (Bergerud *et al.* 2007). The formula for estimating caribou population size via King Census is:

$$N= nA / 2LR$$

where *N* is the total estimated population size, *A* is the area censused, *n* is the number of animals observed along the transects, *L* is the length of transects and *R* is the mean sighting distance to observed animal or animals (Leopold 1933; Robinette *et al.* 1974).

Population estimates of the Slate Islands caribou were also recorded through mark-recapture sightings via the Lincoln Index (Lincoln 1930). For this population estimate, caribou were captured through use of bait and water-crossing traps, in which they were restrained and tagged (Bergerud *et al.* 2007). The mean number of tagged caribou each year (1975 to 1997) was 44 individuals. Sightings of tagged and non-tagged animals were recorded during transect surveys, blind observations and casual encounters at camp sites, and used in an estimate of the

population (Bergerud *et al.* 2007). The formula for estimating caribou population size via Lincoln Index is:

$$N = (n_1 \times n_2) / m$$

where N is the total population, n_1 is the total number of animals first marked during the capture period, n_2 is the total number of animals re-captured in the second effort of sampling during the re-capture period and m is the total number individuals found during the recapture period that were marked from the capture period (Lincoln 1930; Gregory *et al.* 2004).

Based on King census transect results, estimates of the Slate Islands caribou population have historically ranged from 104 to 606 individuals (mean = 262 ± 22 individuals; Bergerud *et al.* 2007). Population estimates via the Lincoln Index yielded a narrower range of 181 to 482 individuals (mean = 303 ± 64 individuals; Bergerud *et al.* 2007). These population estimates result in caribou population densities of approximately 7.3 caribou/km^2 and 8.4 caribou/km^2 for the King census transect and Lincoln Index, respectively.

The dietary preferences of the Slate Islands caribou have been well recorded. Bergerud *et al.* 2007 compared the availability of vegetative species reported by Bergerud in 1985 to Cringan's (1956) reporting of caribou vegetative preferences in 1949. Bergerud *et al.* (2007) documented preferred caribou summer forage to include highbush cranberry (*Viburnum edule* Michx), mountain ash (*Sorbus decora* Schnied), mountain maple (*Acer spicatum* Lam), dwarf bush honeysuckle (*Diervilla lonicera* Mill), trembling aspen (*Populus tremuloides* Michx), thimbleberry (*Rubus parviflorus* Nutt), and elderberry (*Sambucus pubens* L). Preferred summer herbs include big-leafed aster (*Aster macrophyllus* L Cass), wild sarsasparilla (*Aralia nudicaulis* L), fireweed (*Epilobium angustifolium* L Holub), ferns, dog berry (*Clintonia borealis* Aiton

Raf.), Canadian bunchberry (*Cornus canadensis* L.) and twinflower (*Linnaea borealis* L; Bergerud *et al.* 2007).

Though forage preferences have been determined for the Slate Islands caribou, broader habitat preferences of this population have not been identified. The Slate Islands caribou population is located in the Boreal Shield Ecozone, which includes also the Pukaskwa, Pen Islands, Rupert and La Sarre caribou populations. Broad summer habitat use of these populations is described as open canopies of mature black spruce forests and mesic peatlands with ericaceous species for calving habitat (Environment Canada 2008). Summer forage consists of *Equisetum spp*. and graminoids, which contain beneficial nutrients (specifically protein) for lactating cows (Helle 1980 *in* Rettie and Messier 2000). Winter habitat use has been described as contiguous mature coniferous forest (consisting of black spruce [*Picea mariana* Mill] and balsam fir) containing lichen species (Environment Canada 2008).

The main difference between the Slate Islands and mainland caribou populations is that the Slate Islands caribou can deplete their preferred forage due to their confined habitat. Subsequently, the caribou will consume less-preferred forage available in the park in order to avoid starvation (Bergerud *et al.* 2007). Species documented to compete for forage with the Slate Islands caribou include snowshoe hare (*Lepus americanus*) and Canadian beaver (*Castor canadensis*), although neither of these herbivores functionally deplete available forage (OMNR 2011).

Bergerud *et al.* (2007) hypothesized that summer forage is the foremost limiting factor of the Slate Islands caribou population during periods without predators (Bergerud *et al.* 2007). Data collected between 1974 and 2003 revealed two major caribou die-offs during the winters of 1984/1985 and 1989/1990 (**Error! Reference source not found.**; Bergerud *et al.* 2007).

Analysis of the Slate Islands caribou demographic data found that winter mortality rate was positively correlated with population density and the weights of female caribou in the fall, but was uncorrelated with abundance of winter lichens or snow depth during the winter months (Bergerud *et al.* 2007). These starvation events also coincided with little to no recruitment in the spring and summer following the winter, suggesting a high level of calf abortion (Bergerud *et al.* 2007). This resulted in a low recruitment level for several years post starvation event, contributing to a population decline (Bergerud *et al.* 2007). Bergerud postulated that these trends reflected a density-dependent population regulation based on the availability summer forage (Bergerud *et al.* 2007). Long term trend in caribou demographics relative to climatic factors (e.g. precipitation, mean temperatures, ect.) were not determined for this population due to the closure of the Slate Islands weather station in 1989.

Unlike the majority of woodland caribou populations across Canada, the Slate Islands caribou population existed for approximately 100 years without predation (OMNR 2011). The only occurrence of predation was during 1994 and 1995, when two grey wolves (*Canis lupis*) crossed the ice of Lake Superior during the 1993/1994 winter (Bergerud *et al.* 2007; Carr *et al.* 2012). During this period, annual female adult survivorship declined from a historical mean of 82% to 71% in 1994 (Bergerud *et al.* 2007). Overall, the caribou population declined to approximately 100 individuals during this period. In spring 1996, one of the wolves disappeared and evidence of poison was found on the islands which was suggested to have been deployed by locals of Terrace Bay. The other wolf was thought to have survived the poison and may have continued to live on the islands, but this is yet to be confirmed.

3.3 Data Collection

3.3.1 Caribou locations

Slate Islands caribou location data was collected via King census strip transects surveys (hereafter referred to as "King census"; Figure 5; Table 4). King census surveys used in this thesis were conducted by A. T. Bergerud and co-workers together with the Ontario Ministry of Natural Resources (OMNR) select years from 1974 to 1995. Surveys were conducted by solo observers on days with little to no wind, resulting in less interference for good listening conditions. Observers walked transects recording all caribou (individual or multiple) seen and heard during the survey. Observers also recorded habitat type caribou were observed in, caribou sex, body condition and number of caribou when and where that level of detail was observable. Upon encountering or hearing a caribou, observers measured the distance to flushed caribou by walking to the spot where the caribou was observed and estimating the distance to the observer's location. Locations of dead caribou were recorded and date of death was estimated based on caribou decomposition.
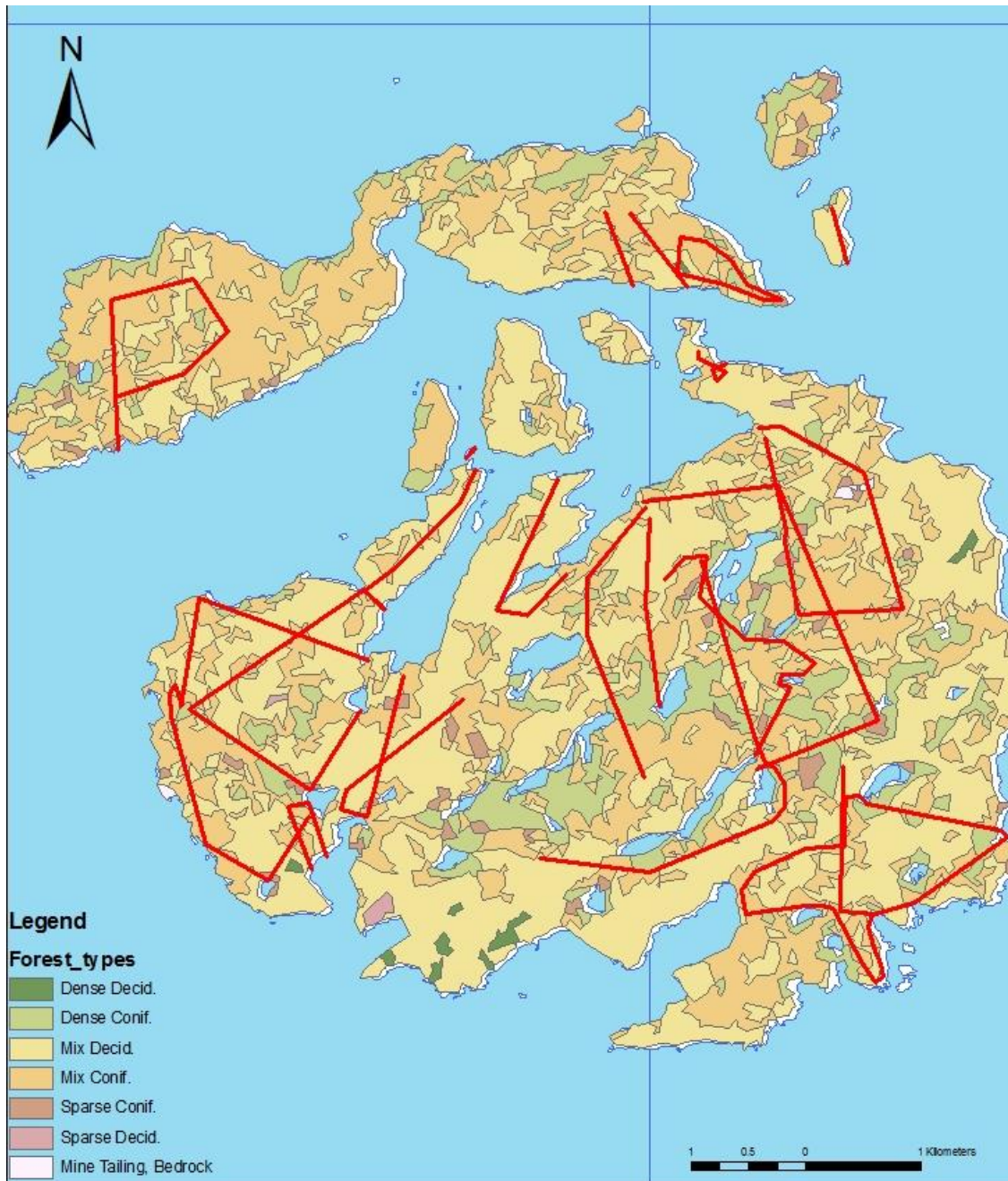
Figure 5. Example map of transects walked during the 1985 King census survey relative to
Forest Resource Inventory data. Red lines represent transects walked by solo observers. Map was
created through ArcMap GIS using data provided by the Ontario Ministry of Natural Resources.

Table 4. A summary of the available data collected on the woodland caribou on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995.

Year	Kilometers surveyed via King Census	Number of Caribou counted via King Census	Population Estimate Provided via King Census	Population Estimate Provided via Lincoln Index	Influence of Predation
1978	130	43	180	186	Pre-Predation
1979	101	43	184	201	Pre-Predation
1980	162	59	248	326	Pre-Predation
1981	83	74	203	238	Pre-Predation
1984	158	87	608	444	Pre-Predation
1985	154	37	336	294	Pre-Predation
1986	62	43	259	355	Pre-Predation
1987	93	38	500	443	Pre-Predation
1991	40	28	105	237	Pre-Predation
1994	n/a	76	200	350	Predation - Wolf
1995	n/a	65	220	215	Predation - Wolf

Annual King census transects were as evenly distributed by vegetation cover type within the archipelago as was possible while taking observer pick-up and drop-off locations into consideration. Daily transect routes were selected to avoid areas recently disturbed by transects conducted and to reduce the risk of "double counting" animals. All caribou locations were catalogued and mapped by hand (Bergerud *et al.* 2007; Carr *et al.* 2012).

The total kilometers surveyed annually during the King census surveys from 1978 to 1995 ranged from 62 to 162 km (Table 4). The mean number of kilometers surveyed during the annual King census survey was 99.5 ± 9.05 km, while mean flushing distance of caribou was calculated to be 33.3 ± 1.12 m (Bergerud *et al.* 2007). The number of caribou counted annually during King census surveys ranged from 28 to 87 individuals (Table 4).

3.2. Forest resource inventory data

Forest Resource Inventory (FRI) data was provided by staff at the Thunder Bay Ontario Ministry of Natural Resources office. The information was collected via aerial photography in 1974 and was analyzed in this thesis using ArcMap 9.3. The FRI data distinguished broad forest cover types. Cover types included in the Slate Islands Provincial Park FRI dataset were 1) Dense Deciduous, 2) Dense Coniferous, 3) Mixed Deciduous, 4) Mixed Coniferous, 5) Sparse Deciduous, 6) Sparse Coniferous, and 7) Bedrock.

3.4 Available Data and Statistical Analysis

Data collected during annual King census surveys was provided with permission by Dr. A.T. Bergerud and Dr. B. McLaren (Lakehead University, Ontario). Locations of caribou recorded during surveys were digitized using ArcMap 9.3 software (© ESRI 2010) and mapped in relation to the Slate Islands topography. I studied nine years of pre-predation caribou distribution data and two years of data when wolves were present on the island (Table 4).

Generalized linear models were used to build resource selection functions to analyze Slate Islands caribou habitat preferences (Table 5). Generalized linear models were selected for analysis of Slate Islands caribou distributions because the observed caribou dataset was found to have a skewed, non-normal distribution (Appendix A: Tests for normality with the observed caribou dataset).

Generalized linear models allow for the joint analysis of continuous and categorical data, and they can be made robust to datasets with non-normal error structures (Koper and Manseau; 2009, 2012). Generalized linear models were used to analyze 1) caribou distributions across Slate islands forest and landscape types, 2) caribou distributions across anthropogenic and

natural features, 3) the effect of population size on caribou distributions and 4) potential effects of the presence of predators on these distributions (Table 5).

Observed caribou distributions (n=593) were compared to randomly generated points representing available caribou locations on the Slate Islands (Koper and Manseau, 2012). Random points were populated across the park area (Figure 6) using the *Generate Random Points* sampling function of Hawth's Tools (Beyer 2005) in ArcMap excluding areas of the park with ponds and lake as they were not surveyed via King census. In order to avoid biasing datasets toward years with greater number of caribou observations (Table 3) an equal number random points were created for each year of study. Koper and Manseau (2012) suggested that the number of random points per observed locations can range from one to ten times the number of observed points. Because the lowest number of observed caribou within a given summer was 28 (Table 3), 280 different random points were created for every year of study (n=3080) for use in models.
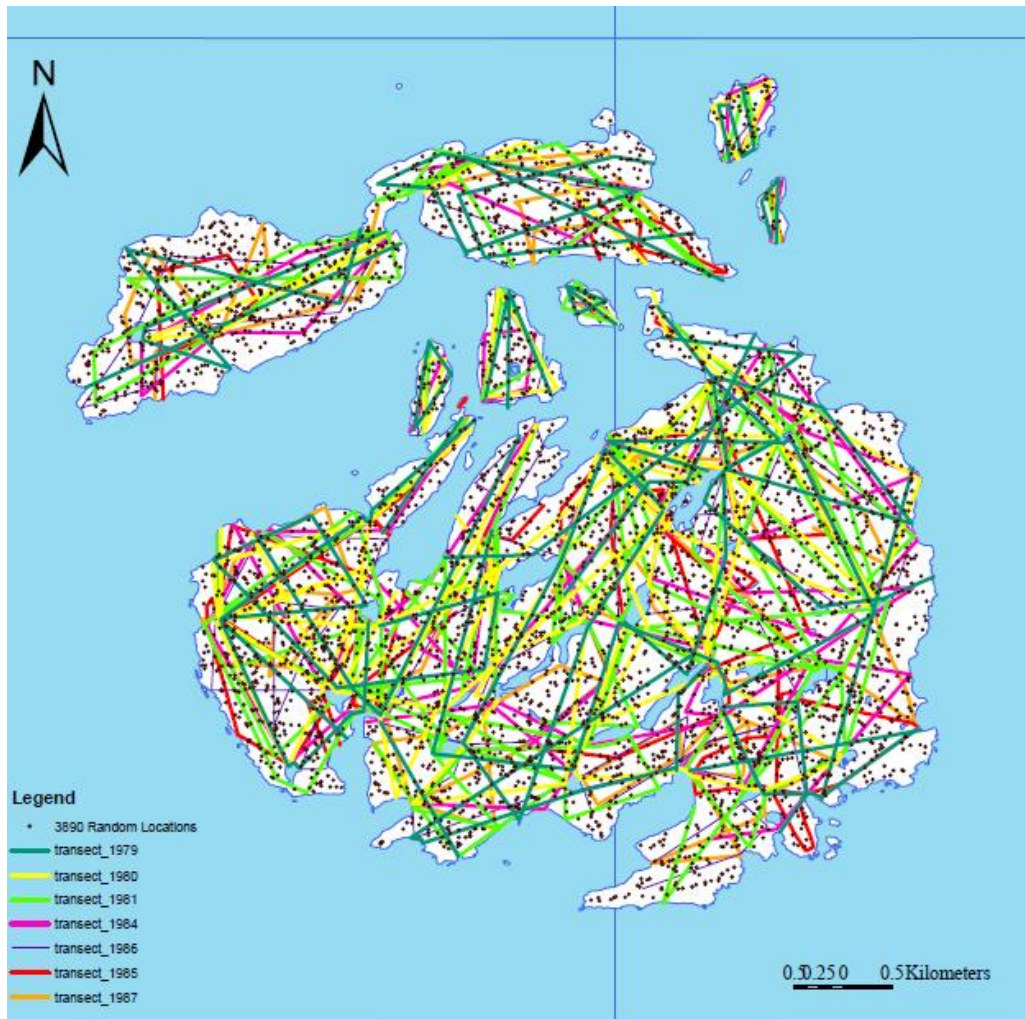
Figure 6. Map of 3890 random points generated using the Hawth's tools function for use in generalized linear models. Points plotted relative to 1979 to 1987 king census transects conducted by Berguerd *et al*. (2007) in the Slate Islands Provincial Park (Ontario, Canada). Transect data was not available for 1978, 1994 and 1995 transects.

Information regarding year of survey, point location relative to habitat, landscape, anthropogenic features, predation pressure and population size was associated with each observed and random caribou location using the intersect function in ArcMap. Caribou locations

were treated as a single point in space and were not assigned a buffer area. This information was

then compiled into a spreadsheet using Microsoft Excel®. All GLMs were performed in SAS 9.2

software (SAS 2010; Appendix B). Additionally, partial correlation matrices were compiled for

all variables within each of the models outlined in Table 5.

Table 5. Generalized linear models used to analyze caribou distributions across the Slate Islands Provincial Parks (Ontario, Canada) from 1978 to 1995.

Model Objective	Model Name	Model Number	Model Variables
To determine if caribou distributions varies across habitats and landscape features	Caribou-Forest Distribution Over Time Model	1	Dense Coniferous + Mix Deciduous + Mix Coniferous + Sparse Coniferous + Year + Dense Coniferous*Year + Mix Deciduous*Year + Mix Coniferous*Year + Sparse Coniferous*Year
	Forest Distribution Model	2	Dense Coniferous + Mix Deciduous + Mix Coniferous + Sparse Coniferous
	Landscape Distribution Model	3	Distance_to_water + LogPatchSize + Slope + Elevation
	Nearest Neighbour Model	4	Distance_to_nearest_neighbour
To determine if caribou distributions vary anthropogenic and natural features	Anthropogenic Features Model	5a	Distance_to_Old_Barn + Distance_to_Mortimer_Beach +Distance_to_Come_n_Rest + Distance_to_Puds_Bay + Distance_to_Lighthouse + Distance_to_South_Camp
	Natural Features Model	5b	Distance_to_Mud_Lake
To determine if habitat selection is density dependent	Forest Distribution - Population Size Model	6a	Dense Coniferous + Mix Deciduous + Mix Coniferous + Sparse Coniferous + Population Size + Dense Coniferous*Population Size + Mix Deciduous*Population Size + Mix Coniferous*Population Size + Sparse Coniferous*Population Size
	Landscape Distribution - Population Size Model	6b	Distance_to_water + LogPatchSize + Slope + Elevation + Population Size + Distance_to_water*Population Size + LogPatchSize*Population Size + Slope*Population Size + Elevation* Population Size
	Nearest Neighbour - Population Size Model	6c	Distance_to_nearest_neighbour + Population_size+ Distance_to_nearest_neighbour *Population_size
To determine if habitat selection changes with the presence of predators	Forest Distribution - Predation Model	7a	Dense Coniferous + Mix Deciduous + Mix Coniferous + Sparse Coniferous + Predation + Dense Coniferous*Predation + Mix Deciduous*Predation + Mix Coniferous*Predation + Sparse Coniferous*Predation
	Landscape Distribution - Predation Model	7b	Distance_to_water + LogPatchSize + Slope + Elevation + Predation + Distance_to_water*Predation + LogPatchSize*Predation + Slope*Predation + Elevation*Predation
	Nearest Neighbour - Predation Model	7c	Distance_to_nearest_neighbour + Predation + Distance_to_nearest_neighbour *Predation

3.4.1 Caribou distribution across habitat and landscape

As stated in Section 1.4 of the introduction, the first hypothesis of my thesis was that if the Slate Islands caribou selected habitat based on availability of forage, they would prefer deciduous forest stands, which contain more palatable plant species (Bryant *et al.* 1983) preferred by caribou. To test hypothesis 1, observed and available caribou locations were plotted across the Slate Islands and geometrically intersected with habitat and landscape variables (Table 6) using ArcMap. Habitat variables included forest stand type as indicated by FRI data.

Mixed deciduous and mixed coniferous are the first and second most common forest types on the archipelago (Table 3). To investigate the use of mixed deciduous forest by the Slate Islands caribou, mixed coniferous forest type was used as the reference level for the habitat use GLM (Boyce *et al.* 2002). Landscape variables included forest stand patch size, slope, elevation and the distance from caribou to the nearest water body. Patch size was calculated for all forest patches on the Slate Islands using Hawth's tools function in ArcMap. Observed caribou data relative to patchsize was negatively skewed, thus a base 10 logarithm of patch size was used transform and normalize the data. A raster file containing landscape variable data of the Slate Islands Provincial Park was provided by the Ontario Ministry of Natural Resources (OMNR) in Thunder Bay. Distance to nearest water bodies was calculated for all caribou points using Hawth's tools. Differences between use of habitat and landscape variables at observed and available caribou locations was quantified using GLMs using a binomial distribution (Table 5).

There was a very low number (<2) of observed caribou locations and/or random points in rare cover types (i.e. dense deciduous, sparse deciduous and bedrock), making it difficult to compare caribou habitat use relative to habitat availability in these cover types. I therefore removed rare habitat types from the models. In addition, caribou observations and random points

located in water bodies were removed from the FRI dataset because hypothesis 1 is focused on forest types caribou use for foraging.

In addition to habitat and landscape variables, distance to nearest caribou (nearest-neighbour statistics) was calculated for observed and available caribou locations on the Slate Islands using the Hawth's tools function in ArcMap. A separate random points dataset consisting of a 1:1 ratio of random:observed dataset was used for all near-neighbour analysis. GLMs were used to test whether distance to nearest neighbour differed across observed and available caribou locations (Table 5; Table 6). A normal distribution was used for this data analysis based on preliminary analysis of the nearest-neighbour dataset.

Table 6. Available habitat data for the Slate Islands Provincial Park (Lake Superior, Ontario, Canada) from 1978 to 1995. Raster and shapefile data provided by the Thunder Bay Ministry of Natural Resource Management.

Variable	Description
Forest Resource Inventory (FRI)	1) Dense Deciduous, 2) Dense Coniferous, 3) Mixed Deciduous, 4) Mixed Coniferous, 5) Sparse Deciduous, 6) Sparse Coniferous, and 7) Bedrock*
Forest Patch Size (m)	Continuous variable
Range of Elevation (m)	Continuous variable – 0 to 400
Range of Slope (degrees)	Continuous variable – 0 to 45
Range of Distance to Water (m)	Continuous variable
Distance to Nearest Neighbour (m)	Continuous variable

* Dense deciduous, sparse deciduous and bedrock cover types were not included in analysis.

Caribou Distributions across Forest Types over Time

To complete testing of Hypothesis 1 in my thesis, I investigated if caribou use of forest stand type changed over time. To test this, observed and available caribou locations were

mapped across Slate Islands Provincial Park. This was accomplished using geometrically

intersecting caribou locations and available locations with FRI data (Table 6). The effect of year

on habitat selection was analyzed using GLMs (Table 5).

3.4.2 Caribou distributions across anthropogenic and natural features

During a 2008 King census survey (Carr *et al.* 2012), I observed that some woodland

caribou frequented campsites and occasionally caribou would attempt to obtain food from

humans or would dig up in campfire pits eating ashes (Figure 7). The literature I reviewed here

suggested avoidance of anthropogenic habitats by mainland caribou population. Thus,

Hypothesis 2 of my thesis predicted that if the caribou selected habitat for avoidance of human

presence, the caribou would prefer areas of the park further away from camp sites and human

lodgings. To determine if anthropogenic features influence caribou distribution, areas with

regular human presence in Slate Islands Provincial Park (Table 7) were mapped and caribou

distances to anthropogenic features were measured using Hawth's tools in ArcMap. Differences

between distance to anthropogenic features of observed and available locations were compared

using GLMs (Table 5).

Figure 7: A Slate Islands caribou coming into campsite and approaching researcher in attempt to obtain food. Photo credit Jeff Renton (used with written permission).

Table 7. A summary of anthropogenic features on the Slate Islands Provincial Park (Lake Superior, Ontario, Canada).

Feature	Description
Old Barn Camp	Tourist campsite.
Mortimer Beach	Tourist destination.
Come n' Rest Camp	Tourist and researcher campsite.
Pud's Bay Camp	Tourist campsite.
Lighthouse and Cabins	Cabins and lighthouse used by federal Slate Islands staff.
Southern Camp	Tourist campsite.

In addition to anthropogenic features, a natural salt lick located beside Mud Lake on Patterson Island was maintained by Bergerud *et al.* throughout their duration of studying the Slate Islands caribou (Figure 8; Bergerud *et al.* 2007). This salt lick was used to draw in caribou in order to monitor their body condition. To determine if natural features (the Mud Lake Mineral Lick) significantly influenced the distribution of the Slate Islands caribou, the Mud Lake Mineral Lick was mapped on the Slate Islands Provincial Park in ArcMap and caribou distances to the salt lick were measured using Hawth's tools. Differences between distance to the salt lick across observed and available locations were compared using GLMs (Table 5).

Figure 8: Picture of caribou being drawn into and using a salt lick, maintained and located at Mud Lake on Patterson Island (July 2008; Slate Islands Provincial Park, Lake Superior, Ontario).

3.4.3 Effect of population size on habitat selection

To address Hypothesis 3 of my thesis and determine if habitat selection for deciduous forage varied with population size, observed and available caribou locations across habitat and landscape variables across varying populations sizes (Table 4) were tested using GLMs (Table 5). In addition, GLMs were used to test whether distance to nearest neighbour changed with population size.

In addition, Hypothesis 3 of my thesis outlines that competition for enemy-free spaces may have effected on how the caribou used their surround habitat relative to population size. I predicted if caribou compete for enemy free space, they should be either be 1) closer to water, 2) using higher elevations or 3) using coniferous forest types during low population density years. To address this hypothesis, observed and available caribou locations across habitat and landscape variables across varying populations sizes (Table 4) were tested using GLMs (Table 5).

3.4.4 Effects of predation on habitat selection

Hypothesis 4 of my thesis outlines three potential effects the introduction of wolves to the Slate Islands may have had on the caribou population. I predicted that i) caribou would use areas closer to shorelines to stay closer to potential escape routes; ii) caribou would space themselves out to maintain a lower prey density on the landscape and; iii) caribou would shift their habitat use away from high quality foraging areas and use areas that may provide a lower predation risk (i.e. higher elevations and shorelines) when wolves were present on the islands.

To investigate Hypothesis 4, GLMs were used to evaluate whether habitat selection changed between predation and non-predation years, using predation-habitat interactions (Table 5). To investigate if predation influences caribou distributions, GLMs were used to test whether distance to nearest neighbour changed with predation. Due to low sample size (n=1), selection for sparse coniferous habitat could not be evaluated.

CHAPTER 4: RESULTS

4.1 Effects of habitat type, landscape and anthropogenic features on caribou distributions

Forest stand type had a significant influence on caribou distributions on the Slate Islands, though proportion of each forest type used by Slate Islands caribou did not change over time (Model 1; Table 8). From 1978 to 1995, caribou avoided areas of the park with dense coniferous forest and selected areas with mixed deciduous forest relative to the selection of mixed coniferous forest on the islands (Model 2; Table 8; Figure 9).

With respect to landscape variables, the Slate Islands caribou selected areas of the park further from water bodies, larger patch sizes, and areas with flatter slopes, and areas at lower elevations (Model 3; Table 8; Figure 10). On average, caribou were 20.7 m further from water bodies, located on slopes 0.7 degrees flatter and at elevations 1.64 m lower than randomly distributed points (Figure 10). Additionally, caribou used forest patches averaging 68.5 ha larger in area relative to random points on the landscape (Model 3; Figure 10). Caribou were located on average 139 m closer to one another compared to random points distributed across the Slate Islands (Model 4; Table 8; Figure 10).

Table 8: Forest type selection, landscape selection and distance to nearest neighbour models for

the Slate Islands caribou (Ontario, Canada) from 1978 to 1995, analyzed using generalized linear

models.

Model Name	Model Number	Habitat Parameter	β	SE	p
Caribou-Forest Distribution Over Time Model	1	Intercept	1.666	0.734	0.023*
		Year	0.149	0.117	0.202
		Dense Coniferous	-0.383	0.339	0.259
		Sparse Coniferous	0.408	0.211	0.054
		Mix Deciduous	0.208	0.595	0.726
		Year* Dense Coniferous	-0.014	0.050	0.778
		Year* Sparse Coniferous	-0.023	0.031	0.460
		Year* Mix Deciduous	-0.132	0.098	0.179
Forest Distribution Model	2	Intercept	2.522	0.351	<0.001*
		Dense Coniferous	-0.468	0.157	0.003*
		Sparse Coniferous	-0.545	0.289	0.060
		Mix Deciduous	0.270	0.098	0.006*
Landscape Distribution Model	3	Intercept	-3.528	0.600	<0.001*
		Distance to water body (m)	0.096	0.028	0.001*
		Log PatchSize (log m^2)	0.546	0.063	<0.001*
		Slope (degrees)	-0.030	0.008	<0.001*
		Log Elevation (m)	-0.005	0.002	0.008*
Nearest Neighbour Model	4	Intercept	4.648	0.057	<0.001*
		Distance to Nearest Neighbour (m)	-1.370	0.147	<0.001*

*indicates significance at $\alpha = 0.05$
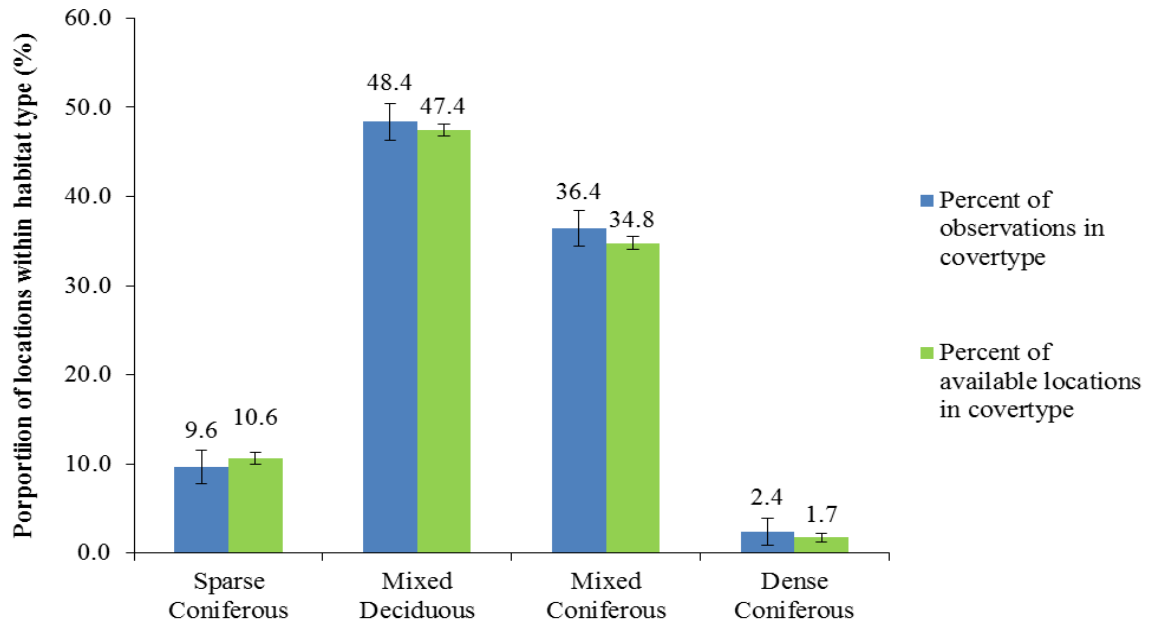
Figure 9. Proportion (%) of available and observed caribou locations (and associated standard deviations) within cover types located on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995.
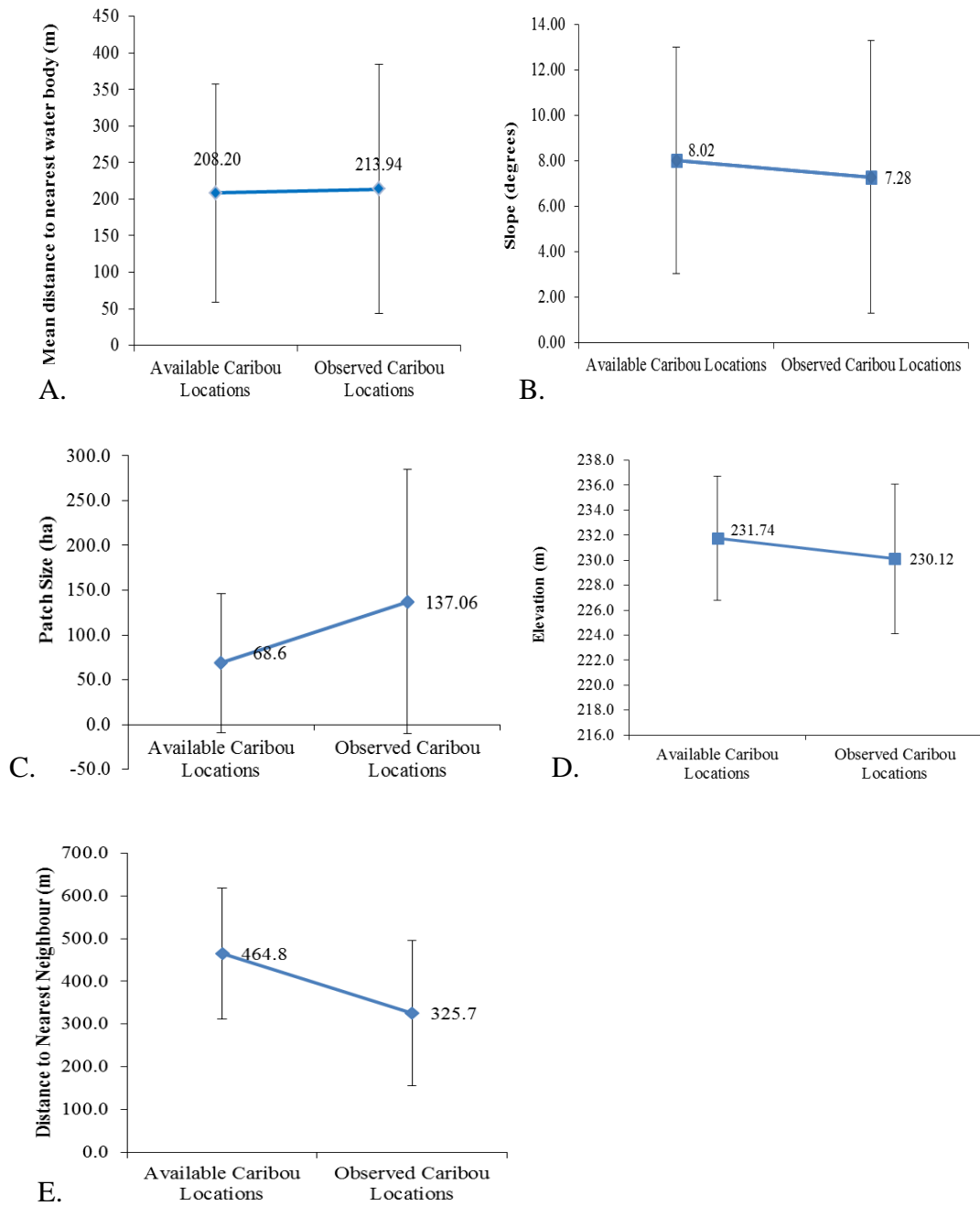
Figure 10. Comparison of mean distance to nearest water body (A.), mean slope (B.), forest patch size (C.), elevation (D.), nearest neighbour distance (E.) and associated standard deviations for available and observed caribou locations on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995.

4.2 Effects of anthropogenic and natural features on caribou distributions

Among anthropogenic features in the park, the caribou preferred areas further away from the Old Barn Campsite and areas closer to Mortimer Beach, the Come 'n Rest Campsite, Pud's Bay Campsite and the Lighthouse (Model 5a; Table 9, Figure 11). Distance to the Mud Lake Mineral Lick did not significantly influence caribou distribution (Model 5b; Table 9).

Table 9: Anthropogenic and natural features models for the Slate Islands caribou (Ontario, Canada) from 1978 to 1995, analyzed using generalized linear models.

Model Name	Model Number	Habitat Parameter	β	SE	p
Anthropogenic Features Models	5a	Intercept	-2.054	0.452	<0.001*
		Distance to Old Barn Camp (km)	0.704	0.230	0.002*
		Distance to Mortimer Beach (km)	-0.301	0.112	0.007*
		Distance to Come n' Rest Camp (km)	-0.446	0.189	0.019*
		Distance to Pud's Bay Camp (km)	-0.367	0.131	0.005*
		Distance to Lighthouse (km)	-0.460	0.058	<0.001*
		Distance to Southern Camp (km)	-0.056	0.068	0.413
Natural Features Model	5b	Intercept	1.594	0.092	<0.001*
		Distance to Mud Lake Mineral Lick (km)	0.053	0.033	0.110

*indicates significance at $\alpha = 0.05$
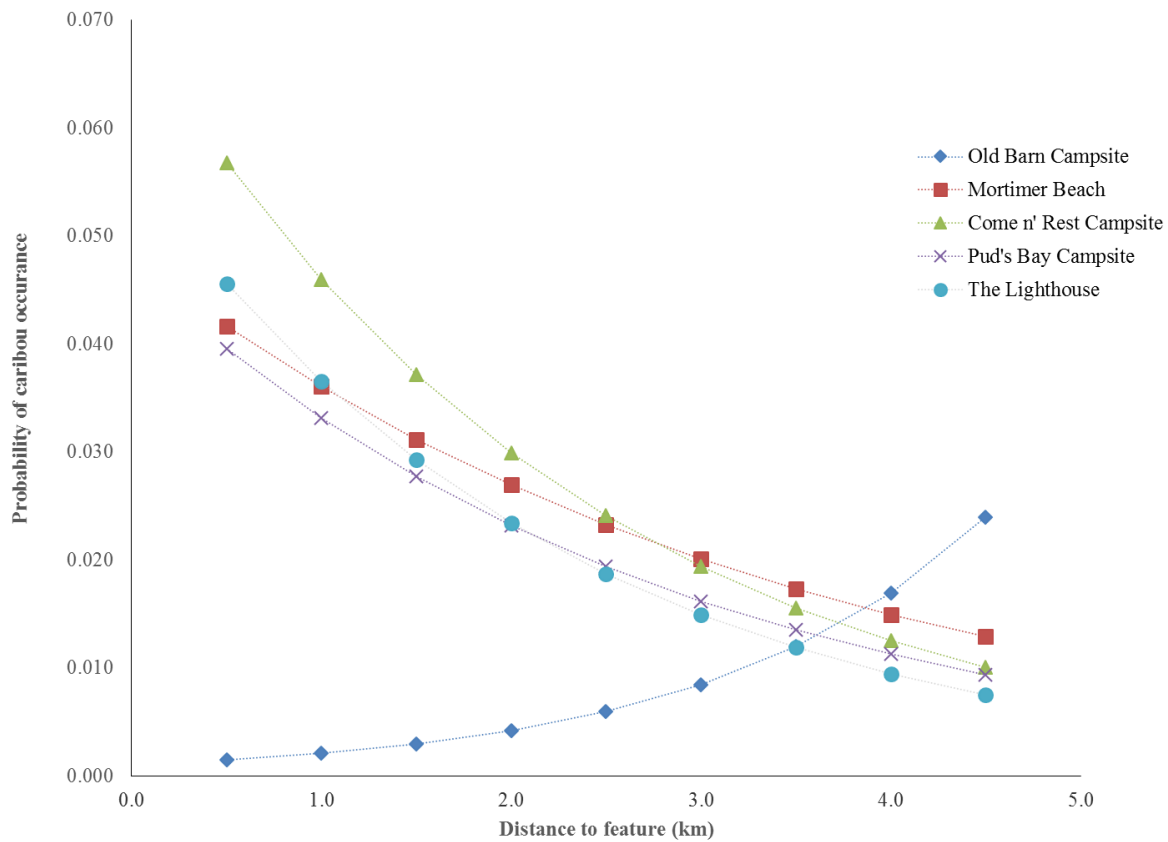
Figure 11. Probability of caribou occurrence on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995 relative to distance to anthropogenic features.

4.3 Effects of population size on habitat selection

The Slate Islands caribou forest type use did not vary with population size (Model 6a) Among landscape variables, there was an interaction between distance to water body and population size, such that when the caribou populations rose above 110 individuals, caribou began to use areas of the park further from waterbodies (Model 6b; Table 10; Figure 12). Additionally, there was a significant interaction between slope and population size; as the Slate Islands caribou population size increased, caribou selected areas with flatter slopes (Model 6b;

Table 10; Figure 13). Finally, Model 6c., in combination with Figure 14, indicated that as

population size increased for the Slate Islands caribou, distance to nearest neighbour declined

(Table 10; Figure 14).

Table 10: Forest type, landscape and distance to nearest neighbour models for the Slate Islands

caribou (Ontario, Canada) from 1978 to 1995, and interactions between main effects, analyzed

using generalized linear models.

Model Name	Model Number	Parameter	β	SE	p
Population Size Model	6a	Intercept	2.218	0.378	<0.001*
		Dense Coniferous	-0.500	0.174	0.004*
		Sparse Coniferous	0.089	0.338	0.793
		Mix Deciduous	0.040	0.105	0.703
		Population Size	0.001	-0.003	<0.001*
		Dense Coniferous*Population Size	0.001	0.001	0.078
		Sparse Coniferous *Population Size	-0.002	0.001	0.270
		Mix Deciduous *Population Size	<0.001	<0.001	0.309
Population Size Model	6b	Intercept	3.190	5.458	0.559
		Distance to water body (m)	-0.064	0.065	0.322
		Log PatchSize (m)	0.643	0.137	<0.001*
		Slope (degrees)	0.020	0.018	0.271
		Log Elevation (m)	-3.666	2.266	0.106
		Population Size	-0.004	0.017	0.832
		Distance_to_water*Population Size	0.001	0.000	0.004*
		Log PatchSize*Population Size	<-0.001	0.000	0.386
		Slope*Population Size	<-0.001	0.000	0.002*
		Log Elevation*Population Size	0.003	0.007	0.703
Population Size Model	6c	Intercept	4.442	0.123	<0.001*
		Point Type (Observed vs Rnd)	-0.473	0.314	0.132
		Population Size	<0.001	<0.001	0.060
		Point type *Population Size	-0.003	0.001	0.001*

*indicates significance at 0.05
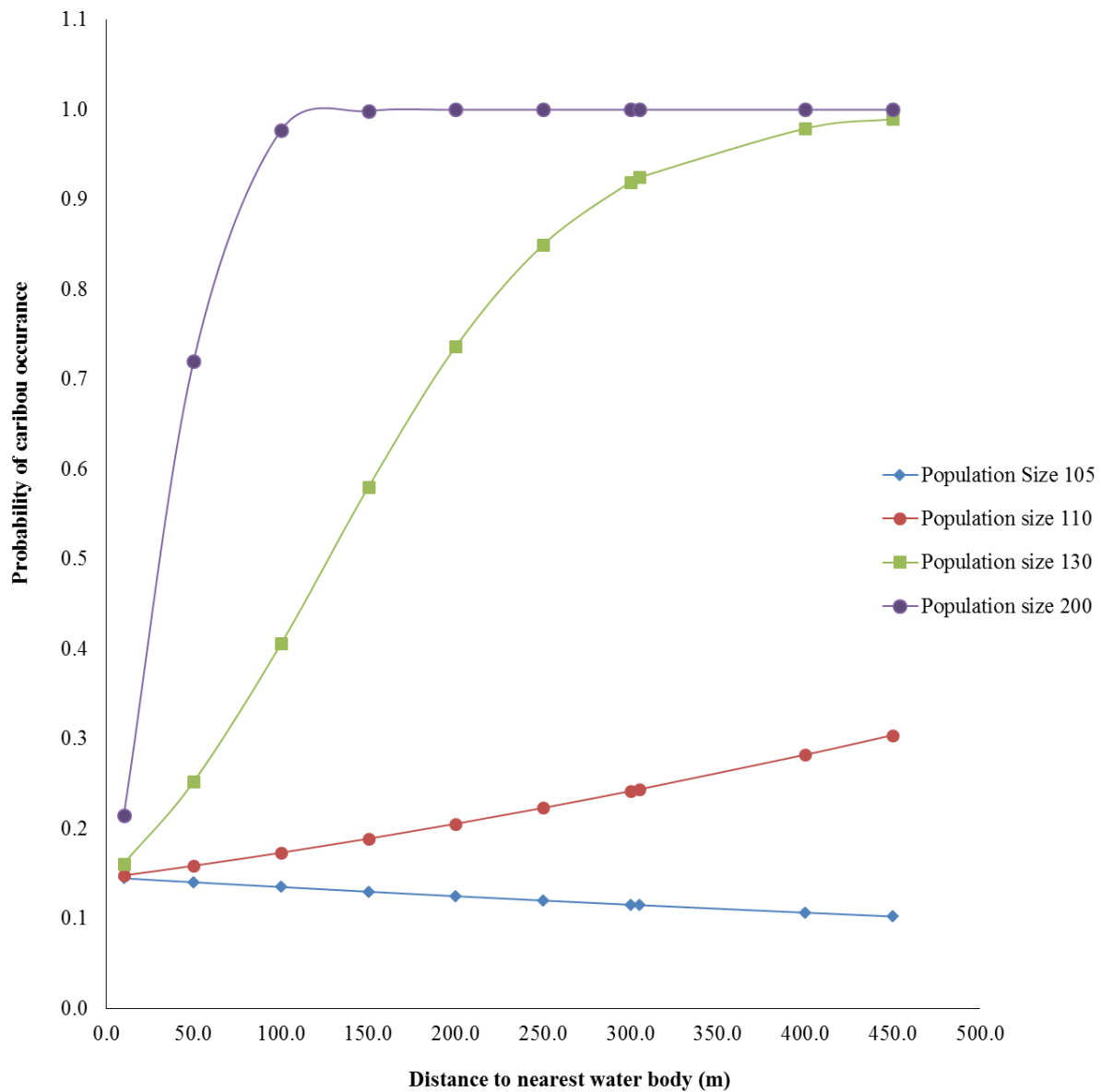
Figure 12. Probability of caribou occurrence on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995 relative to distance to nearest water body.
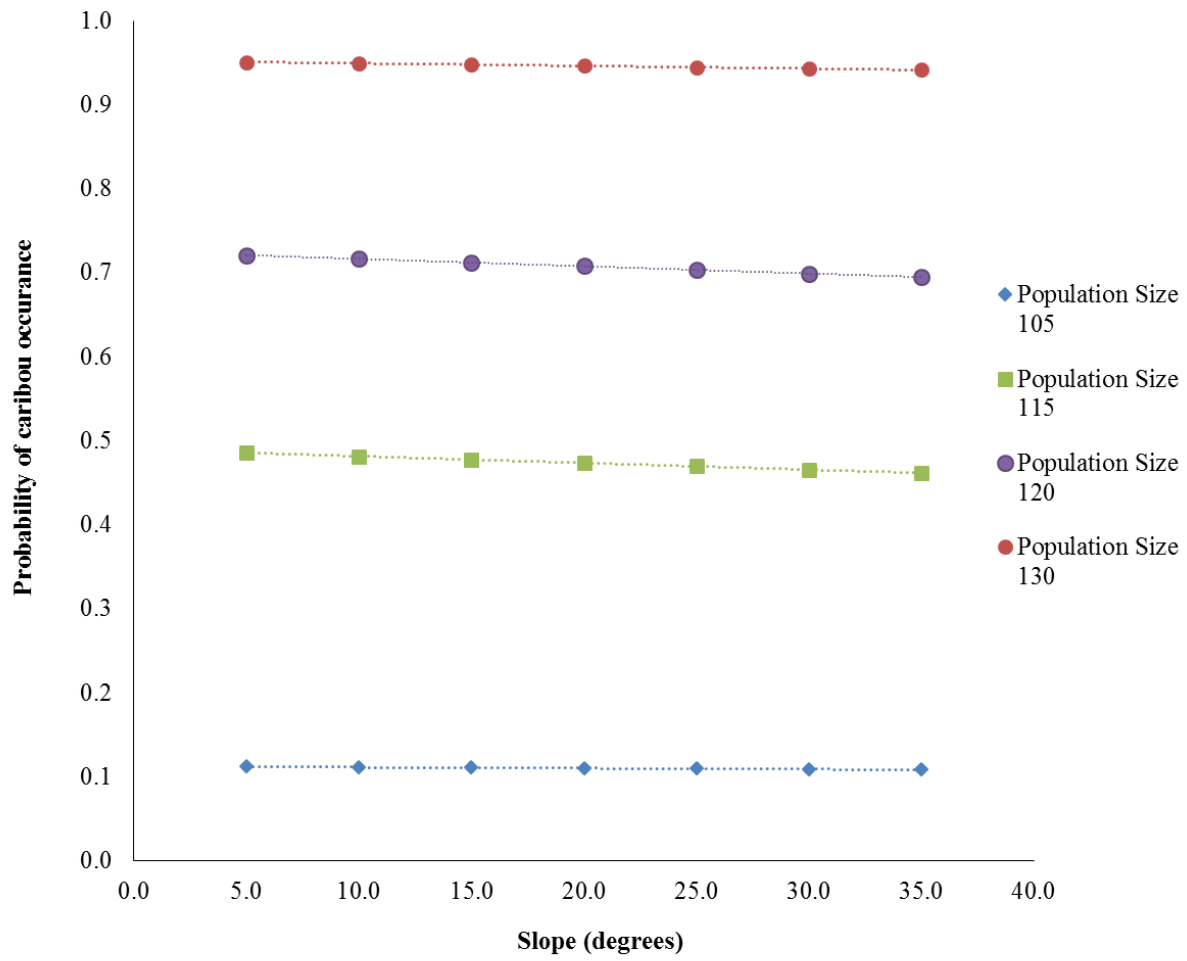
Figure 13. Probability of caribou occurrence on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995 relative to slope (degrees).
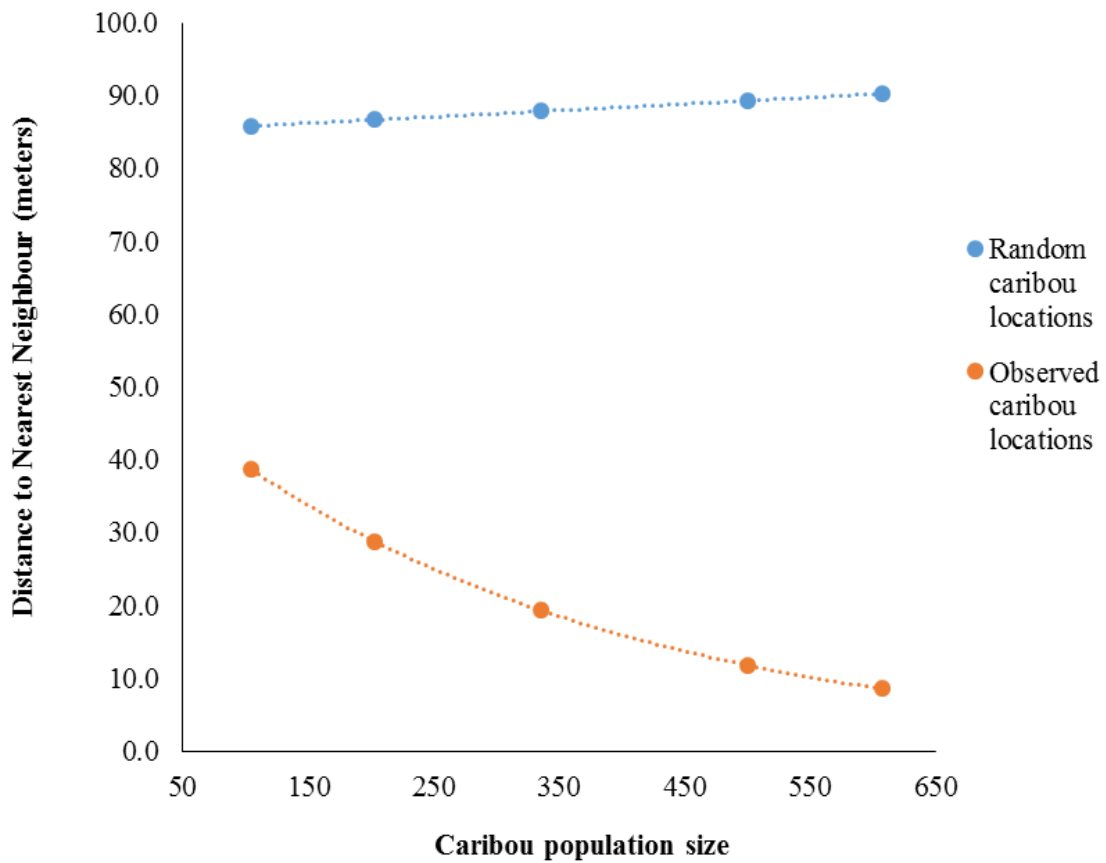
Figure 14. Equation of the line for Model 6c relative to distance to nearest neighbour (m) for observed and available caribou values on the Slate Islands Provincial Park (Ontario, Canada) from 1978 to 1995. Population estimates provided via King Census estimates conducted by A.T. Bergerud *et al* (2007).

4.4 Effects of predation on habitat selection

There was no effect of the presence of predators on caribou use of Slate Islands forest types (Model 7a; Table 11), landscape variables (Model 7b; Table 11), or distance to nearest neighbour (Model 7c; Table 11).

Table 11: Forest type, landscape and distance to nearest neighbour models for the Slate Islands caribou (Ontario, Canada) from 1978 to 1995 and interactions between main effects, analyzed using generalized linear models.

Model Name	Model Number	Parameter	β	SE	P
Predation Model	7a	Intercept	23.642	0.465	<0.001*
		Dense Coniferous	-21.390	0.407	<0.001*
		Sparse Coniferous	-0.521	0.331	0.115
		Mixed Deciduous	-21.898	0.295	<0.001*
		Predation	0.245	0.203	0.227
		Dense Coniferous*Predation	1.000	0.075	0.841
		Sparse Coniferous*Predation	0.000	21.675	n/a
		Mix Deciduous*Predation	0.037	0.231	0.872
Predation Model	7b	Intercept	-4.885	5.250	0.392
		Distance to waterbody (m)	-0.056	0.063	0.375
		Log PatchSize (m)	-0.662	0.138	<0.001*
		Slope (degrees)	0.030	0.016	0.062
		Log Elevation (m)	4.026	2.178	0.065
		Predation	2.703	5.979	0.651
		Distance_to_water*Predation	-0.051	0.070	0.473
		LogPatchSize*Predation	0.146	0.155	0.348
		Slope*Predation	0.002	0.019	0.928
		Log Elevation*Predation	-1.310	2.481	0.598
Predation Model	7c	Intercept	4.616	0.133	<0.001*
		Distance to Nearest Neighbour	-1.399	0.309	<0.001*
		Predation	0.039	0.147	0.792
		Distance to Nearest Neighbour*Predation	0.057	0.351	0.870

*indicates significance at 0.05
Note: significance of sparse coniferous forest type could not be estimated due to a low number of caribou locations for this forest type (*n*=1)

CHAPTER 5: DISCUSSION

The results of my thesis indicate that caribou were selective for particular forest types, landscape characteristics, and anthropogenic features. The strength of these associations were sometimes influenced by the population size of the year.

5.1 Caribou distribution across habitat and landscape

Mainland woodland caribou populations regularly select mature conifer stands at the forest patch scale (Courtois 2003; McLoughlin *et al.* 2005; Wittmer *et al.* 2007; Courbin *et al.* 2009; Hins *et al.* 2009), however preferred summer forage types of mainland caribou include forbs, sedges and grasses (Thomas and Gray 2002). In my study, I found that the Slate Islands caribou selected deciduous forest types and did not select coniferous forest types at the forest-patch scale. Similarly, Bergerud *et al.* (2007) suggested that the Slate Islands caribou preferred to browse deciduous species. Given the level of intraspecific competition on the Slate Islands, it is not surprising that in this study caribou selected the more nutritious and more palatable species in deciduous forest types (Bryant *et al.* 1985) over coniferous forest types.

Relative to mainland populations, the lower use of dense coniferous forest patches is an anomaly. Mainland caribou are thought to select coniferous forest stands because there are fewer heterospecific ungulates, thereby reducing attraction of potential predators (Courtois 2003; McLoughlin *et al.* 2005; Wittmer *et al.* 2007; Courbin *et al.* 2009; Hins *et al.* 2009). Within my thesis, predation did not influence caribou distributions; thus, the Slate Islands caribou may not have been selecting forest types typically associated with lower predation risk. The non-selection of forest types associated with lower predation risks can also be seen as a trade-off for the selection of forest types associated with higher nutrition (i.e. deciduous cover types; Bryant *et al.* 1985) that typically have higher predation risks for mainland populations (Belovsky 1991;

Bergerud *et al.* 2007). While this behaviour has not been documented in other woodland caribou populations, it has been previously hypothesized that individuals may select preferred foraging habitats over habitats with lower predation risk in situations where predation is not as high of a risk factor (Belovsky 1991).

Landscape features also influenced the Slate Islands caribou distribution. Similar to trends seen within mainland populations, the Slate Islands caribou tended to select larger habitat patches. Mainland woodland caribou populations may use larger forest stands as a method of increasing foraging efficiency (Johnson *et al.* 2000) and decreasing predation risk (Pearce and Eccles 2004; McLoughlin *et al.* 2005; Culling et al. 2006). Similar to mainland populations, Slate Islands caribou may select larger patch sizes as a method of increasing foraging efficiency in preferred forest patches (Johnson *et al.* 2000).

Through this thesis I found that the Slate Islands caribou preferred interior areas of the park during periods of higher population density. Caribou preference for interior areas of the park is contrary to many other studies evaluating caribou summer habitat use in Ontario (Bergerud *et al.* 1984; Bergerud and Page 1987; Belovsky 1991). In other populations, cow-calf pairs may select habitat near shorelines as a predator avoidance strategy (Bergerud *et al.* 1984; Bergerud and Page 1987). Mainland caribou populations normally do not forgo habitats with lower predation risks because predation is generally more limiting than forage in the summer (Wittmer *et al.* 2007). In the case of the Slate Islands caribou, I hypothesize that the Slate Islands caribou prefer using areas further from shorelines at high population levels because the threat of predation on the islands is generally low, so preference for enemy-free habitats is not as valuable as other landscape variables. Additionally, the caribou may be actively avoiding shorelines because they contain more open habitat (i.e. rocky shorelines) and less forage than areas such as

the interior of the islands. However, it is important to note that caribou distributions and landscape use change at higher density within the Slate Islands caribou population (see section 5.3 for further discussion).

Slope and elevation had small but significant influences within the landscape distribution model (Model 3). It is important to note that both slope and elevation had small coefficients relative to other landscape variables in the model (-0.030 and -0.005, respectively). This indicates that while these variables are statistically significant in the model, they likely play a small role in influencing the Slate Islands' caribou distribution relative to other influencing features on the archipelago.

It is interesting to note that Bergerud (1996) observed that the Slate Islands caribou sometimes used areas with steep slopes and higher elevation in search of forage, sometimes falling to their death. In contrast to Bergerud's work, I found that the Slate Islands caribou prefer areas with lower elevations. Additionally, my study found that the caribou preferred areas of the archipelago with flatter slopes, with use of steeper slopes declining as caribou density increases. These patterns are consistent with other studies examining caribou summer behavior in areas with more varied terrain. Both Apps *et al.* (2001) and Oosenbrug and Theberge (1980) have previously found that mountain caribou prefer areas with lower elevation and flatter slopes during the spring and summer months, hypothesizing that caribou prefer these areas because the forage is generally more accessible and emerges earlier at lower elevations. Wiens *et al.* (1997) and Johnson *et al.* (2002) proposed that caribou use these types of areas because they require less energetic outputs in transit than areas with high elevations or steeper slopes. Relative to the Slate Islands population, I hypothesize that if slope and elevation does influence the Slate Islands' caribou distribution, the caribou are selecting flatter slopes and lower elevations because the

caribou require less energetic output in these areas than areas with steeper slopes and higher elevations (Wiens *et al.*1997; Johnson *et al.* 2002). Building on these results, Model 6b. further investigated the relationships between landscape variables and caribou distributions relative to caribou density on the Slate Islands. Trends in Model 6b. indicated that caribou use of slope on the archipelago shifted as caribou population size increased. Please see section 5.3 for further discussion.

It was found through this study that the Slate Islands caribou were consistently observed closer to one another than would have been expected through chance alone at higher population densities. This is contradictory to what is most often seen in mainland woodland caribou populations. While mainland caribou will group together in the autumn, they are generally solitary during the spring and summer months (Darby and Puritt 1984). However, grouping behaviour has been noted in some mainland populations, such as the Wabakimi Lake population in northern Ontario (Cumming *et al.* 1994). Cumming *et al.* (1994) concluded that this behaviour may result from caribou spacing themselves away from moose and wolf populations while actively seeking winter forage, resulting in a loose but statistically significant grouping of individuals in the remaining limited number of suitable locations. It is important to note that calves and cows are normally located very close to one another during the summer months (Environment Canada 2011), which may have accounted for some of the close distance to nearest neighbour values. However, upon review of the notes taken by researchers who conducted the King census surveys for this study, few calves were recorded during the surveys. Therefore, it is unlikely that cow-calf observations were the drivers in this model trend.

It is probable that the Slate Islands caribou are located closer to one another at higher population densities than random because of i) the relatively limited area within the Slate Islands

Provincial Park, ii) the high caribou density (relative to other caribou populations in Canada), iii) the population is limited by summer forage, and iv) the caribou selected deciduous forest types (which are associated with preferred forage species) over coniferous habitats (which are most commonly associated with predator avoidance strategies; Bergerud *et al.* 2007). It is important to note that for the majority of this study there were no predators on the islands, therefore was less pressure for the caribou to space away from one another as part of a predator avoidance strategy. It is also important to note that the relationship between the Slate Islands caribou distribution and distances to nearest neighbour varied with increased population sizes (see section 5.3 for further discussion).

5.2 Caribou distribution across anthropogenic and natural features

The Slate Islands caribou tended to select habitats close to campsites and permanent structures, which is dissimilar to mainland populations that most commonly avoid anthropogenic features (Dyer *et al.* 2001, Schaefer and Mahoney 2007; Vors *et al.* 2007; Fortin *et al.* 2013). The Slate Islands caribou may be drawn to anthropogenic forage sources to cope with the high level of competition for forage in the park area. It is probable that this is a learned behaviour and not all of the caribou participate in this type of foraging. The only anthropogenic feature in the park that the caribou avoided was the Old Barn campsite. This site is the most popular camping site in the park and regularly hosts up to 15 - 20 campers. It is possible that the Slate Islands caribou avoided this camp site because it was too busy and noisy for the caribou.

It is not uncommon to find species other than caribou using anthropogenic sites as supplemental foraging areas. It is well known that predators such as black bears visit campsites and recreational areas as a method of searching for and obtaining food (Rogers *et al.* 1976; Ayers *et al.* 1986). Similarly, this behaviour has also been documented in mule deer in Virginia, U.S.A

79

(Hockett 2000). Additionally, it has been hypothesized that in some cases mule deer will select for areas with human presence as a method of predator avoidance; Waser *et al.* (2014) demonstrated that coyotes avoided areas such as townsites, while mule deer selected for townsites as a method of reducing vigilance behaviour and increasing feeding time for fawns. Similar to Waser *et al.*, it is possible that the Slate Islands caribou selected areas on the islands with increased human activity as a method of reducing predation risk. To the best of my knowledge, this thesis is the first documentation of woodland caribou selecting for areas such as campgrounds as a method of foraging or predator avoidance.

5.3 Effects of population size on habitat selection

My results are consistent with the hypothesis that population density can sometimes affect how the Slate Islands caribou interact with their environment. Caribou forest type selection did not vary with population size, while use of select landscape variables (i.e. distance to water bodies and slope) changed as population size increased on the islands.

While the results of the basic habitat and landscape model and the population size models can be discussed and compared from an ecological perspective, it is important to highlight that models without interaction terms are interpreted statistically in different ways from models that include interaction terms. In the absence of interaction terms, parameter estimates of a regression model (i.e. $Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_2 i + \varepsilon i$) means the effect of X_1 when holding X_2 constant (Quinn and Keough, 2002). When an interaction term is added to the model (i.e. $Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{1i}*X_{2i} + \varepsilon_i$), the meaning of the main parameter estimates becomes the effect of the variable when the other variables equal zero (i.e. effect of X_1 when $X_2=0$; Quinn and Keough, 2002). In this example, the interaction term ($\beta_3 X_1 i * X_{2i}$) means the effect of X_1 when X_2 varies (Quinn and

Keough, 2002).Therefore, parameter estimates for the same variable cannot be directly compared between models with and without interaction terms because their meanings are different.

It is difficult to compare the results of the population size vs. forest type model to mainland caribou populations because intraspecific competition for forage has not been studied in boreal woodland caribou populations. It has been suspected that intraspecific competition for forage contributed to boom-bust cycles observed in barren-ground caribou populations located on the Prince of Wales and Somerset Islands in Nunavut (Gunn and Adamczewski 2003), however this hypothesis could not be definitively supported. Studies examining interspecific competition for forage among other ungulate species have also indicated that as population size and/or competition increases, dominant individuals occupy preferred habitat and subordinate conspecifics begin to occupy less-preferred habitats (Collins and Urness 1983; Peterson 1990; Thouless 1990). Finally, a study examining coarse and fine-scale habitat selection of the Sable Islands horses (*Equus ferus caballus*) suggested that the horses selected for more productive forage types (i.e. grasslands) when the population size was low and decreased their use of the preferred grassland habitat as the population approached carrying capacity (van Beest *et al.* 2013). The authors interpreted these results as a possible indication of density dependant competition for preferred forage types (van Beest *et al.* 2013).

The lack of effect of population size on caribou forest type use is surprising given the body of research described above and the fact that my basic forest type model (Model 1) indicated that caribou use forest types differently across the islands. Additionally, Bergerud *et al.* (2007) hypothesized that population size played a strong role in Slate Islands caribou forage competition. It is possible that the model used for this analysis was limited by low statistical power, or conversely, that the population density was too high to permit caribou to significantly

increase their intraspecific distances to a level detectable by this model. Alternatively, other RSF studies examining woodland caribou distributions state that the results of models may vary with the spatial scale (Manly *et al.* 2002; Johnson *et al.* 2004; Polfus *et al.* 2011). Given that this study only examined caribou distributions at one scale (forest-type), it is possible that the scale of the model was too broad to capture habitat selection that may have been occurring at a finer scale (i.e. understory or species scale of forage).

Corresponding with the results of Model 3, the landscape variable vs. population size (Model 6b.) indicated that as slope increased, the probability of caribou occurrence decreased (Figure 13). Further investigation into this relationship revealed that as population size increased, caribou continued to prefer areas with flatter slopes (Figure 13). As noted in section 5.1, these results fall in line with trends reported in other mainland caribou populations (Oosenbrug and Theberge 1980; Wiens *et al.* 1997; Apps *et al.* 2001; Johnson *et al.* 2002). It is important to note that although these results were found to be statistically significant through Model 6b., the trends reported through Figure 13 reveal that the effect of slope on caribou occurrence is relatively small. This means that although slope may play a small roll in influencing caribou distributions across the Slate Islands, its effect may not be biologically significant to the population's distribution.

Bergerud *et al.* (1996) previously suggested that the caribou may use areas with steeper slopes and higher elevations when competition for forage was high. Alternatively, the woodland caribou of the Pic Islands in Lake Superior, Ontario were observed fleeing uphill along steep slopes when chased by dogs (Ferguson *et al.* 1988). Lingle (2002) also demonstrated that mule deer use more steeply sloped areas as a refuge from coyotes, while white-tailed deer employ a strategy of moving downhill when threatened. In the context of the Slate Islands caribou, it is

possible that the caribou were preferring areas with flatter slopes and not using steeper areas as a method of predator avoidance because predation did not influence caribou distributions as evaluated through this study (Model 7a. and 7b.) If slope does influence the Slate Islands' caribou distribution, I hypothesize that the caribou are selecting areas with flatter slopes because the caribou require less energetic output than areas with steeper slopes (Wiens *et al.*1997; Johnson *et al.* 2002). I also hypothesize that as caribou density increases on the archipelago, the caribou begin to use less steep slopes of the park as a method of being more energetically efficient as competition increases for forage (Wiens *et al.*1997).

I also found that the Slate Islands caribou varied their distance to nearest waterbody as caribou density increased on the islands. At lower population levels (approximately 105 individuals and below) the caribou were more likely to occupy areas closer to waterbodies, but as caribou density increased to 110 or more individuals, caribou began shift their distribution and use areas more interior to the park (Figure 12). As noted in section 5.1, these trends are generally contrary to caribou habitat preferences previously documented in the literature (Bergerud 1985; Bergerud and Page 1987; Bergerud *et al.* 1990; Cumming *et al.* 1994).

I hypothesize that distance to nearest waterbody trends reported here may represent a shift in the Slate Islands caribou foraging strategy as population size increases in the park. As noted in section 5.1, it is possible that distributions seen here indicated that the caribou were selecting potential foraging habitat over potentially enemy-free habitats (such as shorelines) when the threat of predation on the islands is low. Additionally, I hypothesize that a population size of 105 individual may represent a threshold for this caribou population, in which individuals begin to shift foraging strategies as a method of compensating for increasing competition levels. Previous research investigating caribou or other ungulate population size thresholds in relation to

habitat distribution is limited. Authors such as Radeloff *et al.* (1999) have previously developed

models evaluate the relationship between habitat selection and population size of German roe

deer (*Capreolus capreolus*) in order to theoretically investigate maximum allowable deer

densities in forested areas. Alternatively, Creel *et al.* (2005) evaluated habitat use relative to

density in elk populations in Montana. While not specifically investigating thresholds associated

with population density, Creel *et al.* found that elk shifted their preferred habitat use in response

to predation pressure, while there was no effect of elk density on habitat selection.

Caribou were, on average, located closer to one another than would be expected through

random chance (Figure 14). As discussed in section 5.1, this observation differs from what is

often seen in mainland woodland caribou populations, in which individuals are spatially

dispersed across their home range to avoid predators (Darby and Puritt 1984; Seip 1991;

Bergerud *et al.* 1992; Courtois 2003). There were no predators on the islands for the majority of

this study, and, as indicated through the results of Model 7c., predation did not affect caribou

distance to nearest neighbour. Therefore, there may have been less pressure for the caribou to be

spatially dispersed in comparison to other caribou populations.

Alternatively, closer than random intraspecific spacing may indicate that the Slate Islands

caribou are clustering together in selected areas of the park. Some mainland caribou populations

have also been found to loosely group together during the summer months, primarily as a result

of attempting to space themselves away from moose and wolf populations in a limited area of

preferred habitat (Cumming *et al.* 1994). Similarly, it is possible that the Slate Islands caribou

are loosely clustering together in the park because there is a relatively limited area of the

archipelago containing the summer forage preferred by the caribou.

Further, observed caribou distance to nearest neighbour declined as caribou population size increased (Model 6c, Figure 14). This makes sense, given that the archipelago is geographically restricted, with limited opportunity for caribou immigration and emigration (Bergerud *et al.* 2007). As a result, caribou may have no choice but to be located closer to one another as population size increases. However, I have insufficient data to confirm whether these trends are the result of a mathematical response in the model or a behavioural response in the caribou as population size increased.

As noted throughout this thesis, woodland caribou are generally considered a solidary species, with individuals normally spacing themselves away from one another during the summer months (Darby and Puritt 1984; Seip 1991; Bergerud *et al.* 1992; Courtois 2003). Additionally, insular barren-ground caribou populations will expand their home ranges in response to increased density and competition for forage (Ouellet *et al.* 1997). In the Slate Islands it is possible that crowding of conspecifics may lead to increased encounters and direct interactions between caribou for preferred habitat, with more dominant individuals attempting to push less dominate individuals out of the preferred habitat areas (Ouellet *et al.* 2007). These trends have been noted in some barren-ground caribou populations (Ouellet *et al.* 2007), and in species such as roe deer (Thouless 1990). This level of competition could lead to less dominant individuals spending more time and energy searching for acceptable habitat on the islands (Ouellet *et al.* 2007). Because there were no predators present throughout most of the study, the caribou could have been grouping together within habitat patches with a lower level of interactions than what would normally be expected compared to other populations.

5.4 Effects of predation on habitat selection

The lack of effect of predation on caribou habitat and landscape selection is an anomaly relative to previous woodland caribou research. The results of my work are also surprising given Bergerud *et al.* (2007) found that the wolves had a strong effect on this population during this time period, reducing adult survivorship by 11% and calf survivorship by 13%. The majority of publications studying caribou population distributions indicate that predator avoidance is one of the primary drivers in caribou habitat selection and movement (Bergerud 1988; Seip 1991; Siep 1992; Rettie and Messier 2000; Johnson *et al.* 2001; Environment Canada 2008). Caribou have also been shown to shift habitat use in reaction to changes in predation rates and new threats. In a study of wolf-caribou spatial overlaps and time delays using GPS data, Whittington *et al.* (2011) suggested wolves can influence caribou movements on an event-by-event basis and at the broader seasonal scales. Other species, such as bighorn sheep (*Ovis canadensis*) have similar reactions to new predation pressures and will shift habitats to adjust to new threats (Festa-Bianchet *et al.* 2006).

Within this study, it is possible either habitat selection was influenced by wolves at a spatial scale other than the one examined here, or there were too few years or too weak of level of predation to detect an effect. Alternatively, given the small area of the park and relatively low number of refuges, it is possible that predation affects the Slate Islands caribou survivorship and fitness (Bergerud *et al.* 2007) without affecting habitat distribution. Similarly, competition for forage may be strong enough within this population that foraging habitat takes priority over selecting anti-predator habitats. While uncommon, the trade-off in favour of forage vs. anti-predator habitat has been documented in other species. Elk in the area of Banff National Park (Alberta, Canada) vary their exposure to habitats associated with higher mortality rates

(Robinson *et al.* 2010). In these circumstances, the costs of avoiding predators may not be outweighed by the costs of avoiding preferred foraging areas, and elk use other methods of reducing predation risk (i.e. grouping behaviour and increased vigilance; Robinson *et al.* 2010). Relative to the Slate Islands caribou, additional information or a larger dataset would be required in order to definitively determine what the drivers are for this population during the threat of predation.

5.5 Conclusions

The Slate Islands caribou selected specific forest types and landscape features (Models 1 – 4), with landscape use varying as population size increases (Model 6). Caribou were also consistently located closer to anthropogenic features than what would be expected through random chance (Model 5). While predation may play a role in other aspects of the Slate Islands caribou ecology (Bergerud *et al.* 2007) its influence was not detected on caribou distributions examined through this thesis (Model 7).

The Slate Islands caribou distributions were most consistent with the hypothesis that caribou compete for foraging resources as opposed to enemy-free spaces on the Slate Islands. In context of this population, the hypothesis that caribou avoid areas containing human presence was not found to apply to the Slate Islands caribou. It is important to note that this study did not incorporate behavioural monitoring and that in order to confirm any behaviour-based aspects of these hypotheses, further study would be required.

CHAPTER 6: MANAGEMENT IMPLICATIONS

Population-specific action plans and recovery actions are recommended for the recovery of woodland caribou populations by Environment Canada (Environment Canada 2011). They recommend activities such as land use planning and habitat restoration/management for critical habitat, in addition to other measures such as predator and alternate-prey management (Environment Canada 2011). While many of Environment Canada's goals are focused on increasing caribou fitness and population growth (and habitat selection can lead to increased individual fitness [McLoughlin *et al.* 2002]), it is important to note that caribou fitness was not specifically tested as part of the scope of this thesis.

As documented through my thesis, the Slate Islands caribou select for areas with deciduous forest types and avoid areas with coniferous forest types. The caribou's selection for deciduous forest types may become more difficult over time as the archipelago has not experienced any recent disturbances that would restore the park to an early-seral state that would encourage growth of deciduous forest (Bergerud *et al.* 2007). Given that Bergerud *et al.* (2007) found that forage was one of the most limiting factors for the Slate Islands caribou on the islands, investigating methods for maintaining or increasing preferred-forage types for the Slate Islands caribou may be useful as a tool to help maintain this population on the archipelago. Given the remote nature of Slate Islands, the status of the caribou and the public use of the area for recreation, maintenance of the preferred deciduous habitat on the Slate Islands may prove to be a difficult task.

Some research groups have begun to experiment with non-traditional methods of caribou habitat with mainland caribou population which could be applied in difficult-to-manage areas such as the Slate Islands. For example, the Canadian Oil Sands Innovation Alliance (COSIA)

has begun to experiment with tree planting programs in efforts to maintain and regenerate preferred caribou habitats in British Columbia (Golder Associates 2012; COSIA 2014). Learning from this research, planting programs could be used to simulate natural deciduous plant growth on the Slate Islands. Alternatively, patch-cut or partial harvest practices (i.e. clear-felling small areas of forest to encourage early-seral growth of deciduous species; Gotmark *et al.* 2005) could be used over a one to three year period to replenish preferred caribou forage and habitats in late-seral areas of the archipelago.

While either planting programs or partial harvest practices could offer promising results for encouraging growth of deciduous forest type for the Slate Islands caribou, potential negative effects of these programs should also be considered. For example, either of these programs may result in a temporary loss of caribou habitat while cleared areas regenerate, or through avoidance of edge habitats (which are normally associated with a higher predation risk; Schaefer and Mahoney 2007), thus reducing available caribou habitat in the short term and negatively affecting the population. Additionally, given the remote nature of the Slate Islands, there would be a high financial cost associated with the establishment of either the planting program or partial harvesting on the islands and an innovative approach would be required execute either program.

My thesis also highlights that caribou generally selected areas of the islands that were frequented by tourists. While this behaviour has been documented in other ungulate species as a foraging technique (Hockett 2000) and as predator avoidance strategy (Waser *et al.* 2014), this is to best of my knowledge this is the first documentation of woodland caribou selecting for tourist areas or campsites. The Slate Islands caribou presence at the campsites may indicate selection for a desired food source at those locations or a potential refuge from predators. Alternatively,

caribou may use anthropogenic sites because of the high level of competition for forage within the park, resulting in caribou having to approach campsites and tourists in search of food. While the woodland caribou are a main attraction for tourists who visit the park, tourist injury due to wildlife interactions poses risks for both sightseers and wildlife. Signage discouraging feeding the caribou and proper disposal of food wastes could be beneficial at popular tourist areas of the Slate Islands and could prevent possible tourist injuries (Hockett 2000).

I found that the Slate Islands caribou selected for specific landscape variables as population density increased in the park, while wolf presence did not influence the caribou distribution. It is worth noting that while it is important to increase caribou populations in order to maintain this species nationally, it has been shown through this thesis that the Slate Islands caribou may shift how they use the landscape as the population size increases. Decision makers should be mindful of this potential effect on the Slate Islands caribou populations as biologists manage the area to maintain or increase caribou population size in the park.

The Slate Islands caribou are an important economic and cultural feature of northern Ontario and Lake Superior. While this population is at risk of local extirpation, steps can to be taken to maintain this population. Maintaining the Slate Islands caribou will be important in maintaining this threatened species as a whole and preserving one of Canada's most symbolic species.

LITERATURE CITED

Apps, C. D., McLellan, B. N., Kinley, T. A., & Flaa, J. P. (2001). Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. The Journal of wildlife management, 65-77.

Atwood, T. C., & Weeks Jr, H. P. (2003). Sex-specific patterns of mineral lick preference in white-tailed deer. Northeastern Naturalist, 10(4), 409-414.

Ayres, L. A., Chow, L. S., & Graber, D. M. (1986). Black bear activity patterns and human induced modifications in Sequoia National Park. Bears: Their Biology and Management, 6, 151-154.

Ballard, W. B., Lutz, D., Keegan, T. W., Carpenter, L. H., & deVos Jr, J. C. (2001). Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin, 99-115.

Ballard, W. B., & Van Ballenberghe, V. (1997). Predator/prey relationships. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, DC, 247-73.

Banfield, A. W. F., & Brooks, A. (1974). The mammals of Canada (Vol. 4, No. 3). Toronto, Ontario, Canada: University of Toronto Press.

Barrette, C., & Vandal, D. (1986). Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour, 118-146.

Beckmann, J. and Berger, J. (2003). Using black bears to test ideal-free distribution model experimentally. Journal of Mammalogy. Vol. 84, No. 2, pp. 594-606.

Belovsky, G. E. (1991). Insights for caribou/reindeer management using optimal foraging theory. Rangifer, (7), 7-23.

Belovsky, G. E. (1986). Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70:35–52.

Bergerud, A. T. (1974). Decline of caribou in North America following settlement. The Journal of Wildlife Management 38:757–770.

Bergerud, A. T. (1983). Prey Switching in a Simple Ecosystem. Scientific American 130–141.

Bergerud, A. T., & Page, R. E. (1987). Displacement and dispersion of parturient caribou at calving as antipredator tactics. Canadian Journal of Zoology, 65(7), 1597–1606.

Bergerud, A. T. (1988). Caribou, wolves and man. Trends in Ecology & Evolution, 3(3), 68-72.

Bergerud, A. T. (1992). Rareness as an antipredator strategy to reduce predation risk for moose and caribou. In Wildlife 2001: populations (pp. 1008-1021). Springer Netherlands.

Bergerud, A. T. (1996). Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer Special Issue No. 9: 95-116.

Bergerud, A. T., and J. P. Elliott. (1998). Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology 76:1551–1569.

Bergerud, A. T., Dalton, W. J., Butler, H., Camps, L., & Ferguson, R. (2007). Woodland caribou persistence and extirpation in relic populations on Lake Superior. Rangifer, (17), 57-78.

Bergerud, A.T. unpublished data. Slate Islands caribou research – 1974-2005

Birch LC, Park T, Frank MB. (1951). The effect of intraspecies and interspecies competition on the fecundity of two species of flour beetles. Evolution. 5:116–132.

Blackith, R. E. (1958). Nearest-neighbour distance measurements for the estimation of animal populations. Ecology, 39(1), 147-150.

Bøving, P.S., and Post, E. (1997). Vigilance and foraging behaviour of female caribou in relation to predation risk. Rangifer, 17: 55– 63.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. (2002). Evaluating resource selection functions. Ecological Modelling, 157(2), 281-300.

Brokx, P. A. J. 1965. The Hudson Bay Lowland as caribou habitat. M.Sc. thesis. University of Guelph, Ontario.

Brown, J. L., & Orians, G. H. (1970). Spacing patterns in mobile animals. Annual Review of Ecology and Systematics, 1, 239-262.

Calef, G. W., & Lortie, G. M. (1975). A mineral lick of the barren-ground caribou. Journal of Mammalogy, 240-242.

Campbell, N. A and J.B. Reece. Biology. 9th Edition. Benjamin Cummings Press.

Carr, N. L., A. R. Rodgers, S. R. Kingston, P. N. Hettinga, M. Laura, J. L. Renton, and P. J. Wilson. (2012). Comparative woodland caribou population surveys in Slate Islands Provincial. Rangifer Special Issue 205–218.

CCWHC (Canadian Cooperative Wildlife Health Centre). (2002). Wildlife Damage Management Internet Center for Newsletter and Publication. Volume 9-1, Winter

Colman, J. E., Jacobsen, B. W., & Reimers, E. (2001). Summer response distances of Svalbard reindeer Rangifer tarandus platyrhynchus to provocation by humans on foot. Wildlife Biology, 7(4), 275-284.

Connelly, G. E. (1978). Predators and predator control. Pages 369-394 in J. L. Schmidt and D. L. Gilbert, editors. Big Game of North America. Stackpole, Harrisburg, Pennsylvania, USA

Collins, W. B., & Urness, P. J. (1983). Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. The Journal of Wildlife Management, 646-663.

COSEWIC. (2002). COSEWIC assessment and update status report on the woodland caribou

    Rangifer tarandus caribou in Canada. Committee on the Status of Endangered Wildlife in

    Canada. Ottawa. xi + 98 pp.

COSIA (Canada Oil Sands Innovation Alliance). 2014. Caribou habitat restoration program.

    Accessed May 15th 2014. Available at: http://www.cosia.ca/caribou-habitat-restoration

Courbin, N., D. Fortin, C. Dussault, and R. Courtois. (2009). Landscape management for

    woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence.

    Landscape Ecology 24:1375–1388.

Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999). Inverse density dependence and the

    Allee effect. Trends in ecology & evolution, 14(10), 405-410.

Courchamp, F., Berec, L., & Gascoigne, J. (2008). Allee effects in ecology and conservation.

    Environ. Conserv, 36, 80-85.

Courtois, R., J.-P. Ouellet, A. Gingras, C. Dussault, L. Breton, and J. Maltais. (2003). Historical

    changes and current distribution of caribou, Rangifer tarandus, in Quebec. Canadian Field

    Naturalist 117:399–414.

Cringan, A. T. (1956). Some aspects of the biology of caribou and a study of the woodland

    caribou range of the Slate Islands, Lake Superior, Ontario. M.A. Thesis, Univ. of

    Toronto. 300pp.

Creel, S., Winnie Jr, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection

    as an antipredator response to wolves. Ecology, 86(12), 3387-3397.

Crete, M., and A. Desrosiers. (1995). Range expansion of coyotes, Canis latrans, threatens a

    remnant herd of caribou, Rangifer tarandus, in Southern Quebec. The Canadian Field-

    Naturalist 109:227–235.

Crisler, L. (1956). Observations of wolves hunting caribou. Journal of Mammalogy, 37(3), 337–346.

Culling, D.E., B.A. Culling, T.J. Raabis, and A.C. Creagh. (2006). Ecology and seasonal habitat selection of boreal caribou in the Snake-Sahtaneh Watershed, British Columbia to 2004. Canadian Forest Products Ltd., Fort Nelson, BC.

Dale, B. W., L. G. Adams, and R. T. Bowyer. (1994). Functional response of wolves preying on barrenground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644–652.

Dalton, W. J. in Carr, N. L., A. R. Rodgers, S. R. Kingston, P. N. Hettinga, M. Laura, J. L. Renton, and P. J. Wilson. (2012). Personal Communitcation between W. J. Dalton and Ontario Ministry of Natural Resources Staff. 2002

Darby, W., and L. S. Duquette. (1986). Woodland caribou and forestry in Northern Ontario, Canada. Rangifer 87–93.

Darby, W. R. W., & Pruitt, W. O. (1984). Habitat use, movements and grouping behaviour of woodland caribou, Rangifer tarandus caribou, in southeastern Manitoba. The Canadian Field-Naturalist, 98(2), 184–190.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66:322-331.

Dressler, B. O., & Sharpton, V. L. (1997). Breccia formation at a complex impact crater: Slate Islands, Lake superior, Ontario, Canada. Tectonophysics, 275(4), 285-311.

Duchesne, M., S. D. Côté, C. Barrette, and S. D. Cote. (2000). Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve , Canada. Behaviour 96:311–317.

Dussault, C., V. Pinard, J.-P. Ouellet, R. Courtois, and D. Fortin. (2012). Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behaviour? Proceedings. Biological Sciences / The Royal Society 279:4481–8.

Dyer, S. J., J. P. O. Neill, S. M. Wasel, and S. Boutin. (2001). Avoidance of industrial development by woodland caribou. The Journal of Wildlife Management 65:531–542.

Elton, C., & Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology, 215-244.

Emlen, J. M. (1966). The role of time and energy in food preference. American Naturalist. 100:611-617

Environment Canada. n.d.a. Slate Island – 45136. Available at: http://text.www.weatheroffice.gc.ca/marine/weatherConditions-currentConditions_e.html?mapID=09&siteID=08503&stationID=45136. Accessed August 8, 2012.

Environment Canada n.d.b. Canadian Climate Normals 1971-2000 for Terrace Bay, Ontario. Available at: http://www.climate.weatheroffice.gc.ca/climate_normals/results_e.html?stnID=4054&lang=e&dCode=0&StationName=TERRACE&SearchType=Contains&province=ALL&provBut=&month1=0&month2=12. Accessed August 8, 2012.

Environment Canada. (2008). Scientific Review for the Identification of Critical Habitat for Woodland Caribou (Rangifer tarandus caribou), Boreal Population, in Canada. August 2008. Ottawa: Environment Canada. 72 pp. plus 180 pp Appendices.

Environment Canada. (2011). Recovery Strategy for the Woodland Caribou, Boreal population (Rangifer tarandus caribou) in Canada [Proposed]. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa. vi + 55 pp.

Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T. & Pelletier, F. (2006) Stochastic predation events and population persistence in bighorn sheep. Proceedings. Biological Sciences∕The Royal Society, 273, 1537–1543.

Festa-Bianchet, M., Gaillard, J. M., & Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. Journal of Animal Ecology, 72(4), 640-649.

Forman, R. T. (1995). Some general principles of landscape and regional ecology. landscape ecology, 10(3), 133-142.

Fortin, D., P.-L. Buono, A. Fortin, N. Courbin, C. Tye Gingras, P. R. Moorcroft, R. Courtois, and C. Dussault. (2013). Movement Responses of Caribou to Human-Induced Habitat Edges Lead to Their Aggregation near Anthropogenic Features. The American naturalist 181:827–36.

Fretwell, S. D. & Lucas, H. L., Jr. (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical Development. Acta Biotheoretica 19: 16–36.

Frey et al. 2003 Frey, B. R., Lieffers, V. J., Landhäusser, S. M., Comeau, P. G., & Greenway, K. J. (2003). An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research, 33(7), 1169-1179.

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution, 13(2), 58-63.

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics, 367-393.

Gese, E. M., and F. F. Knowlton. (2001). The role of predation in wildlife population dynamics. Fort Collins, Colorado. pp. 20.

Given, D. R., & Soper, J. H. (1981). The arctic-alpine element of the vascular flora at Lake Superior. Publ. Bot. Nation. Mus. Nat. Sci.(Ottawa), (10).

Gorden, S. South Purcell Mountain Caribou Augmentation. Presentation – Friday September 28th at the North American Caribou Workshop. Fort St. John, British Columbia. http://nacw2012.ca/images/files/NACW2012-WorkshopBinder_Final.pdf

Götmark, F., Paltto, H., Nordén, B., & Götmark, E. (2005). Evaluating partial cutting in broadleaved temperate forest under strong experimental control: short-term effects on herbaceous plants. Forest Ecology and Management, 214(1), 124-141

Green, R. E. (2008). Assessing the impact of culling on population size in the presence of uncertain density dependence: lessons from a great cormorant population. Journal of applied ecology, 45(6), 1683-1688.

Gullage, S., C. E. Soulliere, S. P. Mahoney, K. Morgan, and T. Porter. (2012). Diversionary Feeding of Black Bear and Coyote in a Caribou Calving Area in Eastern Newfoundland in National Fish and Wildlife Conservation Congress Ottawa, Ontario.

Gunn, A., and, Adamczewski J. (2003). Muskox. Ch. 50. In: Feldhamer, G., Chapman, B.A., and Chapman, J.A., eds. Wild mammals of North America. Baltimore, Maryland: The Johns Hopkins University Press. 1076-1094.

Hairston Jr, N. G., & Hairston Sr, N. G. (1993). Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. American Naturalist, 379-411.

Hebert, D., & Cowan, I. M. (1971). Natural salt licks as a part of the ecology of the mountain goat. Canadian Journal of Zoology, 49(5), 605-610.

Helle, T. (1980). Sex segregation during calving and summer period in wild forest reindeer (Rangifer tarandus fennicuslonn) in eastern Finland with special reference to habitat requirements and dietary preferences. – In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds), Proc. of the Second Int. Reindeer: Caribou Symp. Røros, Norway, Dir. for vilt og ferskvannsfisk, Trondheim, pp. 508–518.

Heinselman, M. L. (1981). Fire and succession in the conifer forests of northern North America. In Forest succession (pp. 374-405). Springer New York.

Hins, C., J.-P. Ouellet, C. Dussault, and M. Stlaurent. (2009). Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. Forest Ecology and Management 257:636–643.

Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. The Canadian Entomologist, 91(07), 385-398.

Holt R.D. (1977) Predation, apparent competition and the structure of prey communities. Theoretical population ecology. 12:197–229

Holt R.D. (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. American Naturalist. 124:377–406

Holt R.D., Lawton JH (1994) The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495–520

Hui, C. (2006) Carrying capacity, population equilibrium, and environment's maximal load. Ecological Modelling, 192, 317–320.

James, A. R., Boutin, S., Hebert, D. M., & Rippin, A. B. (2004). Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management, 68(4), 799-809.

James, A. R. C., and A. K. Stuart-smith. (2000). Distribution of Caribou and Wolves in Relation to Linear Corridors. The Journal of Wildlife Management 64:154–159.

Jeffery, R. A., R. D. Otto, and F. R. Phillips. (2007). George's Island, Labrador - A high-density predator-free refuge for a woodland caribou subpopulation? Rangifer 51–56.

Jeffries, M. J., & Lawton, J. H. (1984). Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society, 23(4), 269-286.

Jenkins, A. K. J., and R. G. Wright. (2013). Resource Partitioning and Competition Among Cervids in the Northern Rocky Mountains. 25:11–24.

Johnson, C. J., Parker, K. L., & Heard, D. C. (2001). Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia, 127(4), 590-602.

Johnson, C.J., Parker, K.L., Heard, D.C., (2000). Feeding site selection by woodland caribou in north-central British Columbia. Rangifer, 159–172.

Johnson, C. J., & Seip, D. R. (2008). Relationship between resource selection, distribution, and abundance: a test with implications to theory and conservation. Population Ecology, 50(2), 145-157.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Keith, L.B. (1974). Some features of population dynamics in mammals. In Proceedings of the 11th International Congress of Game Biologists. pp. 17–58.

Kelsall J. P and Telfer, E. S.1984. Adaptation of some large North American mammals for survival in snow. Ecology 65:1828–1834.

Kelsall, J.P. (1968). The migratory barren-ground caribou of Canada. Monograph no.3, Canadian Wildlife Service, Indian Affairs and Northern Development. Queen's Printer, Ottawa, Ontario. 339 pp.

Klein, D. R. (1968). Latitudinal variation in foraging strategies. - In: Gudmundsson, O. (ed.), Grazing research at northern latitudes. Plenum Pub. Corp., New York pp. 237-246.

Koper, N., and M. Manseau. (2009). Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. Journal of Applied Ecology 46:590–599.

Koper, N., and M. Manseau. (2012). A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. Rangifer Special Issue 195–203.

Leader-Williams, N. (1980). Population dynamics and mortality of reindeer introduced into South Georgia. The Journal of Wildlife Management 44:640–657.

Leopold, A. (1933). Game management. University of Wisconsin Press.

Leopold, A. S. & Daling, F. F. (1953). Wildlife in Alaska. Ronald Press, New York. 129pp.

Levins, R. (1968). Evolution in Changing Environments: Some Theoretical Explorations.(MPB-2) (Vol. 2). Princeton University Press.

Libal, N. S., Belant, J. L., Leopold, B. D., Wang, G., & Owen, P. A. (2011). Despotism and risk of infanticide influence grizzly bear den-site selection. PloS one, 6(9),

Lidicker Jr, W. Z. (1999). Responses of mammals to habitat edges: an overview. Landscape
Ecology, 14(4), 333-343.

Lincoln, F.C. (1930). Calculating waterfowl abundance on the basis of banding returns. – U.S.
Department of Agriculture Circular. No 118, May 1930

Lima 2002 Lima, S. L. (2002). Putting predators back into behavioral predator–prey
interactions. Trends in Ecology & Evolution, 17(2), 70-75.

MacArthur, R. H., and E. R. Pianka. (1966). On Optimal use of a patchy environment. The
American Naturalist 100.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., (2002). Resource Selection by Animals:
Statistical Design and Analysis for Field Studies. Chapman & Hall, London.

McLoughlin, P. D., J. S. Dunford, and S. Boutin. (2005). Relating predation mortality to broad-
scale habitat selection. Journal of Animal Ecology 74:701–707.

Mech, L. D. (1966). The wolves of Isle Royale.

Messier, F. (1991). The significance of limiting regulating factors on the demography of moose
and white-tailed deer. Journal of Animal Ecology 60:377–393.

Messier, F. (1994). Ungulate Population Models with Predation : A Case Study with the North
American Moose. Ecology 75:478–488.

Messier, F., M. Crête, and M. Messier, François, Crete. (1985). Moose-wolf dynamics and the
natural regulation of moose populations. Oecologia 65:503–512.

Middleton, H. (1960). Re: Caribou crossing from the Slate Islands. March 15, 1960. Harold
Middleton to District Forester Geraldton, Ontario. Cited in C. McGregor. A vegetation
inventory of the Slate Islands. Environmental Planning Series, Life Science Report.
Vol.V, No.17. Ministry

Miller, F. L., Edmonds, E. J., & Gunn, A. (1982). Foraging behaviour of Peary caribou in response to springtime snow and ice conditions. Environment Canada, Canadian Wildlife Service.

Monaghan, P., & Metcalfe, N. B. (1985). Group foraging in wild brown hares: effects of resource distribution and social status. Animal Behaviour, 33(3), 993-999.

Mosnier, A., Ouellet, J. P., Sirois, L., & Fournier, N. (2003). Habitat selection and home-range dynamics of the Gaspé caribou: a hierarchical analysis. Canadian Journal of Zoology, 81(7), 1174-1184.

Murdoch, W. W., & Oaten, A. (1975). Predation and population stability. Advances in ecological research, 9, 1-131.

Murray, M. G., & Illius, A. W. (2000). Vegetation modification and resource competition in grazing ungulates. Oikos, 89(3), 501-508.

Murray, C. M., Mane, S. V., & Pusey, A. E. (2007). Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. Animal Behaviour, 74(6), 1795-1804.

Nelson, M. E., and Mech, L. D. (1981). Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs No. 77

OESA (Ontario Endangered Species Act). (2007). (c. 6). [online] Available at: http://www.e-laws.gov.on.ca/html/statutes/english/elaws_statutes_07e06_e.htm

Ontario Ministry of Natural Resources (OMNR). (2011). Slate Islands Terms of Reference: Slate Islands Provinical Park Management plan. Available at: http://www.ontarioparks.com/english/planning_pdf/slat/slat_ToR.pdf Accessed August 1st, 2012.

Oosenbrug, S. M., & Theberge, J. B. (1980). Altitudinal movements and summer habitat

      preferences of woodland caribou in the Kluane Ranges, Yukon Territory. Arctic, 59-72.

Orians, G. H., & Wittenberger, J. F. (1991). Spatial and temporal scales in habitat

      selection. American Naturalist, S29-S49.

Ouellet J-P, Heard DC, Boutin S, Mulders R (1997) A comparison of body condition and

      reproduction of caribou on two predator-free Arctic islands. Can J Zool 75:11-17

Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. (2010). Foraging theory upscaled: the

      behavioural ecology of herbivore movement. Philosophical transactions of the Royal

      Society of London. Series B, Biological sciences 365:2267–78.

Pearce, J., & Eccles, G. (2004). Characterizing forest-dwelling woodland caribou distribution in

      Ontario, Canada. Unpublished report. Canadian Forest Service, Sault Ste. Marie, Ontario.

Pettorelli, N., Gaillard, J. M., Duncan, P., Maillard, D., Van Laere, G., & Delorme, D. (2003).

      Age and density modify the effects of habitat quality on survival and movements of roe

      deer. Ecology, 84(12), 3307-3316.

Pierce, B. M., Bleich, V. C., Monteith, K. L., & Bowyer, R. T. (2012). Top-down versus bottom-

      up forcing: evidence from mountain lions and mule deer. Journal of Mammalogy, 93(4),

      977-988.

Peek, J. M. (1986). A review of wildlife management. - Prentice-Hall, Englewood Cliffs, NJ

      Hall, Englewood Cliffs, NJ.

Peterson, R. O. (1999). Wolf-moose interaction on Isle Royale: the end of natural regulation?

      Ecological Applications, 9(1), 10-16.

Peterson, R. O., and R. E. Page. (1988). The rise and fall of Isle Royale wolves, 1975-1986.

      Journal of Mammology 69:89–99.

Pyke G.H. (1984). Optimal foraging theory: A critical review. . Annual Review of Ecology and Systematics. 15:523-575McLoughlin et al 2005

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. (1977). Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137-154.

Quaintenne, G., van Gils, J. A., Bocher, P., Dekinga, A., & Piersma, T. (2011). Scaling up ideals to freedom: are densities of red knots across western Europe consistent with ideal free distribution? Proceedings of the Royal Society B: Biological Sciences, 278(1719), 2728-2736.

Quinn, G. G. P., & Keough, M. J. (2002). Experimental design and data analysis for biologists. Cambridge University Press.

Radeloff, V. C., Pidgeon, A. M., & Hostert, P. (1999). Habitat and population modelling of roe deer using an interactive geographic information system. Ecological Modelling, 114(2), 287-304.

Rettie, W. J., and F. Messier. (2000). Hierarchical habitat selection by Woodland Caribou: its relationship to limiting factors.

Rettie, W. J., and F. Messier. (1998). Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. Canadian Journal of Zoology 76:251–259.

Ripple, W. J., E. J. Larsen, R. a Renkin, and D. W. Smith. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227–234.

Robinson, B. G., Hebblewhite, M., & Merrill, E. H. (2010). Are migrant and resident elk (Cervus elaphus) exposed to similar forage and predation risk on their sympatric winter range?. Oecologia, 164(1), 265-275.

Rogers, L. L. (1987). Factors influencing dispersal in the black bear. Mammalian dispersal

    patterns: the effects of social structure on population genetics. University of Chicago

    Press, Chicago, 75-84.

Rominger, E. M., & Oldemeyer, J. L. (1989). Early-winter habitat of woodland caribou, Selkirk

    Mountains, British Columbia. The Journal of Wildlife Management, 238-243.

Rupp, T. S., Olson, M., Adams, L. G., Dale, B. W., Joly, K., Henkelman, J., & Starfield, A. M.

    (2006). Simulating the influences of various fire regimes on caribou winter

    habitat. Ecological Applications, 16(5), 1730-1743.

Samuel, W.M. (2007). Factors affecting epizootics of winter ticks and mortality of moose. Alces

    43: 39-48.

Schaefer, J. A., & Mahoney, S. P. (2001). Antlers on female caribou: biogeography of the bones

    of contention. Ecology, 82(12), 3556-3560.

Schaefer, J. a., and S. P. Mahoney. (2007). Effects of Progressive Clearcut Logging on

    Newfoundland Caribou. Journal of Wildlife Management 71:1753–1757.

Schoener, T. W. (1971). Theory of feeding strategies. Annual Review of Ecology and

    Systematics. 2, 369-404.

Seip, D. R. (1991). Predation and caribou populations. Rangifer, (7), 46-52.

Seip, D. R., and D. B. Cichowski. (1996). Population ecology of caribou in British Columbia.

    Rangifer Special Issue 73–80.

Semeniuk, C. A. D., Musiani, M., Hebblewhite, M., Grindal, S., & Marceau, D. J. (2012).

    Incorporating behavioral–ecological strategies in pattern-oriented modeling of caribou

    habitat use in a highly industrialized landscape. Ecological Modelling, 243, 18-32.

Smout, S., Rindorf, A., Hammond, P. S., Harwood, J., & Matthiopoulos, J. (2014). Modelling prey consumption and switching by UK grey seals. ICES Journal of Marine Science: Journal du Conseil, 71(1), 81-89.

Skogland, T. (1974). Villreinens habitat atferd, økologiske og sosiale faktorer. — Progress report Norwegian IBP Program, Direktoratet for Vilt og Ferskvannsfisk, Trondheim, 133 pp.

Skogland, T. (1985). The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54: 359 - 374.

Skogland, T. (1991). What are the effects of predators on large ungulate populations? Oikos 61:401–411.

Smith, R. L., Smith, T. M., Desharnais, R., Bell, J., Palladino, M. A., Hickman, G. C., & Hickman, S. M. (2001). Ecology and Field Biology (pp. 1-766). San Francisco: Benjamin Cummings.

Stephens, D. W., & Krebs, J. R. (1986). Foraging Theory. Princeton University Press. Princeton, NJ, 247.

Stephens, P. A., and W. J Sutherland. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology & Evolution 14:401–405.

Stevenson (1990 Stevenson, S. K. (2010). Managing second-growth forests as caribou habitat. Rangifer, 10(3), 139-144.

Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. (1997). Woodland caribou relative to landscape patterns in northeastern Alberta. The Journal of Wildlife Management 61:622–633.

Terry, E. (1994) Winter habitat selection and foraging patterns of mountain caribou. MSc Thesis. University of British Columbia, Vancouver, BC.

Thomas, D.C., and D.R. Gray. (2002). Update COSEWIC status report on the woodland

  caribou Rangifer tarandus caribou in Canada, in COSEWIC assessment and update status

  report on the Woodland Caribou Rangifer tarandus caribou in Canada. Committee on the

  Status of Endangered Wildlife in Canada. Ottawa. 1-98 pp.

Thouless, C. R. (1990). Feeding competition between grazing red deer hinds. Animal Behaviour,

  40(1), 105-111.

Tilman, D. (2007). Interspecific competition and multispecies coexistence. Theoretical Ecology:

  Principles and Applications, 84-97.

Van Ballenberghe, V., and W. B. Ballard. (1994). Limitation and regulation of moose

  populations: the role of predation. Canadian Journal of Zoology 72:2071–2077.

Van Beest, F. M., L. E. Loe, A. Mysterud, and J. M. Milner. (2010). Comparative Space Use and

  Habitat Selection of Moose Around Feeding Stations. Journal of Wildlife Management

  74:219–227.

Van Beest, F. M., Uzal, A., Vander Wal, E., Laforge, M. P., Contasti, A. L., Colville, D., &

  McLoughlin, P. D. (2014). Increasing density leads to generalization in both

  coarse-grained habitat selection and fine-grained resource selection in a large mammal.

  Journal of Animal Ecology, 83(1), 147-156.

 Vors, L. S. (2006). Woodland caribou extirpation and anthropogenic landscape disturbance in

  Ontario. 155.

Waser, N. M., Price, M. V., Blumstein, D. T., Arózqueta, S. R., Escobar, B. D. C., Pickens, R., &

  Pistoia, A. (2014). Coyotes, deer, and wildflowers: diverse evidence points to a trophic

  cascade. Naturwissenschaften, 101(5), 427-436.

Whittington, J., Hebblewhite, M., DeCesare, N. J., Neufeld, L., Bradley, M., Wilmshurst, J., & Musiani, M. (2011). Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology, 48(6), 1535-1542.

Wiens, J. A., & Milne, B. T. (1989). Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology, 3(2), 87-96.

Wittmer, H. U., B. N. McLellan, R. Serrouya, and C. D. Apps. (2007). Changes in landscape composition influence the decline of a threatened woodland caribou population. The Journal of Animal Ecology 76:568–79.

Wittmer, H. U., Sinclair, A. R., & McLellan, B. N. (2005). The role of predation in the decline and extirpation of woodland caribou. Oecologia, 144(2), 257-267.

Young Jr, D. D., & McCabe, T. R. (1998). Grizzly bears and calving caribou: What is the relation with river corridors? The Journal of wildlife management, 255-261.

APPENDIX A: TESTS FOR NORMALITY WITH THE OBSERVED CARIBOU DATASET

SAS Coding
PROC IMPORT OUT=Residuals
DATAFILE= "C:\Residuals.xls"
DBMS=EXCEL2000 REPLACE;
GETNAMES=YES;
RUN;
proc univariate data=work.Residuals;
var Type_Inversed Distance_to_Water Elevation Slope GRIDCODE Patchsize;
run;

Results of Analysis of Observed Caribou Locations

The UNIVARIATE Procedure
Variable: Distance_to_water (Distance_to_water)

Moments

N	579	Sum Weights	579
Mean	213.382104	Sum Observations	123548.238
Std Deviation	170.12816	Variance	28943.5909
Skewness	1.99700136	Kurtosis	8.65077529
Uncorrected SS	43092378.5	Corrected SS	16729395.5
Coeff Variation	79.7293481	Std Error Mean	7.07028505

Basic Statistical Measures

Location		Variability	
Mean	213.3821	Std Deviation	170.12816
Median	170.2525	Variance	28944
Mode	16.3768	Range	1422
Interquartile Range	229.05035		

110

The UNIVARIATE Procedure
Variable: Elevation (Elevation)

Moments

N	579	Sum Weights	579
Mean	230.120124	Sum Observations	133239.552
Std Deviation	27.0456994	Variance	731.469858
Skewness	0.08975634	Kurtosis	-0.8102877
Uncorrected SS	31083891.7	Corrected SS	422789.578
Coeff Variation	11.7528615	Std Error Mean	1.12398091

Basic Statistical Measures

Location		Variability	
Mean	230.1201	Std Deviation	27.04570
Median	228.7433	Variance	731.46986
Mode	168.0000	Range	130.39008
Interquartile Range	42.70410		

The UNIVARIATE Procedure
Variable: Slope (Slope)

Moments

N	579	Sum Weights	579
Mean	7.27940775	Sum Observations	4214.77709
Std Deviation	5.99415384	Variance	35.9298803
Skewness	1.82706693	Kurtosis	3.97576684
Uncorrected SS	51448.5518	Corrected SS	20767.4708
Coeff Variation	82.343977	Std Error Mean	0.24910853

Basic Statistical Measures

Location		Variability	
Mean	7.27941	Std Deviation	5.99415
Median	5.81258	Variance	35.92988
Mode	11.15746	Range	36.05390
Interquartile Range	6.10523		

The UNIVARIATE Procedure
Variable: GRIDCODE (GRIDCODE)

Moments

N	579	Sum Weights	579
Mean	16.2331606	Sum Observations	9399
Std Deviation	0.90512126	Variance	0.81924449
Skewness	-1.0806446	Kurtosis	1.23338093
Uncorrected SS	153049	Corrected SS	473.523316
Coeff Variation	5.57575496	Std Error Mean	0.03761556

Basic Statistical Measures

Location		Variability	
Mean	16.23316	Std Deviation	0.90512
Median	16.00000	Variance	0.81924
Mode	16.00000	Range	4.00000
Interquartile Range	1.00000		

The UNIVARIATE Procedure
Variable: Patchsize (Patchsize)

Moments

N	579	Sum Weights	579
Mean	1370656.74	Sum Observations	793610251
Std Deviation	1476307.44	Variance	2.17948E12
Skewness	0.94429549	Kurtosis	-0.4860603
Uncorrected SS	2.34751E15	Corrected SS	1.25974E15
Coeff Variation	107.708035	Std Error Mean	61353.2435

Basic Statistical Measures

Location		Variability	
Mean	1370657	Std Deviation	1476307
Median	724111	Variance	2.17948E12
Mode	4220911	Range	4214756
Interquartile Range	2125588		

APPENDIX B: SAS CODE USED FOR MODELS

```
PROC IMPORT OUT= WORK.GLM_feb172013
        DATAFILE= "C:\3080RND_Dataset.xls"
        DBMS=excel2000 REPLACE;
   *GETDELETED=NO;
RUN;

TITLE1 'Forest type GLM.1=Absence, 0=Presence';
proc genmod
data = GLM_feb172013 descending;
class Prop19 Prop20 Prop17 Prop18 ;
model  Type_Inversed = Prop19 Prop17 Prop18 Prop20/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;

TITLE1 'Landscape GLM. 0=Absence, 1=Presence';
proc genmod
data = GLM_feb172013 descending;
class ;
model  Type_Inversed = Distance_to_water_m LogPatchsize Slope Elevation/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;

TITLE1 'GLM with Nearest Neighbour. 0=Absence, 1=Presence';
proc genmod
data = GLM_feb172013 descending;
class Type_Inversed ;
model  Nearest_neighbour_m = Type_Inversed /
dist = normal corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;
```

```
TITLE1 'GLM with Nearest Neighbour and interaction with predation stats. 0=Absence,
1=Presence';
proc genmod
data = GLM_feb172013 descending;
class Type_Inversed Predation;
model  Nearest_neighbour_m = Type_Inversed Predation Type_Inversed*Predation/
dist = normal corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;

TITLE1 'Distance to Feature on Islands. 0=Absence, 1=Presence';
proc genmod
data = GLM_feb172013 descending;
class ;
model  Type_Inversed  = Old_Barn_km Mortimer_km Come_km Puds_km
Lighthouse_Cabins_km South_km/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;

TITLE1 'Distance to Mud Lake salt lick. 0=Absence, 1=Presence';
proc genmod
data = GLM_feb172013 descending;
class ;
model  Type_Inversed  = Mud_Lake_km/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;

TITLE1 'GLM with Nearest Neighbour and interaction with population size stats. 0=Absence,
1=Presence';
proc genmod
data = GLM_feb172013 descending;
class Type_Inversed ;
model  Nearest_neighbour_m = Type_Inversed King_Est Type_Inversed*King_Est/
dist = normal corrb;
*repeated subject = Year/corr =IND modelse;
```

```
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;


TITLE1 'Predation GLM with forest type interaction terms. 1=Absence, 0=Presence';
proc genmod data = GLM_feb172013 descending;
class Predation Prop19 Prop17 Prop20 Prop18;
model Type_Inversed = Predation Prop19 Prop17 Prop18 Prop20 Prop19*Predation
Prop18*Predation Prop17*Predation Prop20*Predation/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;


TITLE1 'Predation GLM with landscape variable interaction terms. 0=Absence, 1=Presence';
proc genmod data = GLM_feb172013 descending;
class Predation ;
model Type_Inversed  = Distance_to_water_m LogPatchsize Slope Log_Elevation Predation
Distance_to_water_m*Predation LogPatchsize*Predation Slope*Predation
Log_Elevation*Predation /
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;


TITLE1 'Population Size GLM include forest type and density with interaction terms.
1=Absence, 0=Presence';
proc genmod data = GLM_feb172013 descending;
class Prop19 Prop20 Prop17 Prop18 Year;
model  Type_Inversed  = Prop19 Prop17 Prop18 Prop20 King_Est Prop19*King_Est
Prop17*King_Est Prop18*King_Est Prop20*King_Est/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;


TITLE1 'Population Size GLM include landscape and density with interaction terms. 0=Absence,
1=Presence';
proc genmod data = GLM_feb172013 descending;
```

```
class ;
model  Type_Inversed  = Distance_to_water_m LogPatchsize Slope Log_Elevation King_Est
Distance_to_water_m*King_Est LogPatchsize*King_Est Slope*King_Est
Log_Elevation*King_Est /
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;


TITLE1 'Year GLM include forest type and density with interaction terms. 0=Absence,
1=Presence';
proc genmod data = GLM_feb172013 descending;
class Prop19 Prop20 Prop17 Prop18 ;
model  Type_Inversed = Year Prop19 Prop17 Prop18 Prop20 Prop19*Year Prop17*Year
Prop18*Year Prop20*Year/
dist = binomial corrb;
*repeated subject = Year/corr =IND modelse;
output out = RESIDS predicted = inverselogit reschi
= pearsresid stdreschi = stpearsresid STDXBETA
= stdxbeta xbeta = logit;
Run;
```

APPENDIX C: CORRELATION MATRICES EVALUATING VARIABLES ANALYZED IN GENERALIZED LINEAR MODELS.

Year GLM include forest type and density with interaction terms.

Parameter Information

Parameter	Effect	Prop14	Prop16	Prop17	Prop18
Prm11	Year_Order*Prop14	0			
Prm12	Year_Order*Prop14	1			
Prm13	Year_Order*Prop16		0		
Prm14	Year_Order*Prop16		1		
Prm15	Year_Order*Prop18				0
Prm16	Year_Order*Prop18				1
Prm17	Year_Order*Prop17			0	
Prm18	Year_Order*Prop17			1	

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm5	Prm7	Prm11	Prm13	Prm15
Prm1	1.0000	-0.8751	-0.5621	-0.4490	-0.8683	0.4970	0.3974	0.7519
Prm2	-0.8751	1.0000	0.4588	0.3644	0.7813	-0.5166	-0.4100	-0.8886
Prm3	-0.5621	0.4588	1.0000	0.3495	0.1240	-0.8858	-0.3085	-0.0966
Prm5	-0.4490	0.3644	0.3495	1.0000	0.1989	-0.3065	-0.8864	-0.1549
Prm7	-0.8683	0.7813	0.1240	0.1989	1.0000	-0.1087	-0.1755	-0.8721
Prm11	0.4970	-0.5166	-0.8858	-0.3065	-0.1087	1.0000	0.3432	0.1074
Prm13	0.3974	-0.4100	-0.3085	-0.8864	-0.1755	0.3432	1.0000	0.1735
Prm15	0.7519	-0.8886	-0.0966	-0.1549	-0.8721	0.1074	0.1735	1.0000

Forest type GLM.1=Absence, 0=Presence

Parameter Information

Parameter	Effect	Prop14	Prop17	Prop18	Prop16
Prm1	Intercept				
Prm2	Prop14	0			
Prm3	Prop14	1			
Prm4	Prop18			0	
Prm5	Prop18			1	
Prm6	Prop16				0
Prm7	Prop16			1	
Prm8	Prop17		0		
Prm9	Prop17		1		

Estimated Correlation Matrix

	Prm1	Prm2	Prm4	Prm6
Prm1	1.0000	-0.5435	-0.8763	-0.4325
Prm2	-0.5435	1.0000	0.1163	0.3446
Prm4	-0.8763	0.1163	1.0000	0.1871
Prm6	-0.4325	0.3446	0.1871	1.0000

Landscape GLM. 0=Absence, 1=Presence

Parameter	Effect
Prm1	Intercept
Prm2	Distance_to_water_m
Prm3	LogPatchSize
Prm4	Slope
Prm5	Elevation

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm4	Prm5
Prm1	1.0000	-0.0833	-0.6022	-0.3604	-0.7925
Prm2	-0.0833	1.0000	0.0455	-0.0856	-0.0447
Prm3	-0.6022	0.0455	1.0000	-0.0450	0.0137
Prm4	-0.3604	-0.0856	-0.0450	1.0000	0.3969
Prm5	-0.7925	-0.0447	0.0137	0.3969	1.0000

GLM with Nearest Neighbour. 0=Absence, 1=Presence

Prm1	Intercept	
Prm2	Type_Inversed	0
Prm3	Type_Inversed	1

Estimated Correlation Matrix

	Prm1	Prm2	Scale
Prm1	1.0000	-0.3869	0.0000
Prm2	-0.3869	1.0000	-0.0000
Scale	0.0000	-0.0000	1.0000

GLM with Nearest Neighbour. 0=Absence, 1=Presence

Parameter	Effect
Prm1	Intercept
Prm2	Old_Barn_km
Prm3	Mortimer_km
Prm4	Come_km
Prm5	Puds_km
Prm6	Lighthouse_Cabins_km
Prm7	South_km

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm4	Prm5	Prm6	Prm7
Prm1	1.0000	0.2591	-0.5577	-0.0662	-0.1527	-0.3708	-0.6180
Prm2	0.2591	1.0000	0.5364	-0.8632	-0.8985	-0.1758	-0.3152
Prm3	-0.5577	0.5364	1.0000	-0.7451	-0.5583	0.2119	0.2320
Prm4	-0.0662	-0.8632	-0.7451	1.0000	0.6872	-0.0841	0.2911
Prm5	-0.1527	-0.8985	-0.5583	0.6872	1.0000	0.3175	0.0370
Prm6	-0.3708	-0.1758	0.2119	-0.0841	0.3175	1.0000	-0.4213
Prm7	-0.6180	-0.3152	0.2320	0.2911	0.0370	-0.4213	1.0000

Distance to Mud Lake salt lick. 0=Absence, 1=Presence
Parameter Information

Parameter	Effect
Prm1	Intercept
Prm2	Mud_Lake_km

Estimated Correlation Matrix

	Prm1	Prm2
Prm1	1.0000	-0.8885
Prm2	-0.8885	1.0000

GLM with Nearest Neighbour and interaction with predation stats. 0=Absence, 1=Presence

Parameter Information

Parameter	Effect	Inversed	Predation
Prm1	Intercept		
Prm2	Type_Inversed	0	
Prm3	Type_Inversed	1	
Prm4	Predation		0
Prm5	Predation		1
Prm6	Type_Inver*Predation	0	0
Prm7	Type_Inver*Predation	0	1
Prm8	Type_Inver*Predation	1	0
Prm9	Type_Inver*Predation	1	1

Estimated Correlation Matrix

	Prm1	Prm2	Prm4	Prm6	Scale
Prm1	1.0000	-0.4314	-0.9044	0.3793	0.0000
Prm2	-0.4314	1.0000	0.3902	-0.8792	-0.0000
Prm4	-0.9044	0.3902	1.0000	-0.4194	0.0000
Prm6	0.3793	-0.8792	-0.4194	1.0000	-0.0000
Scale	0.0000	-0.0000	0.0000	-0.0000	1.0000

GLM with Nearest Neighbour and interaction with predation stats. 0=Absence, 1=Presence

Parameter Information

Parameter	Effect	Predation	Prop14	Prop17	Prop18	Prop16
Prm1	Intercept					
Prm2	Predation	0				
Prm3	Predation	1				
Prm4	Prop14		0			
Prm5	Prop14		1			
Prm6	Prop18			0		
Prm7	Prop18			1		
Prm8	Prop16				0	
Prm9	Prop16				1	
Prm10	Prop17					0
Prm11	Prop17					1
Prm12	Predation*Prop14	0		0		
Prm13	Predation*Prop14	0		1		
Prm14	Predation*Prop14	1		0		
Prm15	Predation*Prop14	1		1		
Prm16	Predation*Prop18	0			0	
Prm17	Predation*Prop18	0			1	
Prm18	Predation*Prop18	1			0	
Prm19	Predation*Prop18	1			1	
Prm20	Predation*Prop16	0				0
Prm21	Predation*Prop16	0				1

Estimated Correlation Matrix

	Prm1	Prm2	Prm4	Prm6	Prm8	Prm12	Prm16	Prm20
Prm1	1.0000	-0.6419	-0.7122	-0.6360	-0.4360	0.5864	.	0.3165
Prm2	-0.6419	1.0000	0.8120	-0.0582	0.4971	-0.9231	.	-0.5679
Prm4	-0.7122	0.8120	1.0000	0.0000	0.3280	-0.8797	.	-0.2872
Prm6	-0.6360	-0.0582	0.0000	1.0000	0.0000	0.0630	.	0.1024
Prm8	-0.4360	0.4971	0.3280	0.0000	1.0000	-0.2886	.	-0.8754
Prm12	0.5864	-0.9231	-0.8797	0.0630	-0.2886	1.0000	.	0.3331
Prm16	.	.	.	.	.	.	.	.
Prm20	0.3165	-0.5679	-0.2872	0.1024	-0.8754	0.3331	.	1.0000

Predation GLM with landscape variable interaction terms. 0=Absence, 1=Presence

Parameter Information

Parameter	Effect	Predation
Prm1	Intercept	
Prm2	Distance_to_water_m	
Prm3	LogPatchSize	
Prm4	Slope	
Prm5	Log_Elevation	
Prm6	Predation	0
Prm7	Predation	1
Prm8	Distance_t*Predation	0
Prm9	Distance_t*Predation	1
Prm10	LogPatchSi*Predation	0
Prm11	LogPatchSi*Predation	1
Prm12	Slope*Predation	0
Prm13	Slope*Predation	1
Prm14	Log_Elevat*Predation	0
Prm15	Log_Elevat*Predation	1

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm4	Prm5	Prm6	Prm8	Prm10	Prm12	Prm14
Prm1	1.0000	0.0438	-0.1542	-0.4317	-0.9885	-0.8779	-0.0391	0.1371	0.3748	0.8679
Prm2	0.0438	1.0000	0.0022	-0.1076	-0.0675	-0.0384	-0.8938	-0.0020	0.0934	0.0592
Prm3	-0.1542	0.0022	1.0000	-0.0783	0.0075	0.1353	-0.0020	-0.8891	0.0679	-0.0066
Prm4	-0.4317	-0.1076	-0.0783	1.0000	0.4308	0.3790	0.0962	0.0696	-0.8682	-0.3783
Prm5	-0.9885	-0.0675	0.0075	0.4308	1.0000	0.8678	0.0603	-0.0066	-0.3741	-0.8780
Prm6	-0.8779	-0.0384	0.1353	0.3790	0.8678	1.0000	0.0371	-0.1542	-0.4259	-0.9887
Prm8	-0.0391	-0.8938	-0.0020	0.0962	0.0603	0.0371	1.0000	0.0131	-0.1019	-0.0621
Prm10	0.1371	-0.0020	-0.8891	0.0696	-0.0066	-0.1542	0.0131	1.0000	-0.0688	0.0091
Prm12	0.3748	0.0934	0.0679	-0.8682	-0.3741	-0.4259	-0.1019	-0.0688	1.0000	0.4234
Prm14	0.8679	0.0592	-0.0066	-0.3783	-0.8780	-0.9887	-0.0621	0.0091	0.4234	1.0000

GLM with Nearest Neighbour and interaction with population size stats. 0=Absence, 1=Presence

Parameter Information

	Parameter	Effect	Inversed
	Prm1	Intercept	
	Prm2	Type_Inversed	0
	Prm3	Type_Inversed	1
	Prm4	King_Est	
	Prm5	King_Est*Type_Invers	0
	Prm6	King_Est*Type_Invers	1

Estimated Correlation Matrix

	Prm1	Prm2	Prm4	Prm5	Scale
Prm1	1.0000	-0.3927	-0.8878	0.3662	0.0000
Prm2	-0.3927	1.0000	0.3486	-0.8840	-0.0000
Prm4	-0.8878	0.3486	1.0000	-0.4125	-0.0000
Prm5	0.3662	-0.8840	-0.4125	1.0000	0.0000
Scale	0.0000	-0.0000	-0.0000	0.0000	1.0000

GLM with Nearest Neighbour and interaction with population size stats. 0=Absence, 1=Presence

Parameter Information

Parameter	Effect	Prop14	Prop17	Prop18	Prop16
Prm1	Intercept				
Prm2	Prop14	0			
Prm3	Prop18			0	
Prm4	Prop16				0
Prm5	Prop17		0		
Prm6	King_Est				
Prm7	King_Est*Prop14	0			
Prm8	King_Est*Prop18			0	
Prm9	King_Est*Prop16				0
Prm10	King_Est*Prop17		0		

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm4	Prm6	Prm7	Prm8	Prm9
Prm1	1.0000	-0.4600	-0.8925	-0.2783	-0.8943	0.4095	0.8050	0.2464
Prm2	-0.4600	1.0000	0.1043	0.3345	0.3167	-0.8903	-0.0740	-0.2997
Prm3	-0.8925	0.1043	1.0000	0.1724	0.8464	-0.1006	-0.9020	-0.1544
Prm4	-0.2783	0.3345	0.1724	1.0000	0.2052	-0.3227	-0.1223	-0.8855
Prm6	-0.8943	0.3167	0.8464	0.2052	1.0000	-0.3557	-0.9384	-0.2317
Prm7	0.4095	-0.8903	-0.1006	-0.3227	-0.3557	1.0000	0.0911	0.3688
Prm8	0.8050	-0.0740	-0.9020	-0.1223	-0.9384	0.0911	1.0000	0.1398
Prm9	0.2464	-0.2997	-0.1544	-0.8855	-0.2317	0.3688	0.1398	1.0000

Population Size GLM include landscape and density with interaction terms. 0=Absence, 1=Presence

Parameter Information

Parameter	Effect
Prm1	Intercept
Prm2	Distance_to_water_m
Prm3	LogPatchSize
Prm4	Slope
Prm5	Log_Elevation
Prm6	King_Est
Prm7	Distance_to*King_Est
Prm8	LogPatchSiz*King_Est
Prm9	Slope*King_Est
Prm10	Log_Elevati*King_Est

Estimated Correlation Matrix

	Prm1	Prm2	Prm3	Prm4	Prm5	Prm6	Prm7	Prm8	Prm9	Prm10
Prm1	1.0000	0.0413	-0.1510	-0.4080	-0.9893	-0.8873	-0.0476	0.1310	0.3316	0.8772
Prm2	0.0413	1.0000	0.0279	-0.1111	-0.0683	-0.0487	-0.8958	-0.0164	0.1179	0.0718
Prm3	-0.1510	0.0279	1.0000	-0.0371	0.0099	0.1292	-0.0162	-0.8869	0.0265	-0.0059
Prm4	-0.4080	-0.1111	-0.0371	1.0000	0.4005	0.3658	0.1282	0.0287	-0.8951	-0.3576
Prm5	-0.9893	-0.0683	0.0099	0.4005	1.0000	0.8788	0.0705	-0.0061	-0.3248	-0.8874
Prm6	-0.8873	-0.0487	0.1292	0.3658	0.8788	1.0000	0.0603	-0.1430	-0.3750	-0.9897
Prm7	-0.0476	-0.8958	-0.0162	0.1282	0.0705	0.0603	1.0000	0.0120	-0.1590	-0.0851
Prm8	0.1310	-0.0164	-0.8869	0.0287	-0.0061	-0.1430	0.0120	1.0000	-0.0256	0.0042
Prm9	0.3316	0.1179	0.0265	-0.8951	-0.3248	-0.3750	-0.1590	-0.0256	1.0000	0.3658
Prm10	0.8772	0.0718	-0.0059	-0.3576	-0.8874	-0.9897	-0.0851	0.0042	0.3658	1.0000
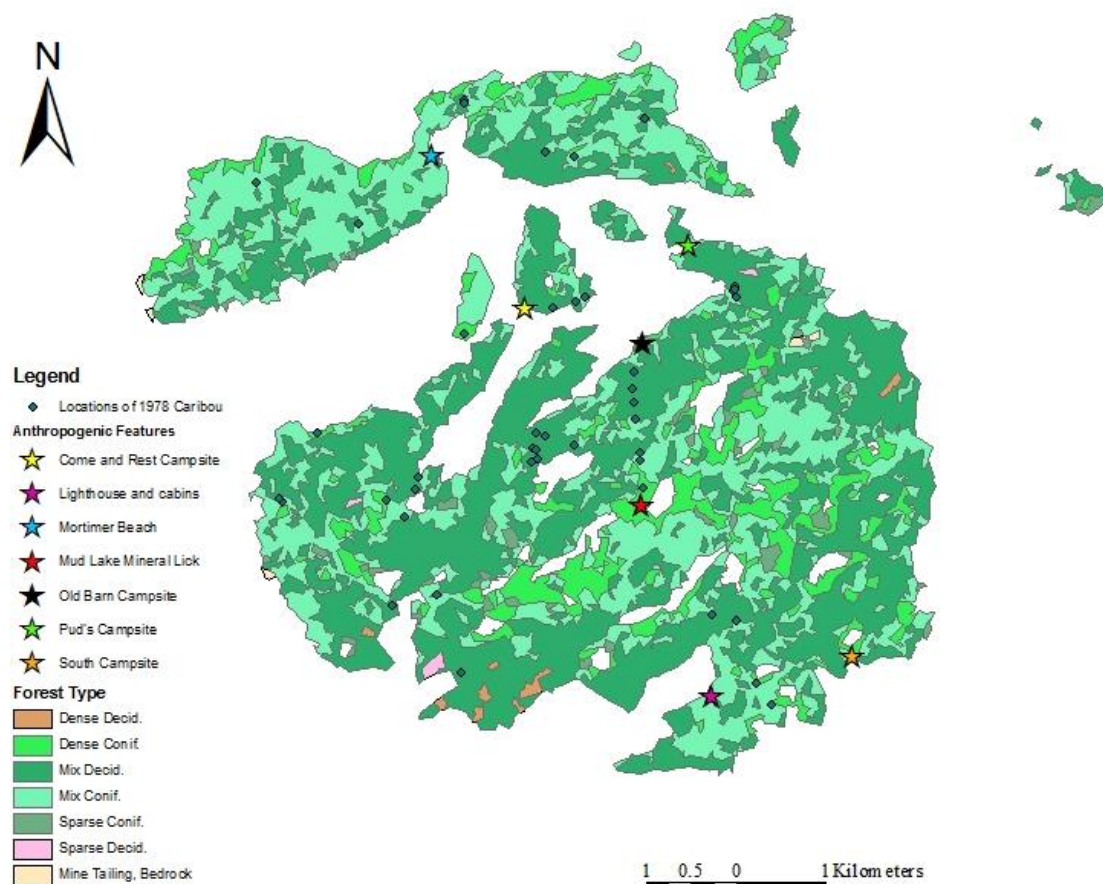
Figure A1: Map of 1978 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
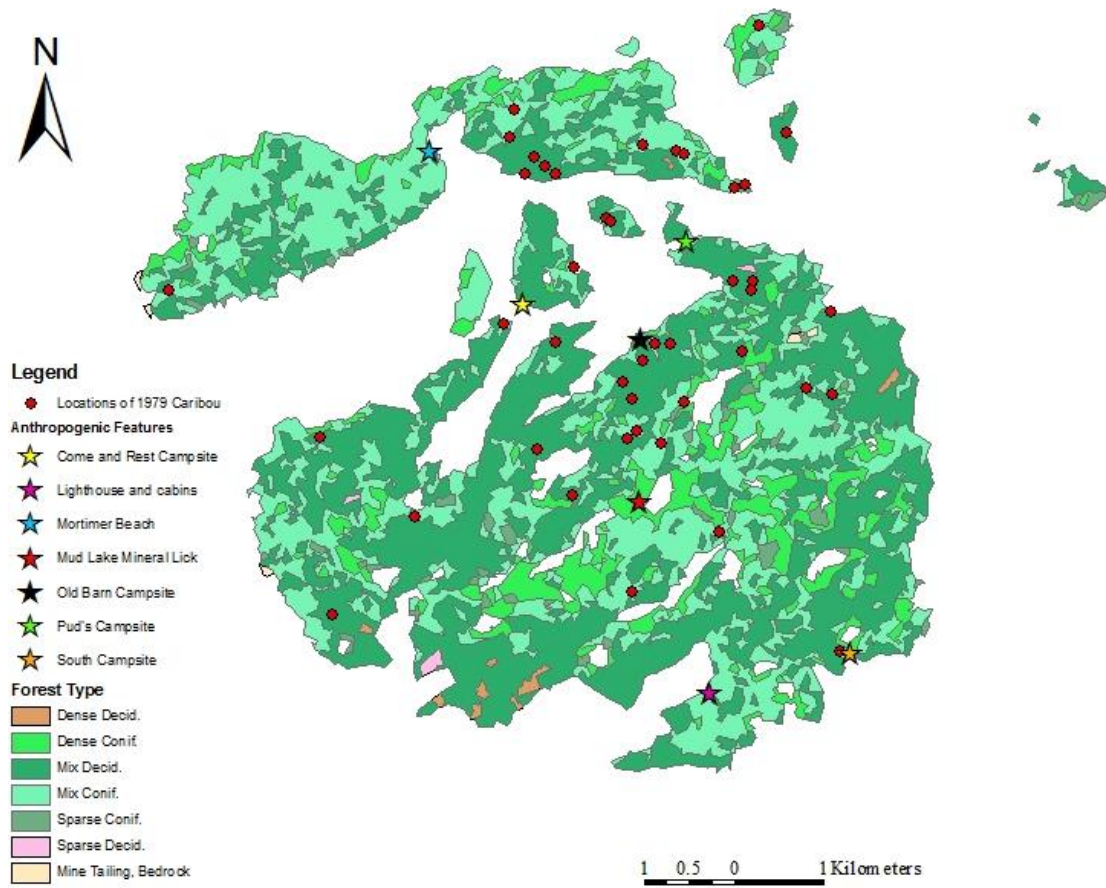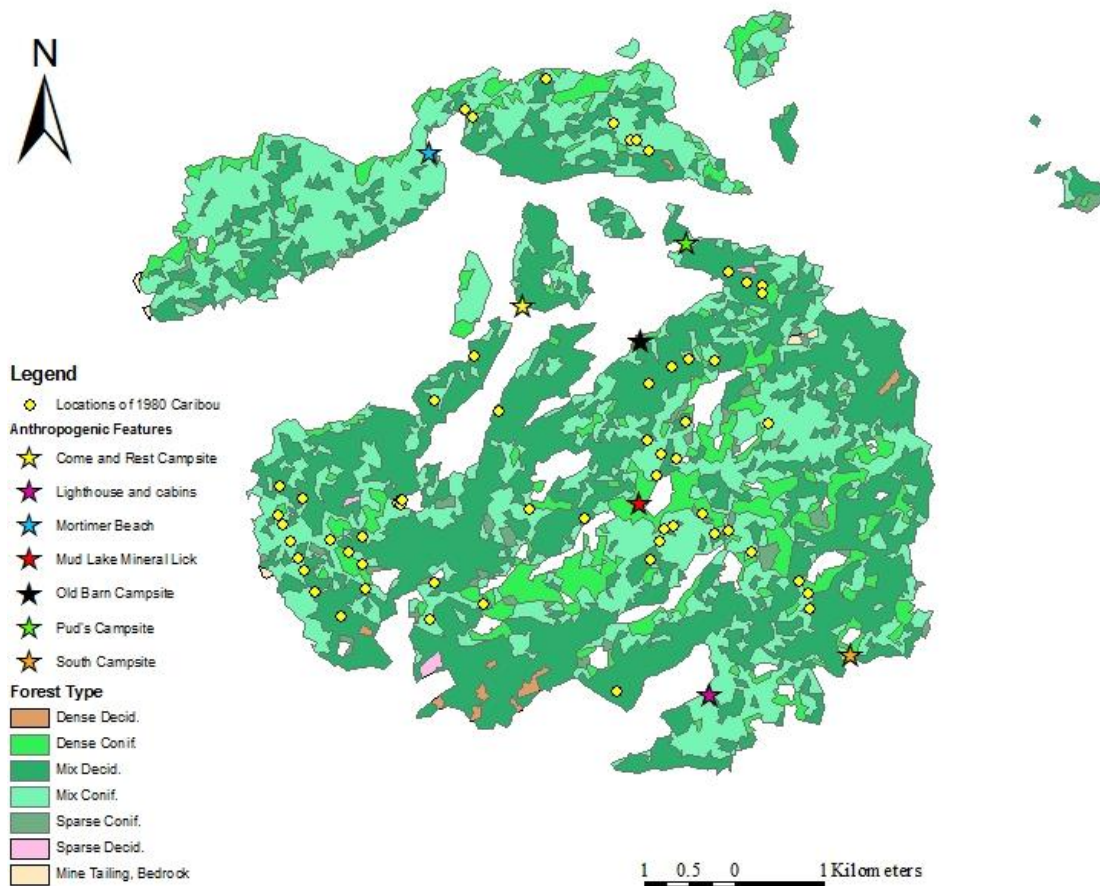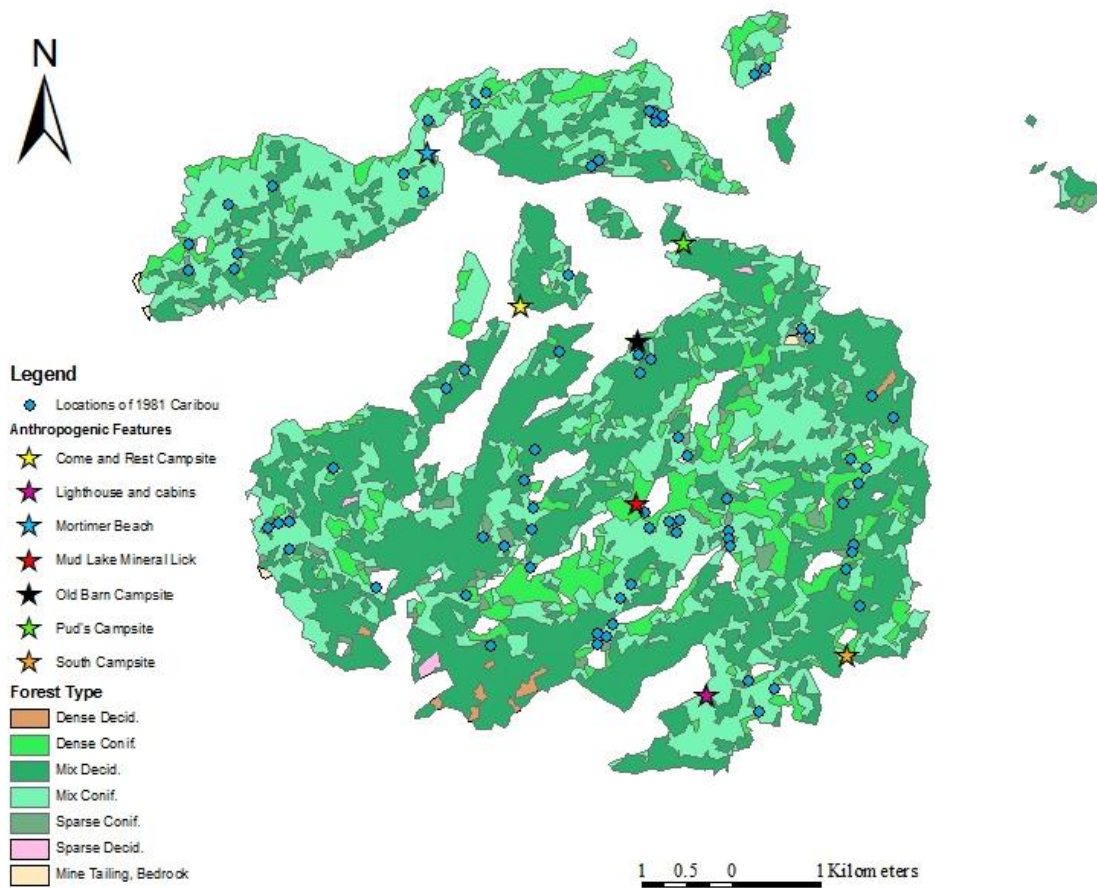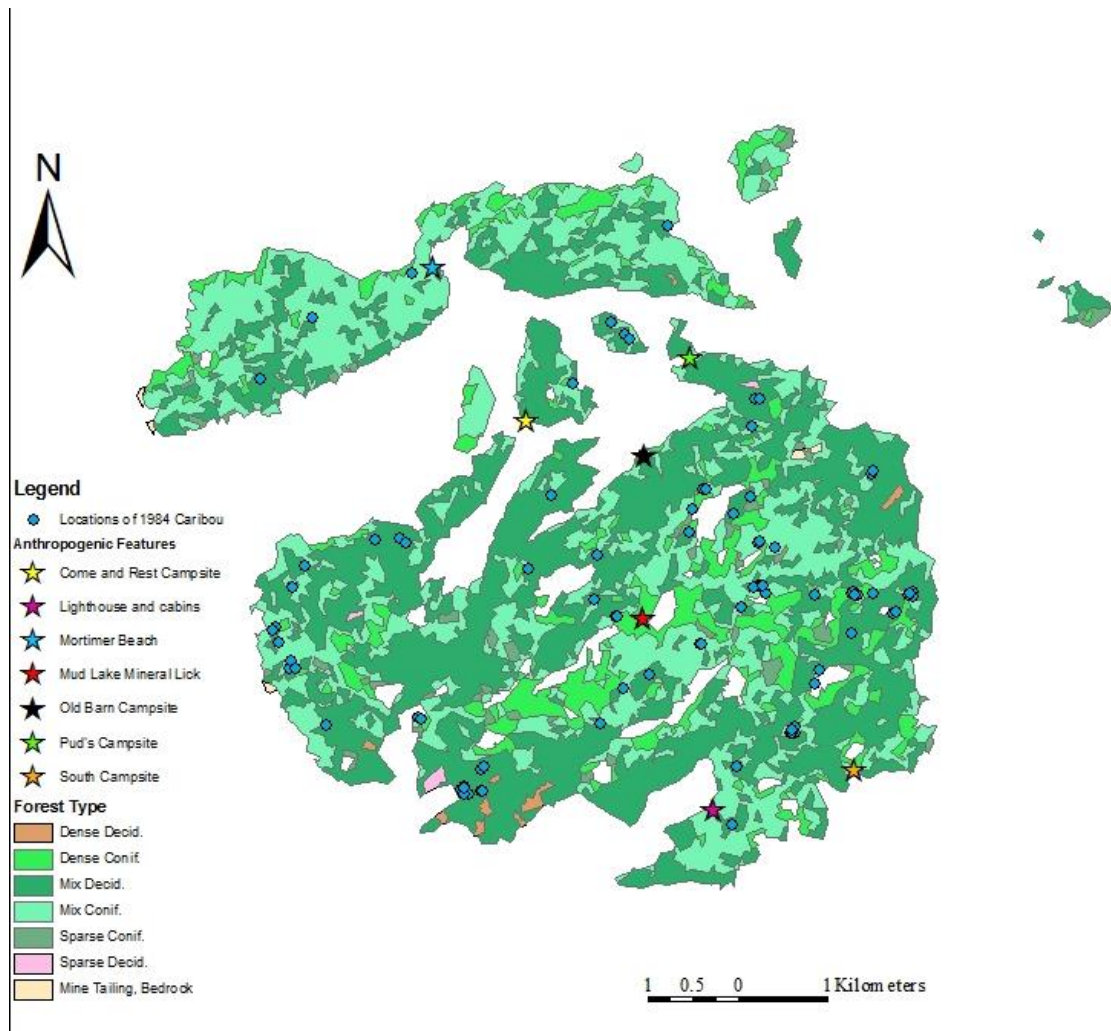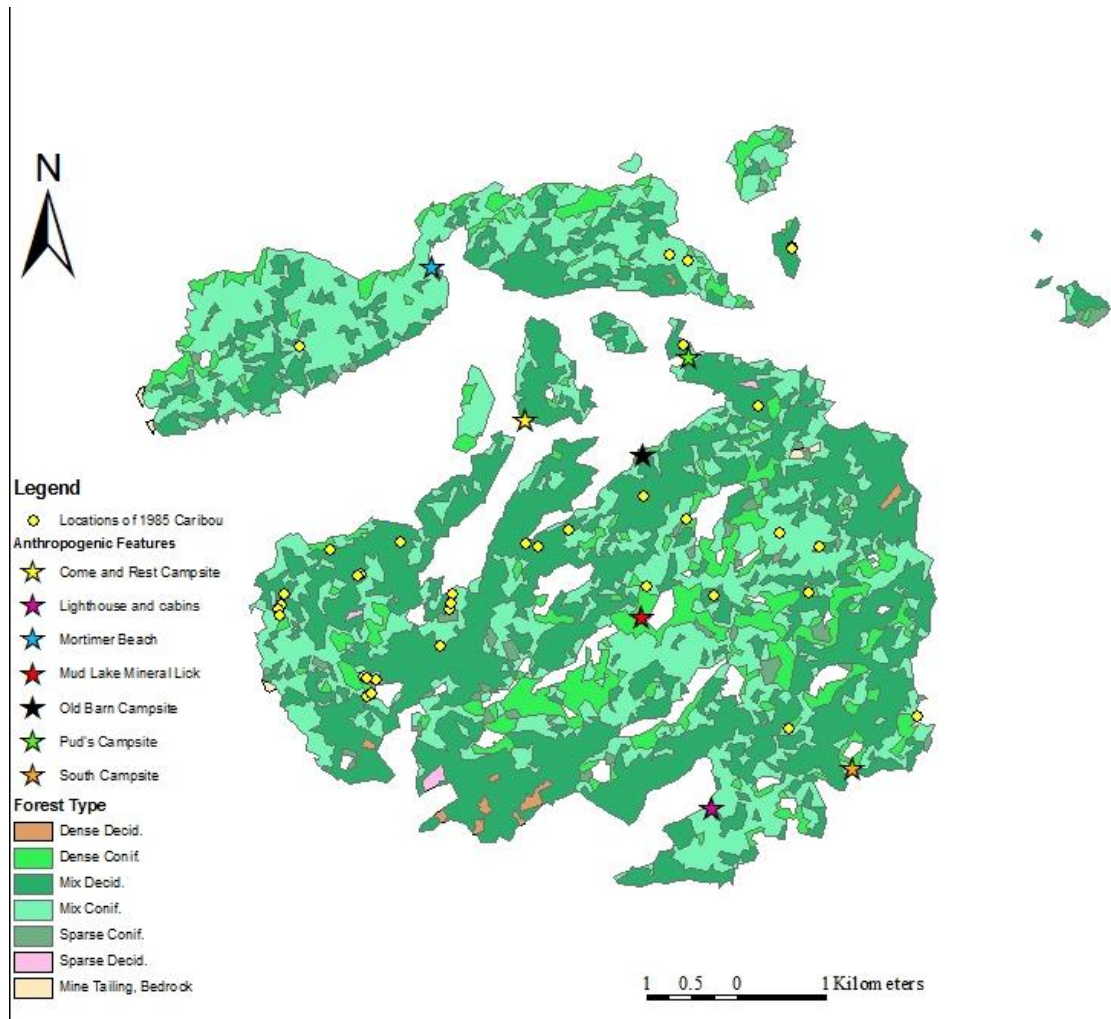
Figure A2: Map of 1979 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
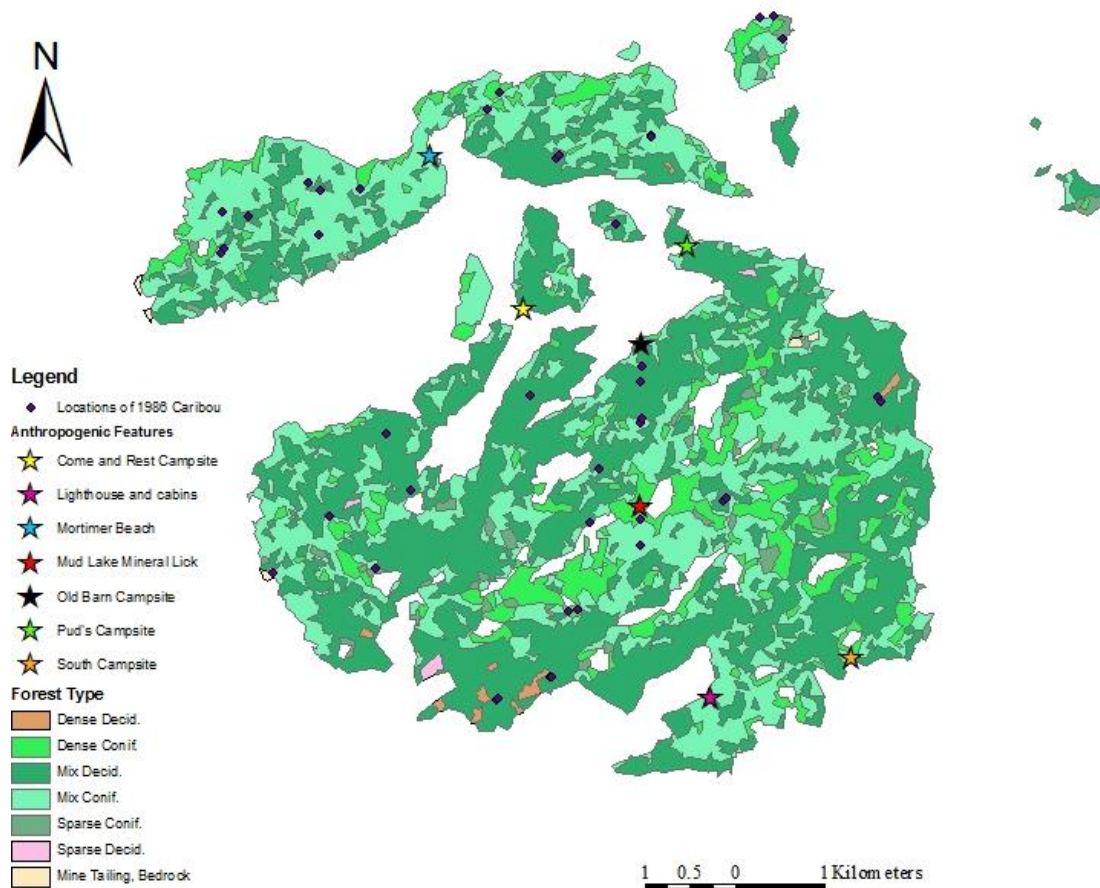
Figure A3: Map of 1980 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features

Figure A4: Map of 1981 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
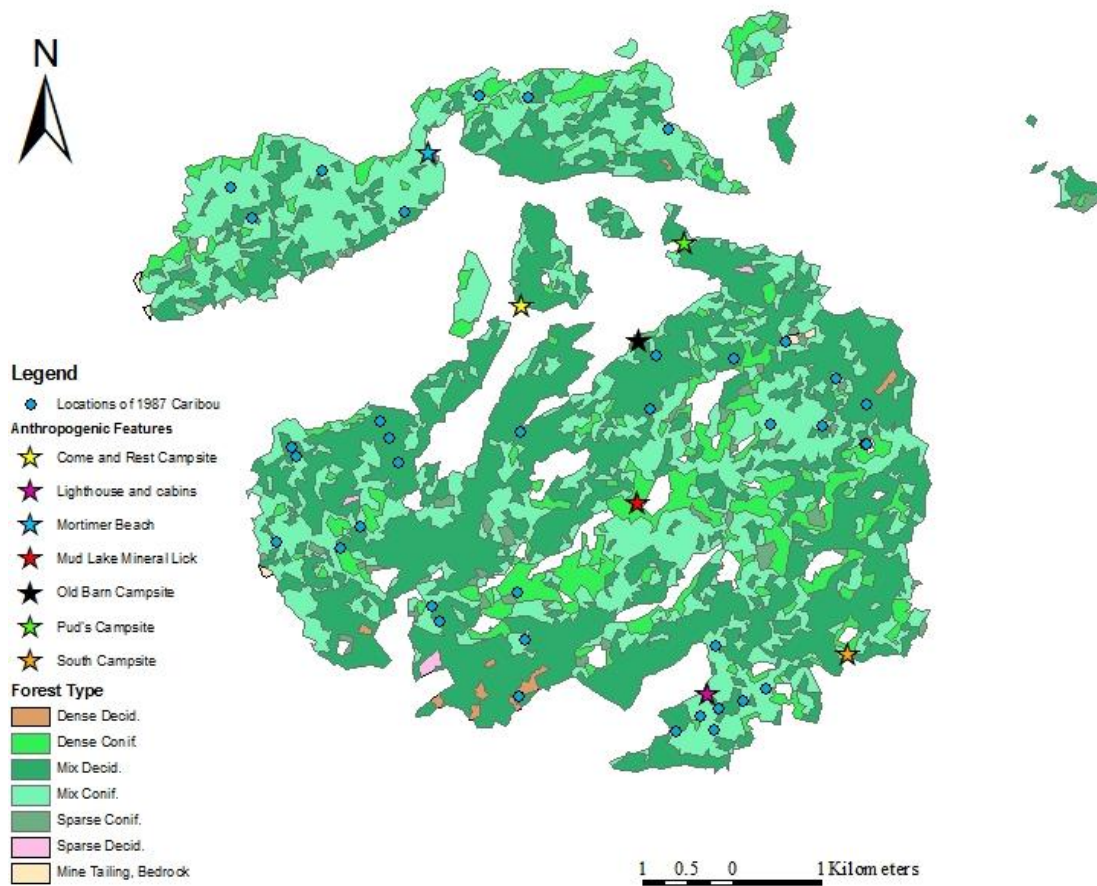
Figure A5: Map of 1984 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.

Figure A6: Map of 1985 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.

Figure A7: Map of 1986 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
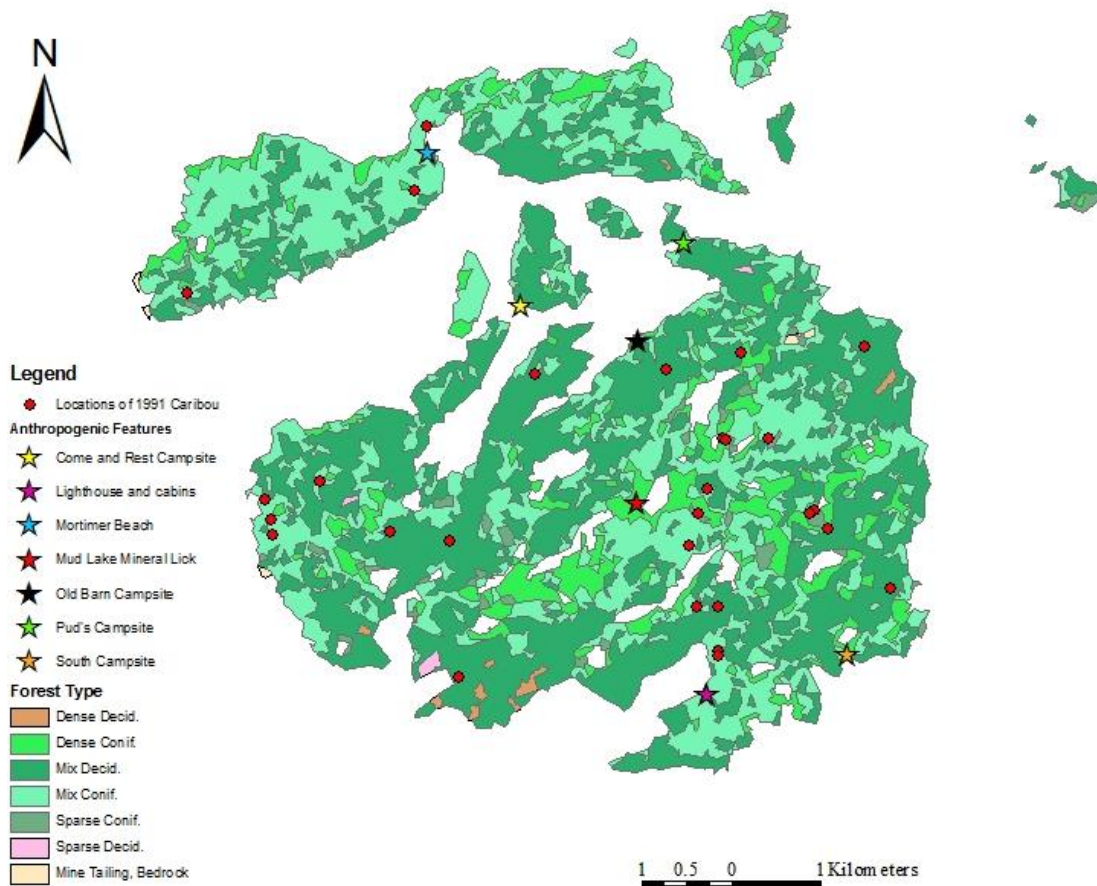
Figure A8: Map of 1987 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.

Figure A9: Map of 1991 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
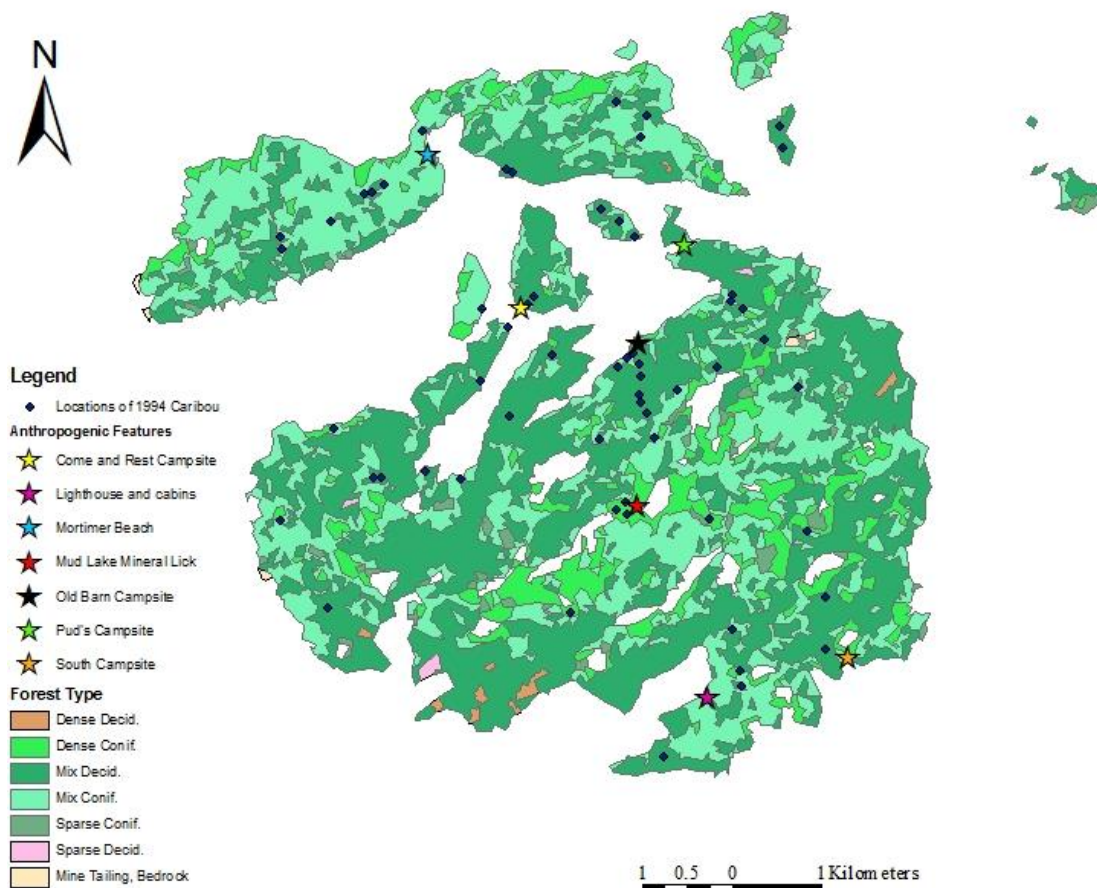
Figure A10: Map of 1994 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features.
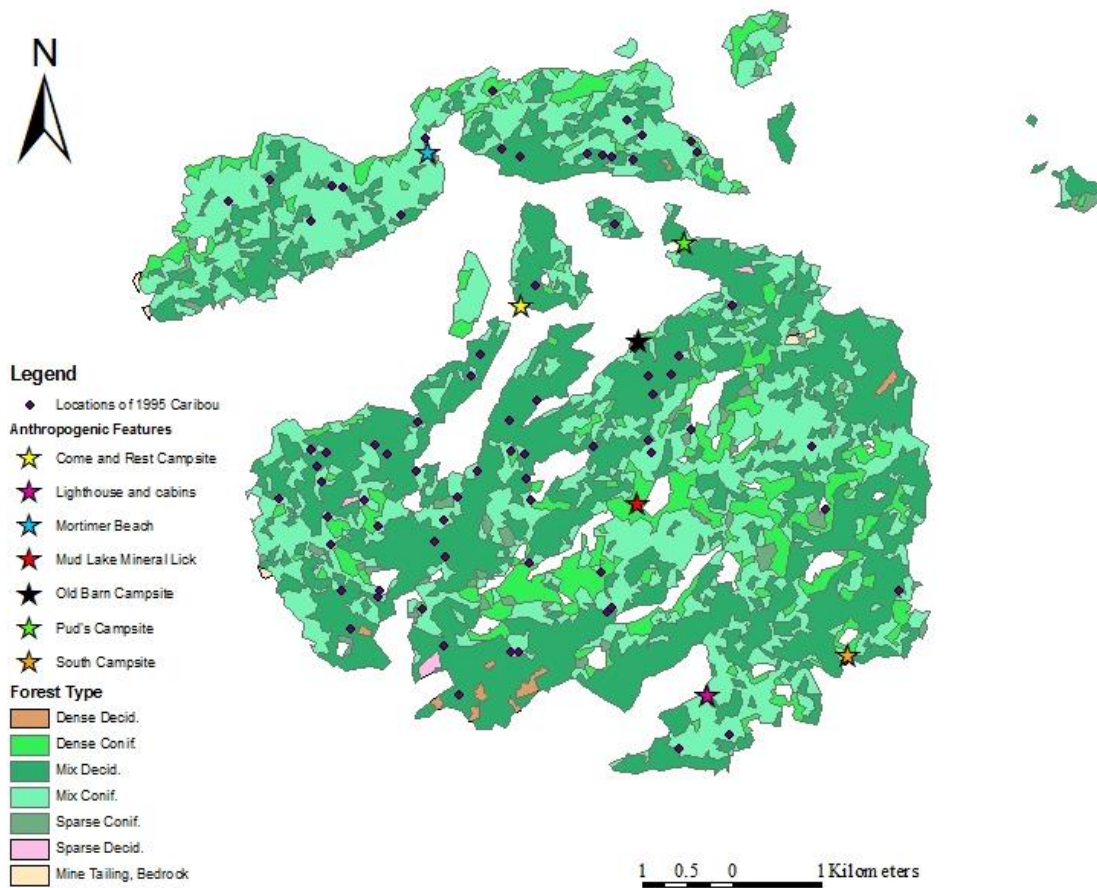
Figure A11: Map of 1995 Slate Island Boreal Woodland Caribou (Slate Islands Provincial Park, Ontario, Canada) distribution relative to forest type and anthropogenic features**.**