University of Alberta

The Impact of Fire, Climate, and Herbivory on the Configuration of Riparian Vegetation and Maintenance of Beaver Ponds in Elk Island National Park

by

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ABSTRACT

The ecosystems of Elk Island National Park have been strongly influenced by flooding by beaver, ungulate herbivory, and the use of prescribed fire. This thesis examines the ecology of beaver within the park in the following chapters: (2) The effects of prescribed fire on beaver, (3) Beaver regulate wetlands during drought, (4) Plant community response to four levels of beaver and ungulate herbivory, and (5) The effects of high ungulate densities on foraging by beaver. In Chapter 2, I examine whether the number of burns, the time since last burn, and the distance from one lodge to its nearest active lodge affected the occupancy of 734 beaver lodges in Elk Island National Park (EINP) over a 13-year period. Both lodges that were exposed to fire at least once and lodges that were never exposed to fire were included in the analyses. Of the variables examined, I found that for each additional time the area around a lodge was exposed to fire, the odds of a lodge being active decreased by 58%. After more than 3 burns, lodges were often permanently abandoned. In Chapter 3, I analyzed 12 separate years of aerial photographs between 1948 and 2002 to measure the area of open water wetlands in unburned areas in Elk Island National Park. These data were then combined with climatic variables, such as temperature, precipitation, and potential evapotranspiration, and beaver lodge activity data to determine the relative importance of climate and beaver on the areas of open water wetlands in the park. Although the best regression model included active beaver lodges, mean maximum temperature, and 2-year mean annual precipitation, the presence of active beaver lodges alone explained over 80% of the variability in the area of open water over the 54-year period. Beaver were also able to maintain open water wetlands during drought. In 1950 (the 2nd driest year during the study period), when beaver were

not present and precipitation was extremely low, wetlands held 61% less open water than in 2002 (the driest year on record and when beaver were well established), despite the fact that 1950 had 47% more precipitation. Chapter 4 examines the effects of four densities of ungulate and beaver herbivory (high beaver + high ungulate, high ungulate + low beaver, low ungulate + high beaver, low ungulate + low beaver) on the composition and structure of riparian vegetation. Ungulate pellet group densities inside EINP were three times higher than those outside the park; therefore all sites considered "high ungulate" were inside the park. In areas of high densities of ungulate pellet groups, shrub heights were less and canopy cover by herbaceous dicots and emergent vegetation decreased compared to areas with lower numbers of pellet counts. *Corylus cornuta*, though stunted, had significantly higher cover values in heavily browsed areas than in areas with lower ungulate densities. In areas with lower densities of ungulate pellet groups and no beaver, species such as *Salix* spp. and *Prunus* spp. were as much as 4 times taller than in areas with both herbivores. In Chapter 5, I used a database independent of the one used in Chapter 4 to examine whether competitive exploitation exists between beaver and ungulates by comparing a system with high ungulate densities to a system with lower ungulate densities. As measures of competition, I examined forage availability (stem densities and stem diameters of woody plants), forage selection and foraging distances by beaver. Both stem densities and stem diameters (forage availability) were smaller inside the park where ungulate herbivory was more intense. Beaver inside EINP harvested more mature *Populus* trees relative to their availability and also foraged closer to their ponds despite a relatively even distribution of plants away from the pond edge. Given that beaver and ungulates are able to coexist with some modifications to foraging choices and behaviour, competition between these herbivores in EINP has not resulted in the complete exclusion of beaver from the landscape, as found in other regions of North America.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1.0 INTRODUCTION

1.1 BACKGROUND AND RATIONALE

Beaver (*Castor canadensis*) are considered a keystone species (Paine 1969) because they actively create and maintain wetland habitats thus affecting riparian vegetation and terrestrial and aquatic faunal communities (Naiman *et al.* 1988, Wright *et al.* 2002, Rosell *et al.* 2005). Many species benefit from increased landscape heterogeneity resulting from water impoundments and foraging activities by beaver, including waterfowl (Renouf *et al.* 1972, McKinstry *et al.* 2001), fish (Ray *et al.* 2004), amphibians (France 1997, Metts *et al.* 2001), mammals (Leighton 1933, Bailey and Stephens 1951), and invertebrates (France 1997). In areas such as Elk Island National Park (EINP) in east-central Alberta, flooding by beaver is considered a key ecological process that has created diverse ecosystems and enhanced ecological integrity on a landscape scale. These effects can be seen long after lodge abandonment and can affect soil chemistry (Johnston and Naiman 1987) and vegetation communities (Donkor and Fryxell 1999) for decades. Along with beaver, other processes - including fire, climate, and herbivory by ungulates - also contribute to the function of ecosystems at broad scales, although the interactive effects of these processes and beaver are not well understood.

The relationship between fire and beaver is often believed to be beneficial to beaver (Kellyhouse 1979, Naiman *et al.* 1988), although this assumption has never been tested. In many areas, fire is used to restore grasslands (Bailey *et al.* 1990, Roques *et al.* 2001) and stimulate growth of woody plants (Bartos and Mueggler 1981, Elliott *et al.* 1999, Hiers *et al.* 2003). As such, fire can improve forage quality for wildlife (Vinton *et al.*

1993) and modify habitat structure (Mushinsky 1985), creating varied age classes by promoting regeneration of disturbance tolerant species such as aspen (*Populus tremuloides*). However, a growing body of literature reveals that, in the context of other ecological disturbances such as high herbivory and climate change (e.g., drought), the use of prescribed fire does not always achieve expected outcomes (White *et al.* 1998, Hessl and Graumlich 2002). Bork *et al.* (1997) found that fire likely increased occupancy of ungulates in burned areas. They also determined that the combination of fire and increased herbivory reduced the extent of the forest overstory and failed to promote regeneration of aspen. Fire, vegetation, and climate are directly related and, with predicted warming climates, fire severity and intensity are expected to increase (Ryan 1991, Hogg and Bernier 2005). Vegetation communities will also change in response to moisture availability and increases in temperature (Stocks *et al.* 1998).

A warming climate also has the potential to negatively affect wetland creation and retention, and therefore associated aquatic and riparian communities. Larson (1995) found that climate explained over 60% of the variation in wet basins in the Prairie Pothole Region (PPR), which in turn influenced the habitat availability for breeding waterfowl. Johnson *et al.* (2005) found that drought conditions displaced waterfowl populations that would normally use the PPR into more northern areas where water levels were more consistently stable. In addition to drought, urban, agricultural, and industrial expansion has accounted for the loss of as much as 70% of the original non-peatland wetlands in Canada (National Wetlands Working Group 1988) and 53% in the United States (Dahl 1990). The importance of beaver in creating water impoundments and modifying channel geomorphic and hydrologic processes has been well researched (Naiman *et al.*1986, Brochart *et al.* 1989). Johnston and Naiman (1990) found that the rate of pond creation paralleled an increase in the population of beaver over a 46-year period, and Syphard and Garcia (2001) determined that, although beaver only accounted for 1% of wetland gains in the Chickahominy River Watershed in Virginia, USA, their activities accounted for 23% of change in wetland types from 1953 to 1994. Despite numerous studies documenting the hydrological effects of beaver, wetland creation and retention by beaver during increased prevalence of drought has not been well studied. In the context of drought and anthropomorphic wetland loss, beaver populations could play a key role in maintaining wetlands and could mitigate the effects of climate change on vegetation, and ultimately, fire behaviour (Westbrook *et al.* 2006).

Regardless of climate, herbivores, such as beaver and ungulates, can produce immediate changes in vegetation communities. Their very use of plants for forage can dramatically alter the composition and structure of vegetation communities. In multiple herbivore systems, varied intensity of foraging activities can cause plants to undergo significant morphological and chemical changes (Basey *et al.* 1990, Hobbs 1996). While beaver crop entire stems of woody plants and remove them to a central place for processing and handling, ungulates - such as moose (*Alces alces*), deer (*Odocoileus* spp.), and elk (*Cervus elaphus*) – generally browse the tops and leaves of woody plants and process them as they search for the next bite. With beaver and ungulates, their foraging activities can increase patch dynamics (Donkor and Fryxell 1999), stimulate compensatory growth in plants (McNaughton 1983, Hobbs 1996, Baker *et al.* 2005), and alter stem densities, species composition, and inducible defences (Barnes and Dibble 1988, Basey *et al.* 1990, Bork *et al.* 1997, Donkor and Fryxell 1999). Although many types of vegetation have evolved with herbivory, browsing and grazing activities by multiple mammalian herbivores can introduce a significant disturbance into plant communities. The combined effect of differing foraging strategies is an important consideration in maintaining diversity and ecosystem function in many areas. In addition, the effects of foraging activities by individual species of herbivores can also affect foraging behaviours of other herbivores using the same resource, or in extreme situations, survival.

In areas where beaver share plant resources with high densities of elk, researchers have documented declines in beaver populations due to a lack of willow (*Salix* spp.) as a winter food resource (Kay 1994, Nietvelt 2001, Baker *et al.* 2005). Extensive browsing by ungulates can result in stems that are small, short, and hedged in appearance (Bork *et al.* 1997, Baker *et al.* 2005) with altered palatability and concentrations of secondary metabolites (Bryant *et al.* 1991, Hobbs 1996). As a central place forager (Orians and Pearson 1979), beaver are limited in their ability to forage beyond a preferred distance from their lodge. All their food is generally obtained within a 0–100 m distance from their pond. Any impacts on the riparian vegetation, be it fire, climate, or herbivory, will have a direct effect on the ability of beaver colonies to survive through winter.

Although rarely examined, competition for shared resources by beaver and ungulates (particularly elk) is an emerging issue for ecologists in areas where ungulate populations have been maintained at high levels. Hardin (1960) predicts that the more niche overlap between competitors, the greater the potential for competition between them. Therefore, one would predict competition between beaver and ungulates to be low because of their different foraging choices and behaviours. Beaver are an aquatic mammal that forages from a central place, while ungulates are free to move around the landscape and process food as they go. Therefore beaver and ungulates should not compete to the point of competitive exploitation or complete exclusion except in extremely restricted habitats. However, in mountainous areas of Wyoming, Colorado and Alberta, studies have shown that high herbivory by elk has likely depressed forage resources for beaver to a level that excludes them from formerly viable areas (Kay 1994, Nietvelt 2001, Baker *et al.* 2005). In areas beyond the mountains, beaver rely on a variety of plant species (Jenkins and Busher 1979, Donkor and Fryxell 1999, Gallant *et al.* 2004), which could mitigate competition with other herbivores.

1.2 THE IMPACT OF FIRE, CLIMATE, AND HERBIVORY ON THE CONFIGURATION OF RIPARIAN VEGETATION AND MAINTENANCE OF BEAVER PONDS IN ELK ISLAND NATIONAL PARK

Elk Island National Park (194 km^2) provides a unique opportunity to examine the impacts of fire, climate, and herbivory on riparian vegetation and the creation and maintenance of beaver ponds. The park has a history of prescribed burning and some of the highest ungulate densities in North America (Blyth and Hudson 1987). Park management conducted the first prescribed burn in 1979. By 2002, over 51% of EINP had been burned (in some areas as many as eight times).

Established in 1906 as a reserve for one of the last remaining herds of Manitoba elk (*Cervus elaphus manitobensis*) in the area, it was fenced immediately after it was created and has been completely fenced since that time. Beaver have recolonized the park area after being successfully reintroduced in 1941. The park is situated in the heart of the Beaver Hills Region, which is defined by the boundaries of the Cooking Lake Moraine. Land surrounding the park ranges from highly developed agricultural and country residential lands to protected areas.

The management of ungulate populations within EINP has been a consistent theme throughout the park's history. In 1907, the park was used as a temporary refuge for 307 plains bison (*Bison bison bison*) en route to Dominion Buffalo Park to the southeast (Blyth 1995). When they were translocated in 1909, 48 avoided capture and became the nucleus of the EINP herd. In 1965, 22 wood bison (*Bison bison athabascae*) from Wood Buffalo National Park were introduced into the southern half of the park. Plains and wood bison have been physically separate throughout the park's history. An estimated 2 or 3 moose (*Alces alces*) were likely in the park area when it was initially fenced (Blyth and Hudson 1987). That population was supplemented with numerous translocations of moose into the park that occurred between 1909 and 1914. There were originally 35 mule deer (*Odocoileus hemionus*) in the park when it was established, although their movements under and over the fence have always been fluid. In 1951, the first white-tailed deer (*Odocoileus virginianus*) was seen in the park and they have now become the more dominant of the two species of deer (Blyth and Hudson 1987). Other than coyotes, there are no large predators resident inside the park and hunting is not permitted. Park management removes live elk and bison from the park every 2 years, to maintain a population density of ungulates in the park of approximately 13 ungulates per km^2.

Elk Island is located in the boreal mixed-wood forest region of east-central Alberta. Trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) are the dominant tree species, while white and black spruce (*Picea glauca* and *P. mariana*) occur in pockets throughout the area. Beaked hazel (*Corylus cornuta*) is the prominent shrub species, although willow (*Salix* spp.), rose (*Rosa acicularis* and *R. woodsii*), serviceberry (*Amelanchier alnifolia*), cherry (*Prunus virginiana* and *P. pennsylvanica*), red-osier dogwood (*Cornus stolonifera*), soapberry (*Shepherdia canadensis*), and snowberry (*Symphoricarpos albus and S. occidentalis*) are also common (see Appendix). Although the climate is cool continental, with cold winters and warm summers (Bowser *et al.* 1962), the area experienced the worse drought on record in 2002; with total annual precipitation almost half the normal values (265 mm in 2002, versus typical values of 400 to 450 mm per year).

1.3 GENERAL OBJECTIVES

I evaluated four aspects of beaver ecology in Elk Island National Park and adjacent sites within the Beaver Hills of east-central Alberta. First, I analyzed data relative to fire history and beaver lodge occupancy using historic records held by Elk Island National Park. Additional research on beaver lodge occupancy was conducted during the course of this study. To assess the relative influence of beaver and climate on the amount of open water coverage over time, I integrated historic aerial photos, along with climate and beaver census data, into a Geographic Information System (GIS, ArcMap by ESRI ^{TM}) for analysis. Next, my field crew and I conducted pellet count and vegetation surveys at 20 ponds that represented four categories of beaver and ungulate herbivory (high beaver + high ungulate, low beaver + high ungulate, high beaver + low ungulate, and low beaver + low ungulate) to examine the interactive effects of beaver and ungulate herbivory on the composition and structure of riparian vegetation. Finally, I assessed the effect of 2 levels of ungulate herbivory ("high" and "low") on forage availability and subsequent foraging choices by beaver within the context of central place foraging theory.

The general objectives of the study were:

1. ***Effects of prescribed fire on beaver:*** To examine whether prescribed fire influences beaver lodge occupancy relative to fire frequency, time since the last burn, and the proximity of a lodge to the nearest active beaver lodge. The data base consisted of 734 lodges, many of which had been exposed to fire at least once and others that were never exposed to fire over a 22-year period. These data, combined with long-term occupancy data for beaver lodges in the park, allowed me to assess the effects of burn frequency (number of times an area was exposed to fire), time since last burn, and distance to the nearest active lodge on lodge occupancy by beaver. In Chapter 2, I examined the following questions: 1) whether beaver lodge occupancy is lower in areas that have been burned than in unburned areas over and above differences in wetland availability, 2) whether a decrease in beaver lodge occupancy in burned areas results in a predictable reoccupation of these areas over time, 3) whether the fire frequency and the time

since the last fire affects lodge abandonment, and 4) whether distances between abandoned and active lodges differ between burned and unburned habitats (such increases in distance could have implications for the recolonization of abandoned areas through juvenile dispersal and dispersal of beaver from burned habitats to more suitable habitats).

2. ***Role of beaver in maintaining open water wetlands*:** To examine whether beaver, climate, or some combination thereof drives retention of open water in wetlands during drought. Specifically in Chapter 3, I determined 1) whether beaver increase open water in wetlands generally, 2) whether beaver maintain areas of open water during drought, 3) the importance of precipitation and temperature in creating and maintaining open water wetlands in the presence of beaver, and 4) the effects of precipitation and temperature on open water in wetlands when beaver were absent from the landscape.

3. ***Effects of varying intensity of herbivory on riparian vegetation*:** To quantify the effects of 4 levels of ungulate and beaver herbivory on the composition and structure of riparian vegetation. In chapter 4, I tested the hypotheses that 1) vegetation cover would decrease in areas with high levels of beaver and ungulate densities, 2) stem heights would be lowest in areas with the highest densities of beaver and ungulates, 3) species diversity would be highest at intermediate levels of herbivory (assumed to be areas lacking either beaver or high densities of ungulates) as suggested by the intermediate disturbance hypothesis (Connell

1978), and 4) species diversity will be lowest at sites with both beaver and high densities of ungulates.

4. ***Competitive exploitation between beaver and ungulates*****:** To examine whether competitive exploitation exists between beaver and ungulates by comparing a system with high ungulate densities to a system with lower ungulate densities. Specifically in Chapter 5, I used a data set that was completely independent of the one used in Chapter 4 to examine how these 2 different degrees of competition influence vegetation availability, diameter classes, and beaver foraging activities relative to these parameters. To determine whether competitive exploitation exists between beavers and ungulates in this system I tested whether 1) densities of ungulate pellet groups in Elk Island National Park are significantly higher than those in the surrounding area, 2) stem densities and diameters of key forage species differ in areas with higher levels of competition, 3) beaver alter their forage selection to less profitable food plants to compensate for a potential decrease in preferred forage in areas with high levels of competition with ungulates, and 4) beaver forage farther from the pond edge in areas with higher ungulate densities than areas with lower densities.

5. ***Synthesis and conclusion*****:** In Chapter 6, I synthesize the findings of all the previous chapters and apply some of the results to beaver management and also to resource management activities such as prescribed burning and the management of riparian vegetation.

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2.0 THE EFFECTS OF PRESCRIBED FIRE ON BEAVER

2.1 INTRODUCTION

Flooding by beaver (*Castor canadensis*) and the effects of fire are viewed as major natural landscape processes that drive vegetation dynamics and alter ecosystems at both local and regional scales (Naiman *et al.* 1988, Johnston and Naiman 1990a, Ford *et al.* 1999, Bisson *et al.* 2003). So important is the beaver's role in maintaining wetlands on the landscape (Naiman *et al.* 1988, Wright *et al.* 2002) that in many areas in North America beaver have been reintroduced to former ranges. The beaver's ability to impound large areas of water, alter vegetation communities, and change sediment loads and water chemistry is well documented (Naiman *et al.* 1986, Smith *et al.* 1991, Klotz 1998). For separate management objectives, fire has also been reintroduced in many places where fire suppression, landscape fragmentation, and climate change have altered historic fire regimes and vegetation communities (Bartos and Mueggler 1979, White *et al.* 1998, Ford *et al.* 1999, Weir *et al.* 2000). The interaction between fire and beaver has been assumed to be beneficial to beaver (Kellyhouse 1979, Naiman *et al.* 1988), although this assumption has rarely been tested.

Prescribed fire, also known as "ecological burning" (Meers and Adams 2003), is often used to restore grasslands (Bailey *et al.* 1990, Roques *et al.* 2001) or stimulate growth of woody plants (Bartos and Mueggler 1979, Elliott *et al.* 1999, Hiers *et al.* 2003). The use of fire to manipulate vegetation communities can also benefit various wildlife species by improving forage quality (Vinton *et al.* 1993) and habitat structure (Mushinsky 1985). A growing body of literature however, reveals that, in the context of other ecological disturbances such as high herbivory and climate change (e.g., drought), the use of prescribed fire does not always achieve expected outcomes (White *et al.* 1998, Hessl and Graumlich 2002). These findings suggest that land managers should adapt their fire management practices (e.g., adapting the timing, size, location, and intensity of fires) to address ecosystem dynamics.

Although one of the preferred forage species for beaver, trembling aspen (*Populus tremuloides*), regenerates well after fire (Bartos and Mueggler 1979, Bartos and Mueggler 1981, Campbell *et al.* 1994, Bailey and Whitham 2002), herbivory by ungulates can significantly suppress or reduce ramet production (Campbell *et al.* 1994, White *et al.* 1998, Bailey and Whitham 2002, Hessl and Graumlich 2002, White *et al.* 2003). Combined with fire, high levels of ungulate herbivory can dramatically reduce the production of woody species (Bailey *et al.* 1990, Bork *et al.* 1997a, White *et al.* 1998). Bailey and Whitham (2002) found that aspen stands exposed to high-severity burns but no elk (*Cervus elaphus*) had 10 times greater aboveground biomass than stands exposed to intermediate burns. The combination of elk and high-severity burns, however, reduced the above-ground biomass 90-fold.

In the Rocky Mountain national parks of Canada and the United States, White *et al.* (1998, 2003) determined that adding fire to a landscape now dominated by high densities of elk hindered the regeneration of aspen. Elk browsed off new aspen suckers before the stems were able to reach 2-m in height, therefore negating the goal of rejuvenating aspen through the use of fire. Meers and Adams (2003) found a similar situation in southeastern Australia where the high levels of preferential grazing by eastern kangaroo

(*Macopus giganteus*) became so concentrated in areas burned with prescribed fire that there were significantly fewer shrubs in burned areas than unburned areas. They also predicted that because habitat condition is closely tied to precipitation, in drought years, grazing pressure after fire could result in even more severe impacts on the vegetation.

Brief references in the literature suggest that beaver benefit from the effects of fire (Bird 1961, Kellyhouse 1979, Lewis 1982, Naiman *et al.* 1988, Fryxell 2001), but little or no empirical evidence has been published to substantiate these comments. Logically, the regeneration of woody species in riparian areas should provide additional forage for beaver. Species such as *Salix scouleriana* are adapted to fire and establish from seed in severely burned sites (Noste and Bushey 1987). The higher soil moisture in riparian areas can provide some protection for plant roots and belowground biomass during fires. Many riparian shrubs and herbaceous dicots recover well after fire (Dwire and Kauffman 2003) and, for some species, reproductive output following a fire increases dramatically (Kauffman and Martin 1990, Pendergrass *et al.* 1999). Climate, it seems, is an overriding determinant of how vegetation and wildlife respond to fire (Weir *et al.* 2000).

However, as reported in the preceding studies, burning in areas with a high level of herbivory does not necessarily result in an increase in the number of woody plants. In addition, during prescribed burns, most vegetation around beaver ponds is either burned or scorched. Morgan (1991) noted that beaver avoided trees on which the lower trunks had been singed or charred. A Slavey informant in H. T. Lewis's (1982) ethnographic study of traditional aboriginal use of fire in Canada's boreal forest reported that beaver do not return to burned areas until 4 years after a burn.

Considering the importance of climate in prescribed fire in typical years, fire occurring during periods of drought could severely compromise the survival of woody plants and dramatically alter vegetation communities. Roques *et al.* (2001) found that combined with drought, fire significantly reduced shrub densities. Fire frequency also determines how plant communities will respond to fire. Elliot *et al.* (1999) determined that repeated fires would be necessary to regenerate declining pitch pine (*Pinus rigida*) stands in the southern Appalachians, while Roques *et al.* (2001) found that frequent fires in the context of low grazing pressures prevented shrub encroachment into the eastern region of Swaziland, southern Africa.

In North America, prescribed fires are usually conducted in the early spring or late fall, when higher soil moisture limits the spread of fire and offers better control of the fire. In dry situations, fire can extend to the water's edge (personal observation), fed by dead vegetation from the past season. Where beaver occupy these wetlands, lodge and dams can be damaged or destroyed. With no food and limited escape cover, beaver might attempt to relocate to more suitable habitat. In such instances, beaver survival could be reduced further by predation risk associated with travel through the open, burned areas.

Given the complex interactions between fire, climate, and herbivory, Elk Island National Park (EINP) in Alberta, Canada is an ideal place to examine the combined effects of these processes on beaver populations in a managed landscape. Park management conducted the first prescribed burn in the park in 1979. By 2002, over 51% of EINP had been burned (in some areas as many as 8 times). In addition, the park has very high densities of large ungulates, a well-established beaver population, and has recently experienced severe drought. Together, prescribed fire, ungulate herbivory, and flooding by beaver have shaped EINP into a complex mosaic of wetlands, grasslands, southern boreal mixed-wood, and aspen forests (Campbell *et al.* 1994). Their influences on one another, separate or in combination, are less obvious. In particular, the effect of fire and ungulate herbivory on the park's beaver populations is not well understood. The long-term data sets for both fire and beaver in EINP offers a unique opportunity to examine the consequence of burning in beaver habitat. This chapter specifically examines the effects of prescribed fire on beaver lodge occupancy in EINP, one component of a larger study addressing fire, herbivory, and climate.

The purpose of this study is to examine whether prescribed fire influences beaver lodge occupancy differently under normal conditions compared to conditions of extreme drought, within the context of high levels of ungulate herbivory. My objectives were to determine 1) whether differences exist between beaver lodge occupancy in burned and unburned areas, 2) whether these differences are due to the presence of fire or due to differences in wetland availability, 3) whether a decrease in beaver lodge occupancy in burned areas results in a predictable reoccupation of these areas over time, 4) whether the fire frequency and the time since the last fire affects lodge abandonment, and 5) whether distances between abandoned and active lodges differ between burned and unburned habitats (such increases in distance could have implications for the recolonization of abandoned areas through juvenile dispersal and dispersal of beaver from burned habitats to more suitable habitats).

2.2 STUDY SITE AND METHODS

Study site

Elk Island National Park is located in the Beaver Hills Region, 40 km northeast of Edmonton, Alberta, Canada (Figure 2.1). The Beaver Hills are part of the previously glaciated Cooking Lake Moraine – a hummocky landscape dotted with small ponds and lakes. The 194 km^2 park is surrounded by privately and publicly owned land, much of which is developed for agriculture. Undeveloped land still borders the park in some areas, although all land outside the park is separated at the park boundary by a 2.1-meter high fence and, in many locations, roads.

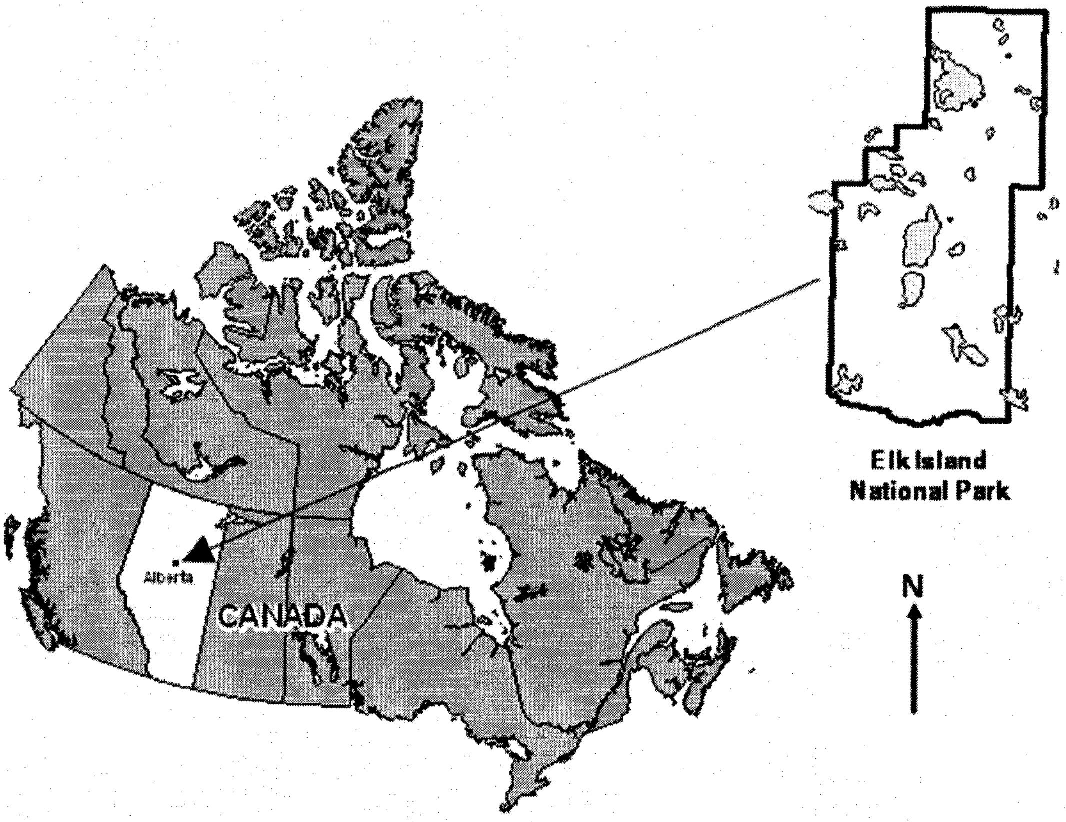

Figure 2.1. Location of the 194 km^2 Elk Island National Park, Alberta, Canada. Shaded areas in inset map are larger water bodies within the park.

Originally established to protect one of the last remaining herds of elk in the region, the park is also home to moose (*Alces alces*), plains bison (*Bison bison bison*), wood bison (*Bison bison athabascae*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*). To protect these species from venturing onto the neighboring agricultural lands, the park is completely fenced and, with the exception of coyotes (*Canis latrans*), lacks any resident species of large predators. Pruss (2002) found that coyotes in Elk Island National Park include beaver in their diet. Good forage and few predators have produced high year-round ungulate densities (13 ungulates/km^2). Parks

Canada controls ungulate populations through a regular culling program that incorporates the removal of live elk and bison from the park.

By the 1880's fur traders had extirpated beaver (*Castor canadensis*) from the area that was to become Elk Island National Park (Lin 1967). A viable population of beaver was finally re-established in 1941 from beaver that were translocated from Banff National Park. Beaver reached their peak population in 1989 (348 active lodges) and have since declined to a 2002 population of 152 active lodges (Figure 2.2).

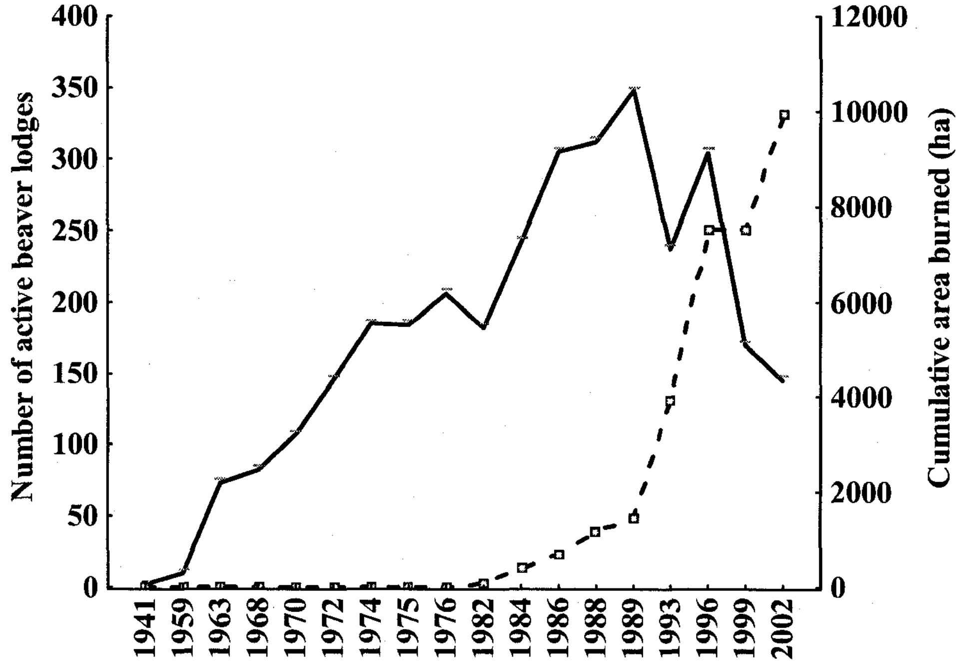

Figure 2.2. Number of active beaver lodges from 1959 – 2002 and cumulative area burned through prescribed fire in Elk Island National Park, Canada. Solid line indicates number of lodges occupied by beaver and dotted line indicates the cumulative area (ha) burned since 1979.

Beaver populations have fluctuated in the park since their reintroduction. Exact causes in these fluctuations have not been well documented or investigated. Tularemia caused a temporary decrease in populations in 1975 (Blyth and Hudson 1987) and has been noted in the park in isolated ponds as recently as 2005. In addition to disease, beaver activities threatening park facilities due to flooding resulted in the removal of the colony. Finally, a severe drought in 2002 caused a decline (less than 7%) in beaver populations from previous a previous survey conducted in 1999.

Provincial Highway 16 bisects the park (70% of the park is to the north of Highway 16 and 30% of the park to the south). Most of the park lies within the southern limits of the boreal mixed-wood forest (formerly considered to be part of the Aspen Parkland Natural Subregion, Achuff 1994). Trembling aspen is the dominant tree species in the park, although balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh) occur in moist areas. Pockets of black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss) also occur, but are more common in the northern part of the park. Shrub understory in the deciduous forests is diverse and includes beaked hazel (*Corylus cornuta*), serviceberry (*Amelanchier alnifolia*), choke cherry (*Prunus virginiana*), willow (*Salix* spp.), prickly and wild red rose (*Rosa acicularis* Lindl. and *R. woodsii* Lindl.), raspberry (*Rubus idaeus*), highbush cranberry (*Virburnum edule* Michx.), red osier dogwood (*Cornus stolonifera* Michx.), and snowberry (*Symphoricarpos occidentalis* Hook). Beaver in the park use many of these tree and shrub species as forage and construction material (Skinner 1984, Chapter 5).

Fire history and beaver lodge occupancy data

All fires since 1979 were mapped and entered into the EINP Geographic Information System (GIS) fire history database. Associated data included date, location, and size of each burn. Parks Canada did not consistently collect data relative to burn severity. There have been 121 prescribed fires in the park since 1979 and all but 6 (in October 1991) were lit between April and June. Fires ranged in size from less than 1 ha to 1,059 ha (Figure 2.3). Some areas of the park, such as areas containing rare patches of spruce and birch, have never been burned (49% of the park); others have been burned repeatedly.

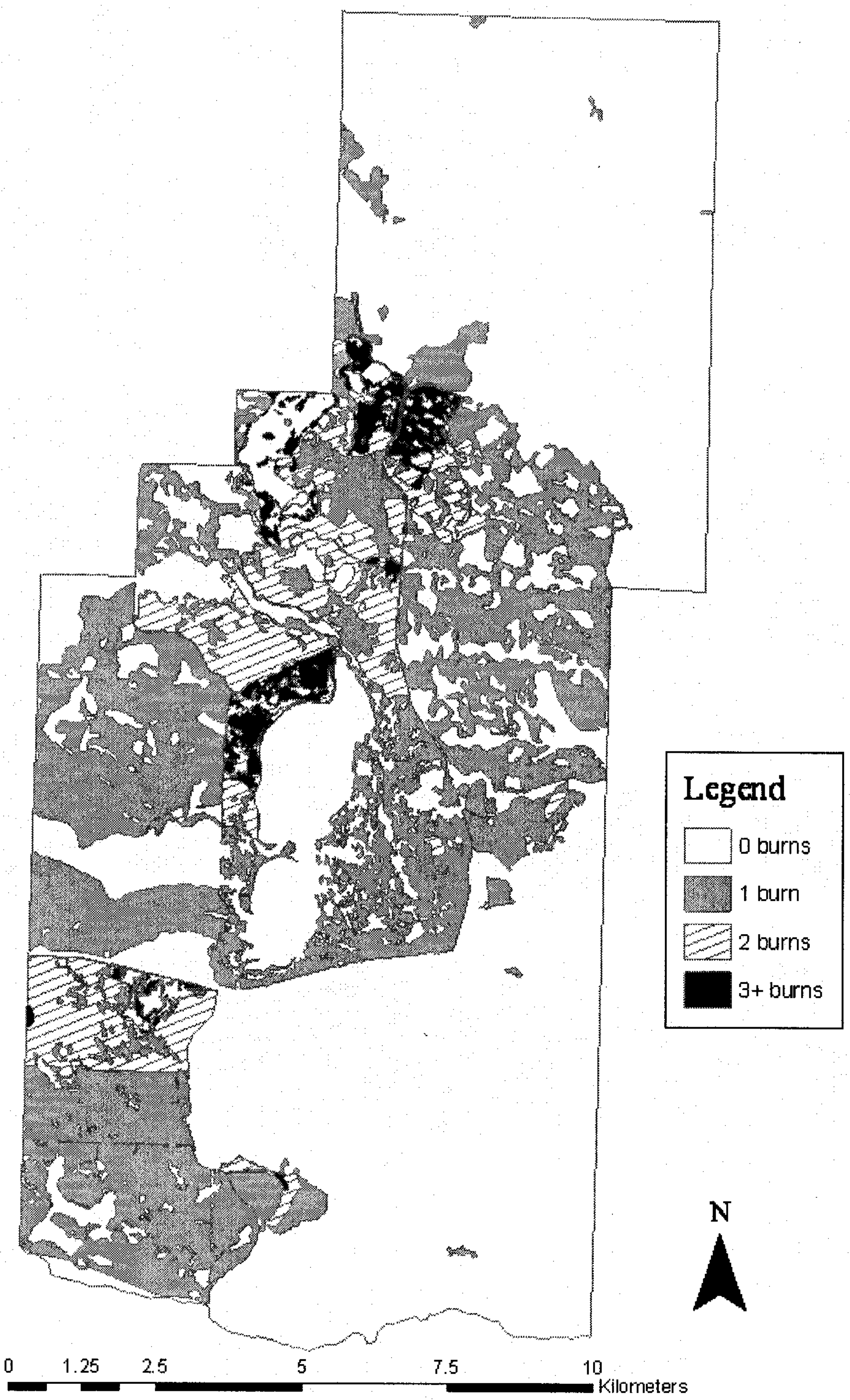

Figure 2.3. Fire frequency (1979 to 2003) in Elk Island National Park, Canada.

Long-term occupancy data for beaver lodges in EINP indicate that beavers 1) construct new lodges, 2) restore abandoned ones, and 3) in some areas occupy the same lodge for more than a decade. Park-wide helicopter and/or ground surveys of fall beaver lodge occupancy have been conducted by Parks Canada every 1 to 3 years since their reintroduction. During these surveys, all lodges within the park are mapped and assessed for occupancy status. A lodge is considered active if a fall food cache is present. Food caches, winter stores of branches and twigs adjacent to the main lodge entrance, are apparent from the both air and the ground. Since 1989, all lodges (active and inactive) have been entered into a GIS where they were each given a unique identifier so their occupancy status can be tracked over time.

Although Parks Canada has conducted regular beaver lodge surveys in EINP, observers did not consistently label individual lodges until 1989. As a result, all beaver lodges that were either visible in, or were constructed after 1989 have excellent data relative to their long-term trends in occupancy. For this reason only the post-1989 data were used to assess occupancy trends relative to fire. By 2001, the end of the survey period, this dataset included 734 lodges.

I used the two GIS databases (fire history and beaver lodge occupancy) to develop a complete fire history for each lodge (e.g., burned vs. unburned, burn frequency, year burned, time since last burned). A lodge was considered to be influenced by fire if the lodge was completely within a burn polygon in the GIS fire history database. If the lodge was outside the polygon it was classified as "unburned" because the beaver colony would have access to adjacent unburned habitats. Elk Island has both bank lodges that are attached to the shoreline, and island lodges, which are completely surrounded by water. Using the occupancy data, I classified lodges in the GIS as either active ("1") or inactive ("0") for each year since 1989.

Wetland coverage within burned and unburned areas

To ensure that differences in beaver lodge occupancy in burned and unburned areas were not confounded by the availability of wetland habitats; I used the GIS to assess existing wetland data (Hardy and Associates 1986) to determine the size of polygons of all the 1,920 wetlands in the burned (n = 814) and unburned areas (n = 1106). Data were first tested for homoscedascity using the Brown and Forsythe test (Brown and Forsythe 1974) and normality using the Shapiro-Wilk's W test (Shapiro *et al.* 1968). I then used a t-test for independent samples to compare differences in the areas of wetland between burned and unburned areas ($\alpha = 0.05$).

Preliminary data analysis for effect of fire on lodge occupancy

To obtain an initial assessment of the effect of fire on lodge occupancy from 1989 to present, I pooled occupancy data for areas burned only once, and compared the percent occupancy immediately prior to and after a fire. Data were then tested, using the Cochran Q test (Bishop *et al.* 1975) to determine whether lodge occupancy was dependent on whether or not the area had been burned. The Cochran Q test is an extension of the McNemar's Chi Square test and is useful for dichotomous data (Zar 1999, Cochran 1950)

To assess the effects of burning on lodge occupancy over time, I also tracked individual years following a burn to examine lodge occupancy rates for up to 12 years following the burn. There were 4 years when fires were lit for which there was a large enough sample size to track lodge occupancy over time (1991, 1994, 1995, and 2000). To avoid the confounding factor of multiple burning, only lodges that were in areas burned once were considered in this initial analysis. I then used linear regression for each of the 4 fire years to determine whether precipitation explained the magnitude of decline in the number of active lodges for the years following a burn. I also tested for correlation between lodges in burned and unburned areas.

Model development and analysis

Further analysis examined the influence of several variables that potentially affected lodge occupancy (including the number of burns). I used the 1989 to 2001 beaver survey data to analyze the effects of fire on beaver lodge occupancy over a 12-year period because this dataset included all lodges surveyed since 1989 that were active at least once during the survey period (n = 734). All lodges that had been permanently abandoned prior to 1989 were removed from the analysis. I used multiple logistic regression to model beaver lodge occupancy based on the presence or absence of beaver (response variable) relative to burn frequency, the years since the lodge area was last burned, and the distance of each lodge to the nearest active lodge for all lodges in the park. The first two variables account for aspects relative to fire history, while the third acts as a spatial variable that provides a context for possible dispersal distances and how fire might affect the overall density of occupied beaver lodges. Akaike's Information Criterion (AIC) was used for model selection (Burnham and Anderson 1998) and allowed evaluation of candidate models using model weights (ω) and ΔAIC. All statistical tests were evaluated using Statistica (StatSoft, Inc. 2003) and R statistical software (R Development Core Team 2005) and were considered significant at $\alpha = 0.05$.

2.3 RESULTS

Wetland coverage within beaver management units

Over 33% of the park is covered by wetlands and lakes (Hardy and Associates 1986); represented by lakes (15%), marsh (11%), swamps (3%), ponds (2%), fens (1%), and bogs (1%). The park lacks any major rivers and streams are generally shallow and intermittent. The burned and the unburned areas had similar wetland area ($P = 0.11$). The average wetland polygon size in burned areas was 2.49 ha ± 14.28 *SD* (range = 0.05 – 393.17 ha) and 4.09 ha ± 26.01 *SD* (range = 0.04 – 559.78 ha) in unburned areas. The edge of the largest lake in the park, Astotin Lake (559.78 ha), was burned along its west and south shores, but because it was not completely surrounded by a burn, its water area was classified as being in an unburned area. Despite the inclusion of this large water body into the unburned class, the average wetland size in the burned and unburned areas was not different ($P = 0.11$). There were large lakes in both burned and unburned areas.

Preliminary effect of fire on beaver lodge occupancy

For lodges burned only once, lodge occupancy for the year immediately prior to a burn was higher (41.1%) than the year immediately after a burn (25.38%, $Q = 10.4716$, $df = 1$, $P = 0.001$). Although the number of active lodges in some of the burned areas did increase in the years after burning, they never recovered to their original occupancy levels over the 12 year period I examined (Figure 2.4). Total annual precipitation did not significantly affect the number of active beaver lodges during any of the 4 fire years that I examined ($R^2 < 0.22$ and $P > 0.29$ in all cases). Although occupancy in the unburned areas in 1991 ($R = 0.98$, $P < 0.001$) and 1994 ($R = 0.89$, $P < 0.02$) showed similar trends to those in burned areas, this trend was not observed in 1995 ($R = 0.34$, $P = 0.51$) and 2000 ($R = 0.04$, $P = 0.96$, Figure 2.5).

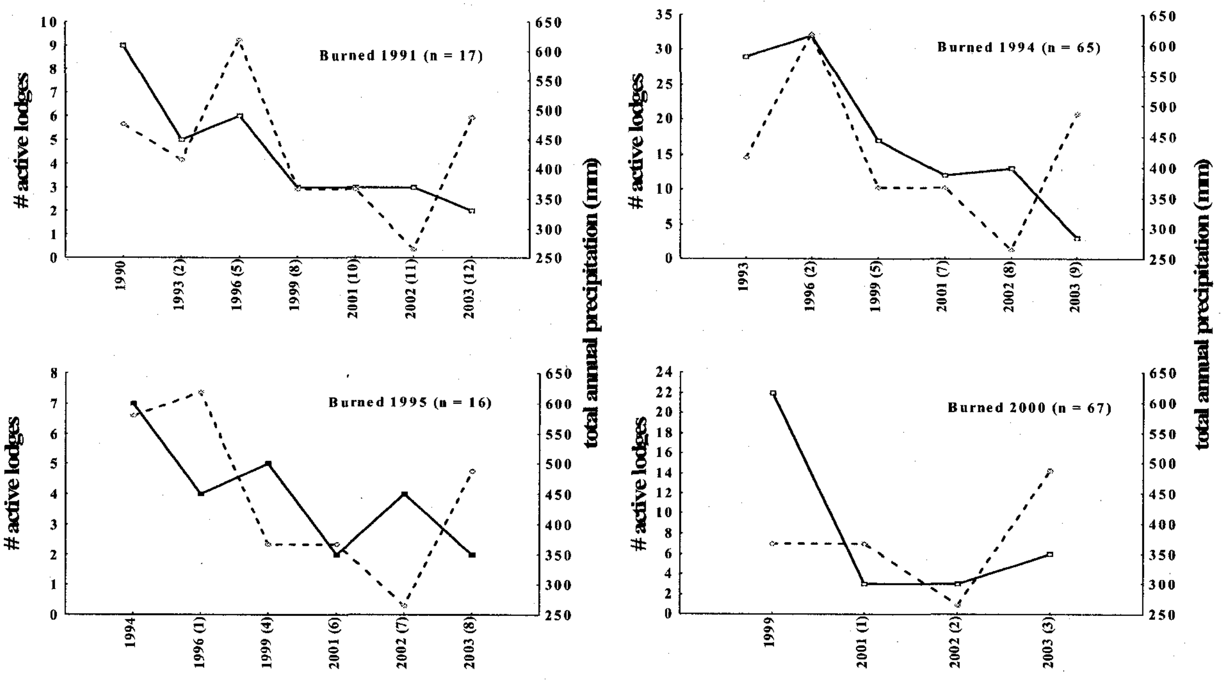

Figure 2.4. Beaver lodge occupancy during 3 to 12 years following burns conducted in 1991, 1994, 1995, and 2000 (number of years post-burn are in brackets following the year). The solid line (–) indicates the number of active lodges, and the dashed line (---) indicates the total annual precipitation (mm) during the same period. Only lodges burned once are included in the graph.

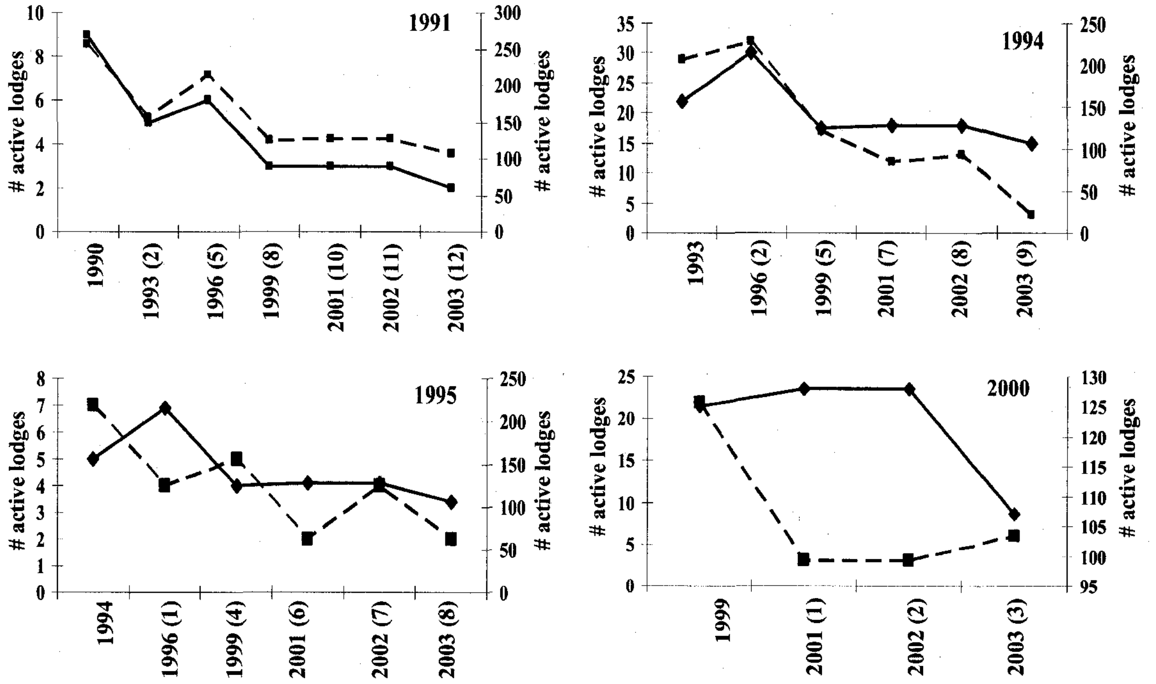

Figure 2.5. Beaver lodge occupancy during 3 to 12 years following burns conducted in 1991, 1994, 1995, and 2000 (number of years post-burn are in brackets following the year). The solid line (–) indicates the number of active lodges in unburned areas, and the dashed line (---) indicates number of active lodges in burned areas during the same period. Only lodges burned once are included in the graph.

Model results for the effects of fire on beaver lodge occupancy

The lowest AIC was for the model that included burn frequency only (Table 2.1). However, the differences in AIC values were small between the model that included burn frequency and the model that included both burn frequency and other variables. I removed "years since last burn" from the analysis (Table 2.2) because this variable was highly correlated with frequency (R = -0.78, $P < 0.05$), and was not a good predictor of lodge occupancy on its own (Table 2.1). When years since last burned was included in the model, the β-coefficient for the frequency of burns was -0.86 and 0.06 for years since last burned (Table 2.3). When years since last burned was removed from the model, the β-coefficient for the frequency of burns was reduced to -0.58. The β –coefficient for distance to nearest active lodge did not show any significant change (β = -0.002 for both models). When the variable "years since last burned" was removed, burn frequency alone accounted for 0.68 of the AIC weight (Table 2.2).

Table 2.1. A comparison of models used for predicting occupancy of beaver lodges relative to the number of burns ("frequency"), the time since the last burn ("years"), and the distance to the nearest active lodge ("distance") in Elk Island National Park (EINP), Alberta. Values include -2 log likelihood scores (-2LL) and number of parameters (*K*). Models were assessed by ranking AIC values (Δ_i) and weights (w_i), which describe the likelihood of the model.

Model	*-2LL*	K_i	AIC	Δ_i	w_i
Frequency	-326.41	2	656.82	0	0.293
Frequency + Years	-325.52	2	657.05	0.23	0.2613
Frequency + Distance	-326.17	3	658.33	1.513	0.1373
Frequency + Years + Distance	-325.36	3	658.71	1.89	0.114
Frequency + Years + Distance + Freq*Years	-325.55	4	659.09	2.273	0.094
Frequency + Years + Distance + Freq*Dist	-326.18	4	660.36	3.54	0.050
Frequency + Years + Distance + Dist*Years	-326.23	4	660.45	3.63	0.0476
Years	-331.21	2	666.42	9.60	0.002
Distance	-333.07	2	670.13	13.31	0.0004

Table 2.2. A comparison of models used for predicting occupancy of beaver lodges relative to number of burns ("frequency") and the distance to the nearest active lodge ("distance") in Elk Island National Park (EINP), Alberta. Values include -2 log likelihood scores (-2LL) and number of parameters (*K*). Models were assessed by ranking AIC values (Δ_i) and weights (w_i), which describe the likelihood of the model.

Model	*-2LL*	K_i	AIC	Δ_i	w_i
Frequency	-326.41	2	656.82	0	0.680
Frequency + Distance	-326.17	3	658.33	1.51	0.319
Distance	-333.07	2	670.13	13.31	0.001

Table 2.3. Estimated coefficients and 95% confidence intervals (CI) for logistic regression models assessing the effects of the number of burns ("frequency"), the distance to nearest active lodge ("distance"), and the years since last burn ("years") on beaver lodge occupancy.

Variable	Complete model				Model = years removed				Model = frequency only			
			95% CI for exp(ß)				95% CI for exp(ß)				95% CI for exp(ß)	
	ß	exp(ß)	lower	upper	ß	exp(ß)	lower	upper	ß	exp(ß)	lower	upper
Frequency	-0.86	0.42	0.23	0.77	-0.58	0.56	0.4	0.8	-0.58	0.56	0.4	0.8
Distance	-0.16	0.85	0.5	1.46	-0.19	0.83	0.48	1.42	—	—	—	—
Years	0.06	1.01	0.97	1.17	—	—	—	—	—	—	—	—
Constant	-1.39	2.66			-1.29	0.27			-1.39	0.25		

According to this model, the odds of a lodge being active decreases by 0.58 for each additional burn to which it was exposed. This decrease is evident in the data: after 3 burns lodges were often permanently abandoned (Figure 2.6). The β – coefficient was the same for the model with frequency alone and the model that included frequency and distance. Although not significant, the odds of a lodge being active decreases by 0.1889 for each additional kilometer a lodge is from its nearest active lodge (Table 2.3).

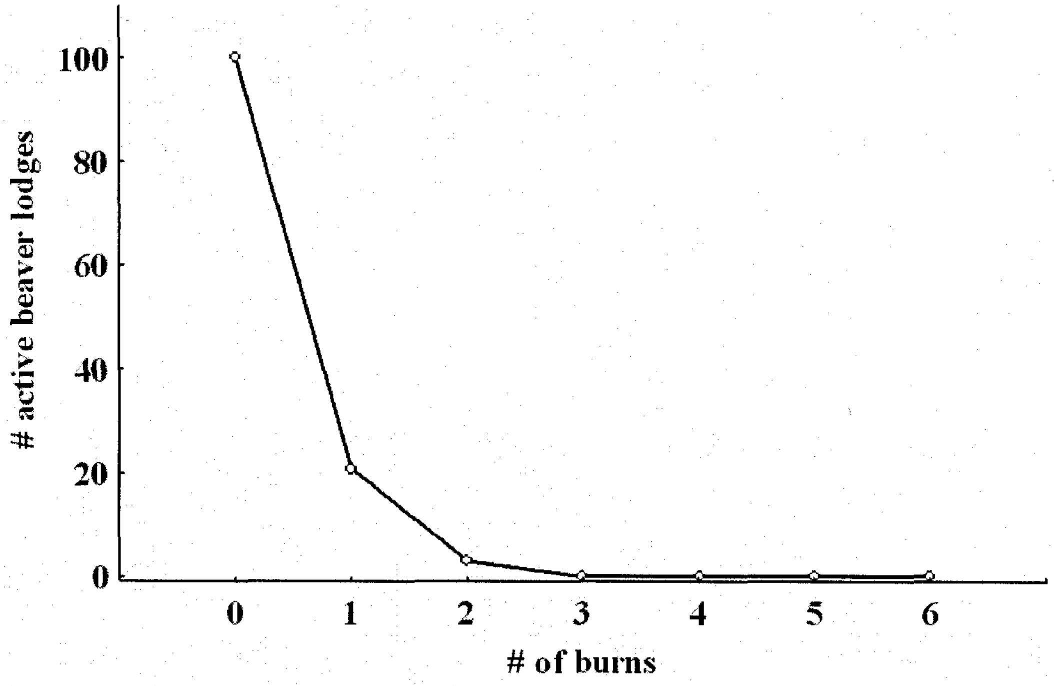

Figure 2.6. Beaver lodge occupancy during 2001 in Elk Island National Park relative to the number of burns the lodge was exposed to since the start of the prescribed fire program in1979.

2.4 DISCUSSION

Fire frequency and timing impacts

As predicted, occupancy of lodges by beavers was significantly lower in areas that had been burned than in unburned areas. There was a marked decrease in lodge occupancy in areas that have been burned more than once. Despite the fact that regeneration of woody plant species and, therefore an increase of forage for beaver, are often predicted after a burn (Bartos and Mueggler 1981, Bailey and Whitham 2002), there did not appear to be a trend in lodge reoccupation in the years following a fire.

Fire frequency has long been understood to regulate grassland ecosystems. In some agricultural systems, a combination of repeated burning, grazing, and season of burn is used as a means to eliminate woody vegetation and produce grassland pastures (Anderson and Bailey 1979, Bailey *et al.* 1990). Historians attribute the combination of aboriginal and natural fires and herbivory to the resilience of the prairie grasslands of pre-colonial North America (Lewis 1982, Campbell *et al.* 1994). In Elk Island National Park, the combination of fire and intensive browsing by ungulates appear to have increased grassland habitats to the detriment of beaver.

Time of year for the burn may also play a role at EINP. In North America, most natural fires occur in the summer, a scenario not replicated by prescribed burning programs. Most of the prescribed burns in EINP during my study period were between April and June. Higher moisture levels in the spring typically allow for safer burning conditions. Fall burning can present greater public safety hazards due to lower moisture levels. Burning in the fall can also dramatically reduce the abundance of grasses and woody plants (Bailey *et al.* 1990), the winter food supply for many herbivores. Unfortunately, early spring is also the time when most emergent wetland vegetation (e.g., *Typha latifolia*) is dry and flammable. In the late spring, summer, or early fall these obligate wetland species are green. Early spring burning in wetland habitats results in fires that extend to the water's edge and, in the case of beaver ponds, right up to and, on occasion, over any adjacent lodges. The impact to beaver lodges may be another cause of the reduced occupancy after a burn and after repeated burns. In EINP, water inputs due to snowmelt are not as pronounced in mountainous regions, because much of the snow is lost through sublimation and areas with significant runoff and standing water that might offer a more significant buffer are not common.

Drought had a devastating effect on beaver in EINP between 2000 and 2002, especially in burned areas. After a particularly hot fire that was lit in 2000, the number of active beaver lodges in the area burned that year declined from 15 active lodges to 3 active lodges over the course of a year. The lodges in this area that were active before the fire have not yet been reoccupied (as of 2006). It is possible that habitats already compromised by drought were not capable of mitigating the effects of burning.

Ungulate herbivory

Unlike many areas where prescribed fire is used for vegetation management, the effects of prescribed fire in EINP are confounded by an unusually high year-round ungulate population. Bork *et al.* (1997b) found that mature forms of *A. alnifolia* and *P. virginiana* were found only outside the boundaries of EINP, where fire and high levels of ungulate herbivory were non-existent. This finding is despite the fact that *A. alnifolia* is a fire tolerant species (Noste and Bushey 1987). Although the presence of *C. cornuta* and *R. idaeus* were positively correlated with burn intensity inside the park, they were significantly shorter and more hedged than those same species found outside the park (Bork *et al.* 1997a, Chapter 4).

Overgrazing by ungulates in burned areas might inhibit plant growth to the point of preventing regeneration of adequate beaver forage (e.g. *Populus tremuloides*). Studies indicate that ungulates are often drawn to areas shortly after a burn (Vinton *et al.* 1993, Bailey and Whitham 2002) and the associated increase in foraging by ungulates in burned areas would delay the regeneration of woody plants. An alternative hypothesis is that beaver have a natural cycle in which they abandon areas where food resources have been exhausted after years of beaver foraging (Ives 1942); however this hypothesis would also assume a similar pattern of lodge abandonment in both burned and unburned habitats, which was not observed for all years (Figure 2.5).

Dispersal and foraging distances

Distance to nearest active lodge had less influence on occupancy than did fire frequency. Along with vegetation patterns, topography often dictates how beaver move across the landscape (Johnston and Naiman 1990a). Regardless of how much area is burned, beaver will always be limited by other environmental factors such as climate, predation by coyotes, the proximity of suitable water bodies, and beaver density. Such limits are reflected in the varying distances to active lodges found from year-to-year in both burned and unburned areas and might explain the lower β-coefficient and higher AIC value of distance in the models.

If an area is burned extensively, however, beaver must increase their foraging distances to find unburned vegetation if they wish to remain in the area. As central place foragers, any increase in foraging distance for beaver would increase their exposure to predation as well as the energy required to bring food and construction materials back to their lodge (Fryxell and Doucet 1991). Conversely, if they chose to move to another wetland, they risk predation and extensive search times, particularly if suitable wetlands are not close by. This aspect of dispersal and foraging in burned areas warrants further study.

Fire is a natural process in many ecosystems and has been used as a management tool in North America since pre-Columbian times (Lewis 1982). Its current use extends to many continents and various ecosystems. The repeated use of fire, especially in grazing systems, controls and suppresses woody vegetation (Bork *et al.* 1997b, Roques *et al.* 2001). Although the maintenance of grasslands is beneficial for many grazing herbivores, herbivores that rely heavily on woody plants could be excluded from these systems. Unlike beaver, ungulates are capable of moving across landscapes in search of better forage and, therefore, are more resilient to localized disturbance such as fire. When beaver habitat is depleted or destroyed, beaver must disperse to a new central location before they resume their foraging and food caching activities.

The long-term reduction in occupancy after repeated burning supports my prediction that multiple fires reduce the number of active beaver lodges. In addition, the interactive effect of fire and drought brings to question whether extensive burning reduces the landscape's ability to mitigate the effects of severe drought in wetland habitats, especially when coupled with high levels of herbivory. Further research is required to fully understand the cumulative impacts of multiple perturbations on beaver populations.

2.5 MANAGEMENT IMPLICATIONS

The use of prescribed fire is often a necessary and irreplaceable tool in the management of natural areas. After a century of fire suppression in many areas of North America, the resultant fuel loading has created an unacceptable risk to public safety. The loss of landscape heterogeneity has reduced habitat diversity, with subsequent impacts on ecological processes (Woodley 1993, White *et al.* 1998). However, prescribed fire must be conducted in ways that sustain existing ecological processes and key species that have long-term benefits to larger ecosystems.

Beaver are considered a keystone species (Paine 1966, Johnston and Naiman 1990b) and their wetland building activities provide habitats for many other organisms. In the context of extremely high density of ungulates, repeated burns in beaver habitat appear to have caused a dramatic decrease in lodge occupancy (and therefore population). Fire could be important for the regeneration of many woody plants species used by beaver (e.g., *Salix* and *Populus*), but these benefits would depend on several factors such as herbivory and fire frequency. Faced with predictions of an increasingly dry climate on the Canadian prairies (Hogg and Bernier 2005), the potential negative impact of fire becomes even more significant. The challenge then, is to broaden our understanding of how beaver and fire coexist in concert with other species competing for the same resources in changing climatic conditions, and apply that knowledge to current management practices to maintain a broad range of species in ever changing environments.

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3.0 BEAVER REGULATE WETLANDS DURING DROUGHT

3.1 INTRODUCTION

During times of drought, the loss of water resources has devastating effects on both agricultural and ecological resources (deMenocal 2001, Schindler and Donahue 2006), to the point of being considered a "landscape hazard" in situations where aridity is directly linked to soil erosion (Sauchyn *et al.* 2002). Although various data, including paleoclimatic (Laird *et al.* 2003), tree ring (Sauchyn *et al.* 2003), and anthropological data (deMenocal 2001), suggest that decadal and multicentennial scale droughts have occurred in North America for at least two millennia; climate models predict the incidence of drought will increase in frequency and duration over the next 100 years (Hengeveld 2000, Hogg and Bernier 2005, Schindler and Donahue 2006). Along with drought and anthropogenic wetland losses, the impact of intensified industrial, urban and agricultural demands upon existing water resources makes concerns of warming temperatures and decreased precipitation even more relevant.

Biotic influences on the maintenance of wetlands, particularly in the context of climate change, have frequently been ignored. Beaver (*Castor canadensis*), in particular, are often overlooked as a potential means to minimize the impacts of drought. This omission exists despite the well-documented role of beaver as a key species in creating and maintaining wetlands at landscape scales (Naiman *et al.* 1988, Johnston and Naiman 1990a). Considering the value of wetlands as habitat for many aquatic and terrestrial species, the absence of information on the influence of beaver (a keystone wetland species) seems critical, if incidence of drought does increase.

Several studies have sought to predict the long-term impacts of drought on wetland availability and function. Larson (1995) assessed the variability of water coverage in wetland basins across the Prairie Pothole Region (PPR) relative to a suite of climatic variables. She found that climate explained over 60% of the variation in wet basins in the PPR, which in turn influenced the availability of habitat for breeding waterfowl. Johnson *et al.* (2005) found that drought conditions displaced waterfowl populations that would normally use the PPR into more northern areas where water levels were more consistently stable. These findings confirmed predictions by Poiani and Johnson (1991), whose climate-based simulation model forecasted lower waterfowl production due to a warmer, drier climate and an increase in dry basins in the PPR. However, despite more stable water availability, the peatlands of the boreal region are also vulnerable to climate change due to a predicted increase in wildfire, the loss of permafrost, and lower water inputs (Camill and Clark 2000, Hogg and Bernier 2005).

Climate change models for the prairie pothole and boreal regions commonly predict reduced groundwater recharge and loss of wetlands due to less precipitation and higher temperatures. In fact, almost all models used to simulate various scenarios relative to global warming predict higher temperatures in these regions (Johnson *et al.* 2005, Hogg and Bernier 2005). In their analysis of temperature data from Canada's western prairie provinces, Schindler and Donahue (2006) calculated an increase in temperature of 1 to 4 °C since 1970, which suggests such a trend has already begun. Although precipitation is more difficult to predict, even if there was an increase in precipitation, rising temperatures would result in greater evapotranspiration, therefore producing drier conditions in the southern boreal region (Hogg and Hurdle 1995, Schindler and Donahue 2006).

Historical and current wetland loss over large expanses of North America due to urban, industrial, and agricultural development only serve to exacerbate wetland loss associated with recent and predicted drought. Since European settlement, as much as 70% of the original non-peatland wetlands in Canada have been lost to development (National Wetlands Working Group 1988) and as much as 53% in the United States (Dahl 1990). This loss of wetlands in turn has eliminated highly valued wetland functions (e.g., groundwater recharge and nutrient removal), which cannot always be mimicked through wetland restoration programs (Zedler 2000). Anthropogenic disturbance causing the loss of wetlands can be as visually obvious as the drainage and infilling of wetlands, or the less visible, but equally as serious, alteration of groundwater and surface-water flows. Recently, wetland ecologists have also identified the potential for wetland loss due to urban and agricultural land use and their associated greenhouse gas emissions (Larson 1995, Poiani *et al.* 1996, Johnson *et al.* 2005).

During this period of wetland loss, a key species associated with the creation and maintenance of wetlands was also removed from the riparian and wetland ecosystems of North America. Beaver were aggressively harvested across North America from the 17th century to the early 20th century. By 1900, beaver were extirpated (Naiman *et al.* 1988) in most regions of North America. Beaver are well known for creating water impoundments and modifying channel geomorphology and hydrology (Naiman *et al.*1986, Brochart *et al.* 1989). Johnston and Naiman (1990a) found that the rate of pond creation paralleled an increase in the population of beaver over a 46–year period. In the context of predicted increases in the incidence of drought and historic and current anthropogenic wetland loss, I hypothesized that beaver populations would play a key role in maintaining local wetlands.

With the creation of beaver impoundments comes an increase in the acid-neutralizing capacity of water flowing through beaver ponds (Smith *et al.* 1991), water storage, groundwater inputs, sediment storage (Naiman *et al.* 1988, Baker and Cade 1995, Westbrook *et al.* 2006), and landscape heterogeneity (Brochart *et al.* 1989, Johnston and Naiman 1990b). On the Colorado River in Rocky Mountain National Park, beaver dams increased both surface water and groundwater in both high- and low-flow periods and were able to attenuate declines in the water table during drier periods (Westbrook *et al.* 2006). High flow periods were generally during spring snowmelt. Beaver dams are also able to transform lentic habitats to a combination of both lentic and lotic habitats (Martell *et al.* 2006). Naiman *et al.* (1988) also found that streams with beaver impoundments have a high resistance to disturbance. Because of its ability to dramatically alter landscape form and function to the benefit of other species, beaver are often considered a keystone species (Jones *et al.* 1994, Baker and Cade 1995).

Given the predicted increase in drought in key wetland regions of central North America, the beaver's ability to create and maintain wetlands over long time periods bring into question whether beaver can mitigate the effects of drought on shallow isolated sloughs, ponds, and lakes in glaciated landscapes. Beavers are known to increase the area of open water wetlands in streams and riverine systems (Johnston and Naiman 1990b), but their ability to maintain relatively isolated wetlands in morainal landscapes has not been demonstrated. The availability of 54 years of aerial photographs and beaver census data from Elk Island National Park (EINP) in east-central Alberta, Canada, during a period that coincided with the most severe drought in the history of the area, provided a unique opportunity to examine the combined effects of climate and beaver on wetlands.

The overall objective of this study was to investigate whether beaver or climatic factors are more important in maintaining open water wetlands. Specifically, I 1) examined whether beaver (number of lodges/area) increase the area of open water in wetlands generally, 2) determined whether beaver also increase open water area during drought, 3) assessed the importance of precipitation and temperature in creating and maintaining open water wetlands in the presence of beaver, and 4) determined the effects of precipitation and temperature on open water in wetlands when beaver were absent from the models.

3.2 STUDY SITE AND METHODS

Study site

Elk Island National Park (194 km^2) is located at the southern fringe of the mixed-wood boreal region of east-central Alberta, Canada (Figure 3.1). The park is in the heart of the Cooking Lake Moraine; a landscape predominantly covered by trembling aspen forest

(*Populus tremuloides*) and defined by a knob and kettle terrain. Balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh) occur in moist areas. Pockets of black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss) also occur, but are more common in the northern part of the park. Fire was suppressed in the park until 1979 when a prescribed fire program was established to restore vegetation communities and enhance wildlife habitat. Approximately 51% of the park area was burned by 2002. Open water areas are represented by lakes, intermittent or slow-moving streams, shallow open water, and marshes. Fens, bogs, and swamps are also present throughout the park.

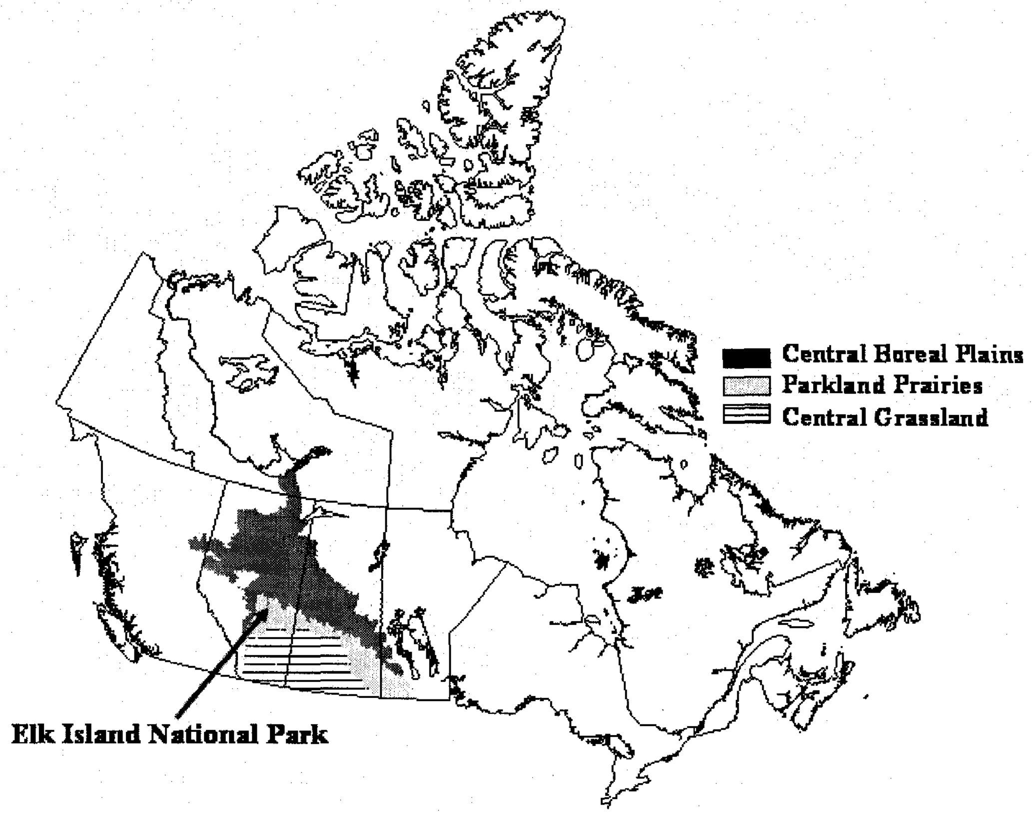

Figure 3.1. Location of Elk Island National Park in Alberta, Canada relative to the prairie ecoprovinces (Marshall and Schut 1999).

Soils in the park overlay glacial till and have generally developed under forest vegetation (Crown 1977). Luvisols account for 75% of the soils in the park, while Mesisolic soils comprise 16%. Brunisols (4%) are found in areas of deep sand deposits and Gleysolic (2%) and Fibrsolic (2%) soils occur in localized pockets throughout the park. A small deposit of Grey Solodized Solenetz soils is located near the east boundary of the park. The climate is classified as continental with warm summers and cool winters (Crown 1977). Much of the atmospheric inputs into wetlands in the park come from rainfall, rather than seasonal snowmelt seen in other areas with rivers originating from mountainous areas. Average precipitation from 1940 to 2002 was 457 mm, although variability from wet to dry years is common (Figure 3.2).

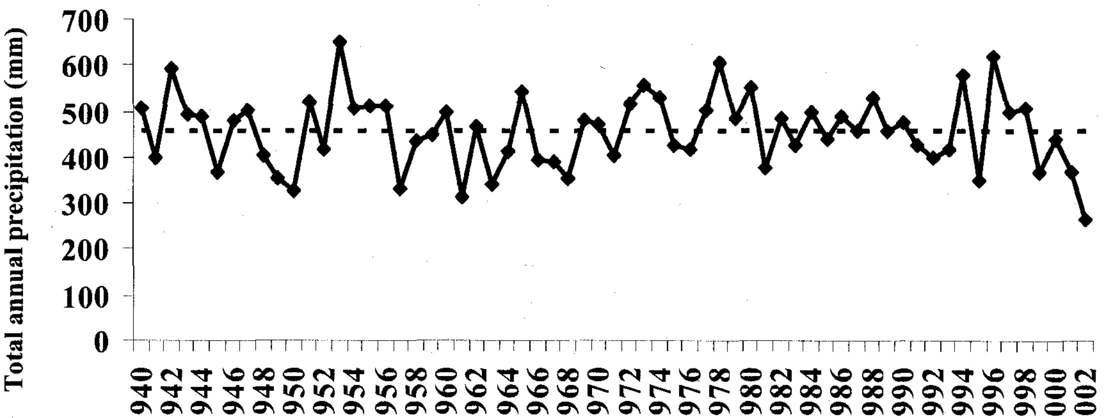

Figure 3.2. Total annual precipitation (solid line) from January 1 to December 31 and average precipitation (dashed line) from 1940 to 2002. Data from Environment Canada ((http://www.climate.weatheroffice.ec.gc.ca/climatedata).

Although there have been no groundwater studies within the park, there have been groundwater assessments in the counties that surround the park (Hydrogeological Consultants Ltd. 1998, 2001). The areas immediately adjacent to the park are almost evenly classed as groundwater recharge and groundwater transition areas. Recharge wetlands are higher than the surrounding groundwater table and water flows out of the wetland to the groundwater (Mitsch and Gosselink 2000), while in groundwater transition areas, groundwater is well below the surface and there is no gradient.

Beaver were extirpated from the park by the mid 1800's (Blyth and Hudson 1987) and not successfully reintroduced until September 1941. Park-wide beaver census data have been gathered since their reintroduction. The initial spread of beaver was very slow. Since the mid to late 1950's there has been a well-established beaver population within the park.

EINP is surrounded by agriculture and private acreages on its north, west, and east boundary and the Cooking Lake – Blackfoot Provincial Recreation Area to the south. Industrial expansion and urbanization are increasing with a growing regional population and strong economic growth in the oil and gas sector. Surrounding land use has resulted in extensive draining of wetlands and the removal of beaver colonies and their habitats.

Data acquisition and development

There is an extensive aerial photo record for Elk Island National Park dating back to 1923 and beaver population data (lodge occupancy) from 1941. For this study I was able to analyze 12 separate years of data between 1948 and 2002 where there were 1) complete vertical aerial photo coverage of the entire park, 2) corresponding beaver census data, and 3) appropriate climate data. Aerial photos for each year were scanned at a minimum of 600 dpi (dots per inch) as greyscale images and made spatially relevant by georectifying them in a Geographic Information System (GIS) using ArcMap 8.1 (ESRI 2001). I then created a mosaic in ArcMap from the aerial photos to develop a single geographically accurate aerial representation of the study area. For 2 of the years, 1995 and 2001, there were existing aerial photo mosaics available in the GIS. For 2002, the driest year on record, Landsat-7 ETM imagery was the only imagery available. Only the black and white band 8 image was used to obtain the best resolution for the area (Table 3.1). Landsat imagery differs from aerial photographs and can pick up on more water reflectance in surrounding emergent vegetation; however, it is commonly used for wetland assessment and offers good results when consistent cover classes are analyzed (Ramsey and Laine 1997). For years where digital and non-digital aerial photographs were available, individual wetlands that were difficult to delineate in the GIS were confirmed with a binocular mirrored stereoscope using the original aerial photos.

Table 3.1. Images used in the analysis of the effects of beaver and climate on the area of open water in Elk Island National Park, 1948 to 2002. (N/A = not available).

Year	# of photos used	Scale and resolution	Date taken
1948	33	1:36 000 (600 dpi)	September 1948
1950	20	1:40 000 (600 dpi)	September 1950
1962	20	1:31 680 (600 dpi)	May 1962
1964	50	1:20 000 (600 dpi)	July 1964
1967	29	1:31 680 (600 dpi)	August 1967
1973	45	1:15 840 (600 dpi)	September 1973
1980	12	1:60 000 (600 dpi)	April 1980
1982	30	1:30 000 (600 dpi)	August 1982
1995	N/A (orthophoto)	1:40 000 (600 dpi)	August 1995
1996	37	1:30 000 (800 dpi)	May 1996
2001	N/A (orthophoto)	N/A, 1200+ dpi	May 1996
2002	Landsat-7, ETM	N/A, 12.5 m	August 2002

The study area comprised approximately 79 km^2 of the park that had never been exposed to fire during the park's history. By excluding the burned areas of the park, I eliminated the possible confounding effects of fire on wetlands and beaver lodge occupancy. In an associated study, it was determined that beaver lodge occupancy is lower in areas that have been burned than unburned areas in the park (Chapter 2).

Using a consistent study area for all years, I digitized all open water in wetlands for each of the 12 sets of aerial photo coverage and calculated their areas in the GIS. Summed areas provided the total area (in hectares) of open water within the study area for each of the 12 years. Because large lakes (> 150 ha) could not be manipulated by beaver, four big lakes within the study area were excluded from the analysis (Flyingshot, Bailey, Goose and Blackfoot Lakes).

Temperature and precipitation data were obtained from Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/climatedata). For the years when accurate climate data were not available for EINP, data from the Edmonton Municipal Airport (approximately 45 km to the west) were used instead. During their analysis of ungulate population dynamics, Blyth and Hudson (1987) found that the Edmonton data provided equivalent climatic values to those in EINP.

Aerial photos were taken in spring and summer months, but the months were not always consistent among the years examined. In addition, extreme weather events after the aerial photos were taken could bias the precipitation values if the typical annual hydrologic year was used (November 1 to October 31). For these reasons, I calculated annual precipitation, temperature, and total annual effective precipitation (precipitation – potential evapotranspiration, Sass *et al.* 2006) as the 12 months prior to the month the aerial photographs were taken. For example, if an aerial photo was taken in June of 1948, annual precipitation and temperature values were calculated from June 1947 to May 1948. Longer climatic intervals (e.g., 3-year average precipitation) were calculated by the same method. This approach is consistent with methodologies in other studies where multiple sets of aerial photographs were used in the analysis of wetland areas (Johnston and Naiman 1990a, Larson 1995). Initial climatic variables included: mean and mean maximum annual temperature, total annual precipitation (P), total annual rainfall, total annual snowfall, and total annual effective precipitation (precipitation – potential evapotranspiration). For total annual effective precipitation, potential evapotranspiration (PET) was calculated using methods by Hamon (1963). I also examined the effects of hydrologic year (November 1 to October 31), seasonal precipitation (3 months prior to the time the photograph was taken), and two-, three-, and five- year time lags for total annual precipitation.

In addition, I examined differences in water area and activity in 80 individual ponds over four separate years - in 1948 and 1950 when there were no beaver present in the study area and in 1996 and 2001 when beaver were well established. The year 1996 represents a year with normal total annual precipitation (377 mm, measured from 12 months prior to the month the air photo was taken), and 2001 represents a year of slightly below average precipitation (370 mm). The year 1948 had the highest precipitation of all 4 years (471 mm), and 1950 was the lowest (342 mm).

I selected all the ponds in the study area that had active beaver colonies in both 1996 and 2001 (*N* = 40) and an additional set of ponds that had no beaver activity in them in both 1996 and 2001 (*N* = 41). By default there was no beaver activity in any of these ponds in 1948 and 1950. Ponds were classified into 2 groups – 1) ponds that did not have beaver in them in 1948 and 1950, but did have active beaver colonies in 1996 and 2001, and 2) ponds that did not have beaver in them in any of the four years. The area of each of these ponds was determined from the digitized 1948, 1950, 1996, and 2001 wetland data. Although it was impossible to find any ponds in 1996 and 2001 that did not have beaver in them at some point in their history, every effort was made to ensure the pond did not have an active colony in it for at least 5 years. Each year provided an individual measure of the area of open water for each pond relative to its future or current beaver activity.

For example, ponds 1 through 40 were given a classification as "active" because they supported beaver in 1996 and 2001. These same ponds were considered as future active ponds in 1948 and 1950. Ponds 41 through 80 were classified as "inactive" because they did not support beaver in 1996 and 2001 and by default in 1948 and 1950.

Park staff have conducted censuses of beaver lodges in the park since 1941 when beaver were re-introduced. Until the mid-1950's the beaver population was limited to Astotin Lake (outside the study area), but in 1952 beaver subsequently recolonized the entire park including my study area. In each census, all lodges were classified as active or inactive and mapped. These data were transferred to the GIS for each of the 12 years. The total number of active and the total number of lodges (active + inactive) were calculated for each year. Elk Island National Park is dominated by knob and kettle terrain and lacks any major riverine systems. Wetlands are generally isolated and lack the linear surface water connectivity found in many other areas with riverine connectivity where beaver are studied extensively (e.g., Naiman *et al.* 1988, Johnston and Naiman 1990b, Syphard and Garcia 2001).

Beaver in EINP construct dams, but dams are generally smaller and less numerous that those found in areas with more rivers and streams. A large dam in EINP would average approximately 20 meters across and 1.7 meters in height. Most dams are much smaller in both height and length than in other areas and serve to block intermittent flows or seepage from a pond to an adjacent low-lying depression. These dams help impound water and increase catchment area. They also enhance connectivity by flooding into adjacent wetlands and low areas. By capturing overland flow in this morainal landscape, beaver are able to facilitate groundwater recharge as well as increase the overall area of open water. Although some form of dam is common, there are active beaver ponds that lack any dams. Counting lodges, rather than dams has been an effective way to monitor beaver activities within the park.

Data analysis

Multiple linear regression was used to determine whether the area of open water in wetlands varied significantly with the number of active beaver lodges, inactive beaver lodges, all beaver lodges (active + inactive), precipitation, and temperature. A suite of 14 variables was derived from the climate and beaver data. From these variables I ran several regression models. To avoid collinearity, no variables that were derivatives of the same data (e.g., using two precipitation variables in the same analysis) were used together when conducting model runs. Only the beaver and climate variables that best explained the variation in open water were included in the final model. The final model was also tested to identify possible interactions between the explanatory variables. Finally, I used a relative Pratt index (d_j) to determine the relative importance of each explanatory variable by attributing the proportion of the overall R^2 to each one (Thomas and Zumbo 1997). A variable was considered "important" if $d_j > 1 / (2 \text{ x } [\text{\# of explanatory variables}])$. The level of significance was $\alpha = 0.05$.

To determine whether beaver are able to mitigate the loss of open water during drought, I compared the open water coverage for the 2 driest years, 1950 (with no beaver) and 2002 (with beaver) by overlaying the water coverage areas in the GIS. To further assess the effects of climate, I developed a regression model that included only precipitation and temperature variables to determine their overall effect on open water cover in wetlands while excluding beaver from the model.

From the data gathered for individual ponds in 1948, 1950, 1996, and 2001, repeated measures ANOVA was used to test for the effect of year and beaver activity over time on the mean change in the area of open water for individual ponds for each of the 4 years. Because the value for total annual precipitation within a year was a single number, the year itself was representative of its annual precipitation. Year was a within-subjects factor while beaver activity (future and current) was a between subjects factor (StatSoft Inc. 2003). I then used a Tukey's HSD test for post-hoc comparisons. All results were significant at $\alpha = 0.05$.

3.3 RESULTS

The area of open water in wetlands closely paralleled the number of active beaver lodges over time (Figure 3.3A). The best model that explained the greatest amount of variability in the area of open water in EINP included active beaver lodges, mean maximum annual temperature, and mean 2-year precipitation ($R^2 = 0.87$, $P < 0.00075$).

$$\textit{area of open water} = -78.14 + 0.81(\textit{active lodges}) + 0.17(\textit{mean max temp}) + 0.18(\textit{2YrPrecip}) + 97.27$$

The presence of beaver had an overwhelming effect on the amount of open water in wetlands in Elk Island National Park (Figure 3.3B). The presence of active beaver lodges was the strongest predictor of open water coverage in the park (relative Pratt index d_j = 0.8492). Neither the mean maximum temperature (relative Pratt index d_j = 0.0784) nor 2–year mean annual precipitation (relative Pratt index d_j = 0.0733) significantly affected the amount of open water in wetlands (Figure 3.4). I did not find any interaction effects between the explanatory variables.

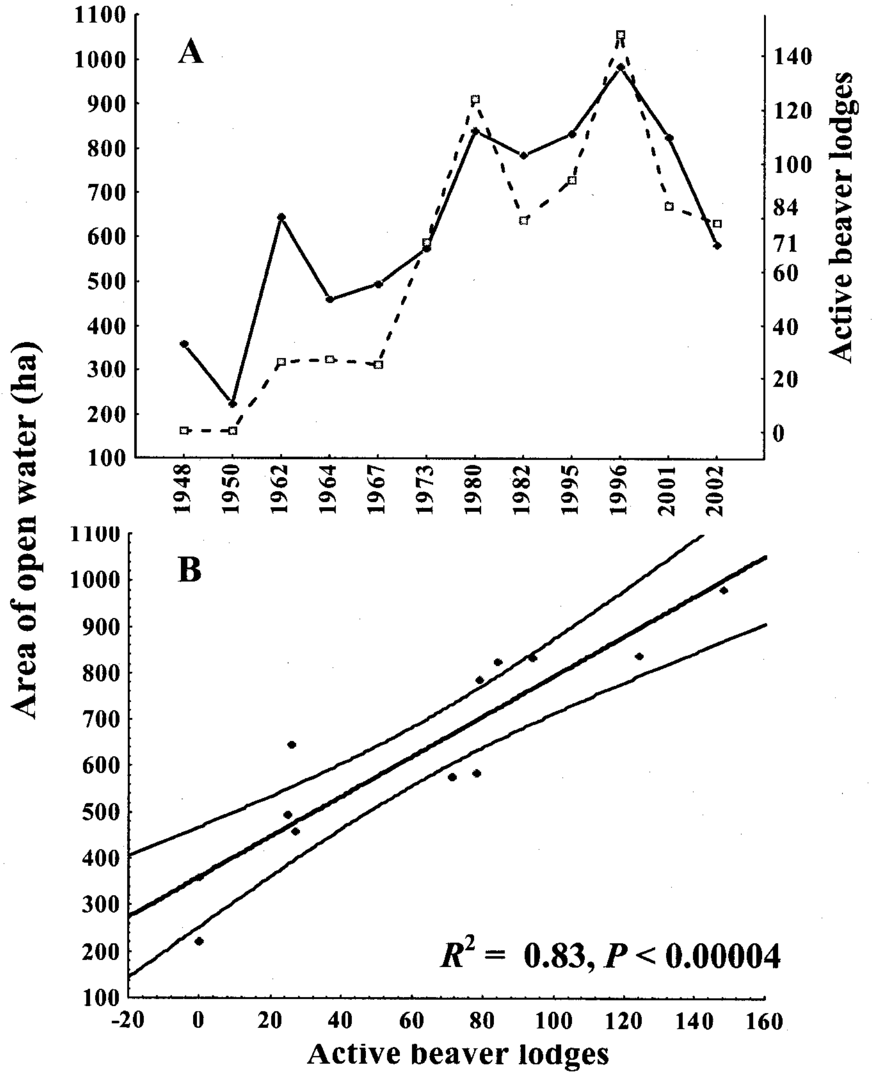

Figure 3.3. Relationship between beaver lodges and area of open water in wetlands. Graph (A) shows the area of open water (solid line) and the number of active beaver lodges (dashed lines) from 1948 to 2002 in Elk Island National Park, and graph (B) represents the regression between the area of open water (Y) and number of active beaver lodges (X) where $Y = -58.43 + 0.19X$. Outer lines represent 95% confidence limits.

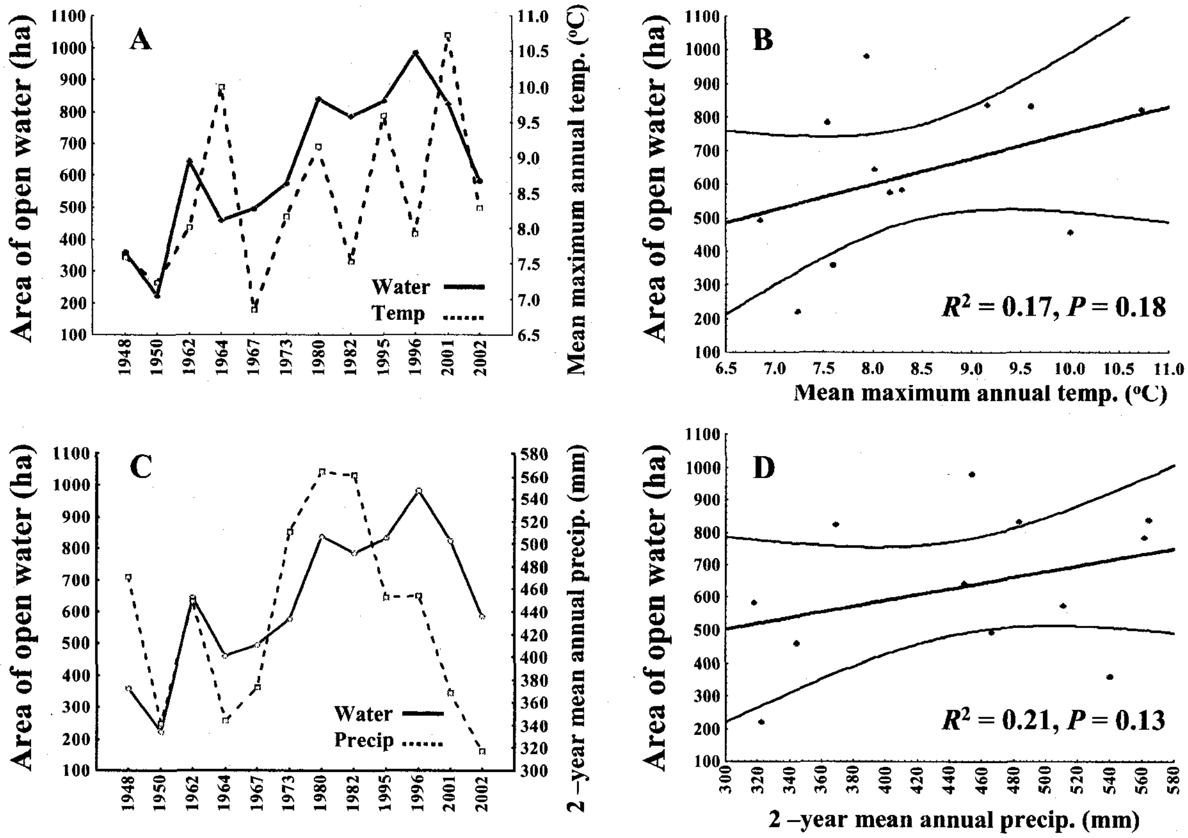

Figure 3.4. Relationship between the area of open water and climatic variables. Graph (**A**) shows the area of open water (solid line) and the mean maximum annual temperature (dashed lines) from 1948 to 2002 in Elk Island National Park; and the regression (**B**) between the area of open water (*Y*) and the mean maximum annual temperature (*X*) where $Y = 7.08 + 0.002X$. Graph (**C**) represents the area of open water (solid line) and the 2-year mean annual precipitation (dashed lines) from 1940 to 2002 in Elk Island National Park; and the regression (**D**) between the area of open water (*Y*) and 2-year mean annual precipitation (*X*) where $Y = 358.78 + 0.14X$. Outer lines represent 95% confidence limits. For graph C, precipitation is extended to 1940 to give a broader context to the drought year in 1950.

Beaver were not present in the study area between 1948 and 1950, but were present in 1962 (the next representative photos, Figure 3.3). They steadily increased in the area until reaching a peak in active beaver lodges in 1996 (348 active lodges). In 1950, the second driest year of the study period, there was 47% more precipitation (316.7 mm) than in 2002, the driest year on record (215.9 mm). In 1950, when beaver were not present, wetlands held 61% less open water (228.7 ha) than in 2002 when beaver were well established (593.90 ha, Figure 3.5).

When active beaver lodges were excluded from the analysis, the remaining variables (mean maximum annual temperature and mean 2-year precipitation) explained 38% of the variability in the area of open water in wetlands ($P = 0.12$). Mean maximum annual temperature was the strongest predictor in the model (relative Pratt index $d_j = 0.5546$) followed by mean 2-year precipitation (relative Pratt index $d_j = 0.4454$).

$$\textit{area of open water} = -720.80 + 0.51(\textit{mean max temp}) + 0.47(\textit{2YrPrecip}) + 197.86$$

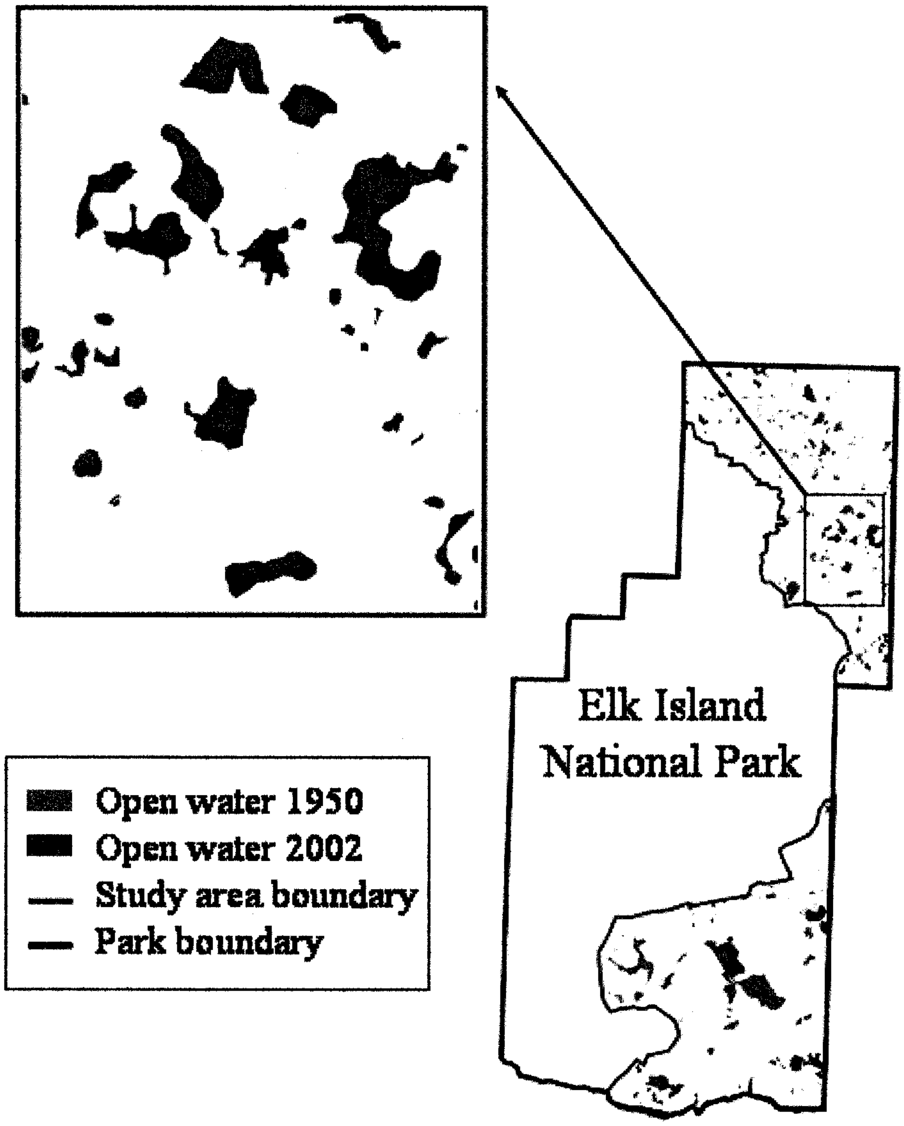

Figure 3.5. The area of open water in 2002 (red) overlaid with the area of open water in 1950 (green). There were no beaver present in the study area in 1950, but they were well established by 2002. The blue line represents the study area boundary and the black line indicates the park boundary.

For all other variables used in the initial analyses, only the variable representing all beaver lodges (active + inactive) had a significant effect on the area of open water in wetlands ($R^2 = 0.45$, $P = 0.017$, Table 3.2). Despite documented residual effects of abandoned beaver dams on water retention (Naiman et al. 1988), in this analysis inactive lodges explained only 29% of the variability in the area of open water in EINP and was not a significant result ($P = 0.07$, Table 3.2). Because the variable representing the number of active beaver lodges was a better predictor of the area of open water than the combined variable representing all beaver lodges, only the data for active lodges were used in the overall model. To show variations in lag time for precipitation 2-, 3-, and 5-year lags were included in the analyses because open water in wetlands might not respond instantly to precipitation events.

Table 3.2. Regression results for the variability in the area of open water (ha) predicted by individual climatic and beaver population variables for the period of 1948 to 2002 in Elk Island National Park, Canada. Values are for simple linear regression models that include only one predictor variable. Results area ranked by the variable's R^2 value.

Ranking	Explanatory variable	R^2-value	P-value
1	number of active beaver lodges	0.83	0.00004*
2	number of all beaver lodges (active + inactive)	0.45	0.02*
3	number of inactive beaver lodges	0.29	0.07
4	2-year total annual precipitation	0.21	0.13
5	total annual rainfall	0.18	0.67
6	mean maximum temperature	0.17	0.18
7	5-year total annual precipitation	0.14	0.23
8	hydrologic year (Nov. 1 to Oct 31)	0.14	0.23
9	3-year total annual precipitation	0.11	0.30
10	seasonal precipitation (3 months prior)	0.05	0.47
11	total annual precipitation	0.032	0.58
12	total annual snowfall	0.031	0.58
13	mean annual temperature	0.028	0.61
14	annual precipitation – potential evapotranspiration (PET)	0.02	0.70

When water areas for individual ponds were repeated measured over 4 years within the study period (1940, 1950, 1996, and 2001) relative to their beaver activity, there was a significant effect of year ($F_{2,237} = 28.5$, $P < 0.001$), beaver activity ($F_{1,79} = 6.53$, $P = 0.01$), and the interaction between year and beaver activity ($F_{3,237} = 6.54$, $P = 0.0003$). Ponds with active beaver colonies had more open water area than those same ponds without beaver in 1948 and 1950. The ponds that did not have active beaver colonies in them during any of the years (i.e., the 41 ponds measured in 1948, 1950, 1996, and 2001) also had less open water area than ponds with active beaver colonies ($F_{1,79} = 6.53$, $P = 0.01$, Figure 3.6). There was no difference in area of open water in any of the ponds measured in 1948 and 1950; however these ponds did have significantly less open water than both active and inactive ponds in 1996 and 2001($F_{1,322} = 43.52$, $P < 0.001$, Table 3.3).

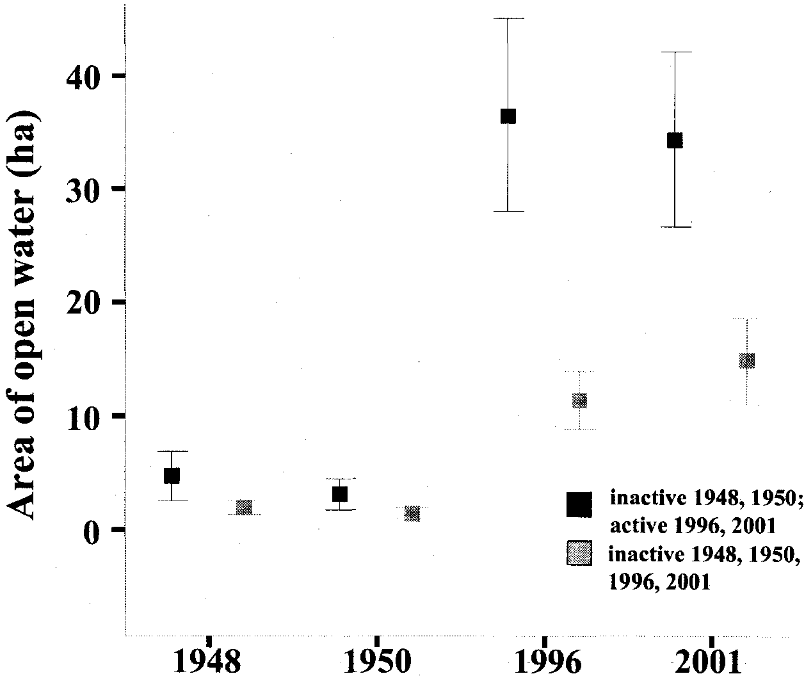

Figure 3.6. Mean are of open water for individual ponds measured in 1948, 1950, 1996, and 2001. Ponds were classified into 2 groups: 1) ponds that did not have beaver in them in 1948 and 1950, but did have active beaver colonies in 1996 and 2001 (black), and 2) ponds that did not have beaver in them in any of the four years (grey). Lines indicate ± 1.0 standard error of the mean.

Table 3.3. Least square means and standard error of the mean for the area of open water (ha) for individual lodges in 1948, 1950, 1996, and 2001.

Pond type	*N*	**1948**	**1950**	**1996**	**2001**
inactive 1948 and 1950 active 1996 and 2001	40	0.46 ± 0.21	0.31 ± 0.14	36.5 ± 0.09	34.4 ± 0.77
inactive all years	37	0.19 ± 0.07	0.13 ± 0.05	11.24 ± 0.25	14.8 ± 0.38

3.4 DISCUSSION

Rarely do we have the opportunity to examine long-term data where we can compare the effects of climate, beaver activity, and open water coverage in wetlands on the same scale. I determined that the presence of beaver increases open water in wetlands despite fluctuations in precipitation and temperature. Specifically, the presence of active beaver lodges accounted for over 80% of the variability in the area of open water in wetlands of EINP over a 54 year period. Although precipitation and temperature were a factor in the amount of open water area, their contributions were minor relative to those of beaver activities. Morainal ponds, such as those found in Elk Island National Park, likely respond quickly to heavy rainfall events as suggested by Ferone and Devito (2004) in their investigations of shallow peatland complexes in the boreal plains. Winter (1999) also proposed that local flow systems are more important than regional flow systems with morainal wetlands. The ponds in the study area are typically isolated ponds and "valleys" are better described as morainal depressions. EINP generally lacks the permanent streams or creeks examined in other studies where researchers have shown beaver to have significant influences on water resources (e.g., Naiman *et al.* 1988, Johnston and Naiman 1990 a, b, Westbrook *et al.* 2006).

A comparison of two of the driest years within the study period showed that even with 47% more precipitation in 1950 (the 2nd driest year during the study), the amount of open water in wetlands was 61% less than in 2002 (the driest year on record), when beaver were well-established on the landscape. These results confirm that beaver have an overwhelming influence on wetland creation and maintenance and can mitigate the effects of drought.

Because beaver are a semi-aquatic mammal, it could be argued that the relationship between the area of open water is correlative rather than causal. However, in all cases where beaver were absent from individual ponds in 1948, 1950, 1996, and 2001, water levels were significantly lower than in areas with active beaver colonies. The area of water in ponds that did not yet have beaver in them, but would in future years was also consistently lower prior to being colonized by beaver. I was unable to find any ponds that were consistently without beaver following recolonization of the park. It is possible that because of lag effects from the presence of abandoned dams and channels, inactive ponds in 1996 and 2001 retained significantly more open water than inactive ponds in both 1948 and 1950. This difference is despite the fact that 1996 and 2001 had less combined total precipitation than 1950 and 1948. Other studies have noted the continued effects of beaver on water resources even after the site has been abandoned (see Naiman *et al.* 1988, Westbrook *et al.* 2006) and it is possible that lag effects from high water also affected groundwater and surface water recharge in EINP, even during drought.

Climate change is a topic of increasing importance on both a global and local scale. The effects of a warming climate are anticipated in many sectors including forestry (Hogg and Bernier 2005, Breshears *et al.* 2005), agriculture (Smit and Skinner 2002), and resource management (Dawson *et al.* 2003, Johnson *et al.* 2005). Climate change is of particular concern within protected areas due to their role in conserving species at risk and associated habitats. An assessment of the potential effects of climate change on Canada's national parks predicted lower soil moistures and increased drought in prairie parks such as EINP, if predictions of current global circulation models (GCM) are accurate (Scott and Suffling 2000). The predicted loss of open water and increased water temperatures would have direct effects on fish, amphibian, and waterfowl populations and could potentially cause more northerly shifts both in vegetation and wildlife populations. Several studies predict biome shifts in forest and grassland ecosystems due to temperature increases predicted in GCMs (Scott and Suffling 2000, Camill and Clark 2000, Hogg and Bernier 2005).

My findings indicate that beaver could mitigate some of the adverse effects of climate change due to their ability to create and maintain areas of open water. Naiman *et al.* (1988) suggest that beaver impoundments have a high resistance to disturbance (e.g., flooding). I argue that this resistance extends to drought. During the drought of 2002, wetlands lacking active beaver lodges were visibly drier than those with beaver or became mudflats. During the height of the drought, many farmers were ranging their cattle into areas with active beaver impoundments to water their animals.

Despite their ability to maintain wetlands, beaver are not impervious to repeated or long-term droughts, which could compromise the survival of beaver colonies. During the drought of 2002, much of the activity around the lodges was spent digging channels in their receding impoundments to maintain critical access to resources and appropriate water depths at the food cache areas in front of their lodges. These caches must be accessible under the water for the duration of the winter for the colony to avoid starvation. I found that some colonies were able to over-winter with as little as 70 cm of water at their food caches. Others, whose food caches were completely frozen into the ice, died from either predation when they tried to escape their lodges in search of food or starvation inside their lodges. The number of beaver lodges in EINP decreased by approximately 7% from 1999 to 2002, some of which can be attributed directly to lack of access to food caches related to low water levels.

Despite fluctuating populations, early fossil records show that the family *Castoridae* have existed in North America since the early Oligocene (34-24 million years ago; Jenkins and Busher 1979) and have survived despite variable climate and hydrological conditions. In fact, beaver are known for their ability to strongly influence hydrology in areas where they are active (Naiman *et al.* 1988, 1986; Johnston and Naiman 1990b; Jones et al. 1994, Syphard and Garcia 2001), although most of these studies were done in riverine systems.

As with my study, both Johnston and Naiman (1990a,b) and Syphard and Garcia (2001) used historic aerial photography to study the influence of beaver activities over a period of 46 and 41 years, respectively. Johnston and Naiman (1990a) found that pond sites increased from 71 to 835 between 1940 and 1986 in northern Minnesota, USA. In the Chickahominy River study, Syphard and Garcia (2001) found that, although beaver only accounted for 1% of wetland gain, their activities accounted for 23% of change in wetland types from 1953 to 1994. In EINP, the area of open water increased from 365 ha in 1948 to a high of 991 ha in 1996 when beaver populations reached their peak. Current levels are somewhat lower due to the ongoing drought (593.9 ha in 2002).

This study differs from other long-term studies in that I was able to examine 12 years of data over a 54-year period, while the other studies were only able to obtain data covering 2 to 6 years of their study period (Johnston and Naiman 1990a,b, Syphard and Garcia 2001). I was also able to use beaver census data that had been mapped at the time of census, while other studies relied on indications of beaver activity from aerial photography. In addition, long-term climate data were readily available and included temperature and precipitation extremes.

Analyses were limited to 12 years of data due to either a lack of photographic coverage when data on beaver were available, or a lack of beaver census data when aerial photographs existed. In addition, no photographic coverage was available for the 1930's; a period when drought was extreme in the area, thus limiting the number of extremely dry years I could examine. The 2002 drought was drier than the drought of the "Dirty '30's" and because current annual precipitation levels continue to be low, its duration may also be comparable to the 1930's. Due to a lack of hydrological data for the park, I was unable to assess possible hydrologic effects on water area in this study. Future hydrologic studies in the area would not only help assess the effects of beaver on groundwater, but also the effects of extreme climatic events such as drought on the overall water resources in the park.

Given the recent predictions of warming and drying trends for the PPR and the southern boreal regions in North America, beaver will likely play an important role in maintaining open water and mitigating the impact of drought. Considering their role as a keystone species in wetlands, their positive impact on biodiversity alone is a significant benefit. Increased removal of wetlands and beaver from the landscape for urban, industrial and agricultural demands warrants further investigation. As with drought, fire is also expected to increase with predicted drying trends and future research that incorporates fire into the model would be warranted.

3.5 CONCLUSIONS

Given their ability to create and maintain areas of open water wetlands, the removal of beaver from aquatic systems should be recognized as a wetland disturbance equivalent to in-filling, groundwater withdrawal, and other commonly cited wetland disturbances (Mitsch and Gosselink 2000, Zedler 2000). Although beaver have recovered in much of their former range after their near extinction at the start of the 20th century, they are often in conflict with human activities and are subject to extensive management. Alternatives to direct removal of beaver colonies have been suggested by Lisle (2003) in his design and use of flow devices. In habitats where potential conflicts are minimal, but the benefits of wetland restoration is high, beaver should be seen as a natural alternative to wetland restoration and enhancement due to their ability to mitigate extreme weather events such as drought.

Acknowledgments

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4.0 RIPARIAN PLANT COMMUNITY RESPONSE TO HERBIVORY BY BEAVER AND UNGULATES

4.1 INTRODUCTION

The boreal-mixed wood forests of North America are home to several species of herbivores and present an excellent opportunity to examine the effects of multiple herbivores on plant community composition and structure. Ungulates and beaver (*Castor canadensis*) forage extensively on terrestrial and emergent vegetation in riparian zones. Despite distinctly different foraging behaviours, they have the potential to transform vegetation communities due to shared resource requirements.

Beaver are central place foragers (Orians and Pearson 1979), browsing in a concentric zone around their ponds (Johnston and Naiman 1987), which facilitates their ability to return with cut stems prior to processing them. Unlike many other mammalian herbivores, beaver cut entire stems and remove them from their original location; a practice that can result in the production of basal sprouts (McGinley and Whitham 1985, Baker *et al.* 2005), thus replacing the original stem with juvenile growth forms (Basey *et al.* 1990). Their removal of woody plants can increase species diversity, decrease canopy cover, alter forest composition (Donker and Fryxell 1999, Rosell *et al.* 2005), increase net primary productivity of existing non-preferred woody species, and reduce the density of trees (Barnes and Dibble 1988). These effects are often confined to areas within 30 to 100 m from the pond edge (Skinner 1984, Barnes and Dibble 1988, Chapter 5).

Beaver occupy a transitional niche, utilizing both terrestrial and aquatic resources. Ungulates, such as moose, have similar foraging patterns. Yet, the impact of foraging along the gradient from aquatic to terrestrial habitats is seldom examined. Along with woody species, beaver also uproot water lily rhizomes (*Nuphar* spp.) and include them in their winter food caches (Ray *et al.* 2001). Although very little research exists regarding the use of non-woody vegetation by beaver in riparian areas, Belovsky (1984) found that beaver ate aquatic macrophytes 4.9% of the time beaver were observed foraging. Sedge and herbaceous dicot species are also eaten throughout the summer months. The effects of herbivory by beaver on aquatic and herbaceous plants is difficult to quantify, however the very presence of aquatic vegetation is often associated with beaver activities such as impounding water and creating wetlands (Ray *et al.* 2001).

Through their creation of wetlands, beaver establish riparian habitats that are used by many other species. Ungulates such as moose (*Alces alces*), elk (*Cervus elaphus*), bison (*Bison bison*), whitetail deer (*Odocoileus virginiana*), and mule deer (*O. hemionus*) use riparian areas for forage and access to water. As with beaver, the effects of ungulates on woody vegetation have been well documented. Ungulates generally browse tips of woody vegetation and remove leaves and new growth, rather than removing entire stems like beaver do. Primary winter forage for elk, deer, and moose include willow (*Salix* spp.), trembling aspen (*Populus tremuloides*), and red-osier dogwood (*Cornus stolinifera*). In Elk Island National Park, beaked hazel (*Corylus cornuta*), rose (*Rosa* spp.) and service berry (*Amelanchier alnifolia*) are also commonly utilized forage species (Blyth and Hudson 1987, Best *et al.* 2003) When exposed to light or moderate use by ungulates, plants can elevate their annual net primary production in the form of compensatory growth (McNaughton 1983, Hobbs 1996). Fecal deposits also increase nitrogen inputs into the soil, thereby indirectly influencing plant growth and available nutrients (Hobbs 1996). As with beaver, ungulates can modify vegetation composition, increase patch dynamics, and alter community structure. In areas where ungulate herbivory is high or very high, compensatory growth is not evident and browsing can substantially decrease shrub heights and biomass (Snyder and Janke 1976, Nietvelt 2001, Baker *et al.* 2005). Browsing by deer can also reduce regeneration of favored species of shrubs and herbaceous dicots (Warner and Cushman 2002, Rooney and Waller 2003). Some authors in other areas attribute declines in aspen forest and willow to high numbers of elk (White *et al.* 1998, White *et al.* 2003, Baker *et al.* 2005).

Although many species of vegetation have evolved with herbivory, browsing and grazing activities by multiple herbivores can still introduce a significant disturbance into plant communities. The combined effect of differing foraging activities is an important consideration in maintaining diversity and ecosystem function in many areas. Given its diverse plant and wildlife communities, the Beaver Hills region of east-central Alberta provides an excellent environment to examine the effects of varying levels of herbivory on plant community composition and structure. Elk Island National Park, in the heart of the Beaver Hills, is an area with some of the highest ungulate densities in North America (Blyth and Hudson 1987) and well-established beaver populations. In turn, it is surrounded by private and protected areas that support beaver populations and significantly lower densities of ungulates.

There is little research on the combined impacts of foraging activities by ungulates and beaver on riparian vegetation. Many of the studies on foraging by ungulates or beaver focus on key forage species such as black cottonwood (*Populus trichocarpa*), willow, and aspen (Singer *et al.* 1994, Case and Kauffman 1997, Donkor and Fryxell 1999, Martell *et al.* 2006). Very few examine the direct effects of these large herbivores on emergent vegetation, and almost none acknowledge the combined effects of other mammalian herbivores naturally present in the study area and the species of interest (e.g., beaver, moose, deer, or elk). Although many studies compare vegetation response under the extremes of herbivory (e.g., vegetation in exclosures *vs.* vegetation exposed to high levels of herbivory), few of these studies address impacts relative to more varied (and typical) densities of beaver or ungulates. Elk Island National Park and the surrounding area provide a unique system that allowed for the study of the impact of varying levels of herbivory by multiple herbivores on riparian vegetation. There were areas with higher and lower densities of ungulates and comparable beaver populations, represented in adjacent, but isolated, managed areas.

The objective of this study was to examine how 4 different combinations of ungulate and beaver presence affected the composition and structure of riparian vegetation. I predicted that 1) vegetation cover would decrease in areas with high levels of beaver and ungulate densities, 2) shrub heights would be lowest in areas with the highest levels of beaver and ungulate densities, 3) as suggested by the intermediate disturbance hypothesis (Connell 1978) I predicted that species diversity would be highest at intermediate levels of herbivory (assumed to be areas lacking either beaver or high densities of ungulates), and that 4) species diversity would be lowest at sites with both beaver and high ungulate densities.

4.2 STUDY SITE AND METHODS

Study area

This study was conducted in the Beaver Hills region of east-central Alberta, Canada during the summers of 2001 and 2002. The area is also known as the Cooking Lake Moraine and includes Elk Island National Park (EINP), the Blackfoot/Cooking Lake Recreation Area and several smaller protected areas and private lands (Figure 4.1). The Beaver Hills are in the southern extent of the boreal mixed-wood forest (Achuff 1994) and represent a transition zone between the boreal forests to the north and the Aspen Parkland subregion to the south. The morainal topography creates a knob and kettle terrain, which in turn results in numerous wetlands and areas of open water. The wetlands of the Beaver Hills function as a regional groundwater recharge area (Mitchell and Prepas 1990) and provide important habitat to many species of plants and wildlife.

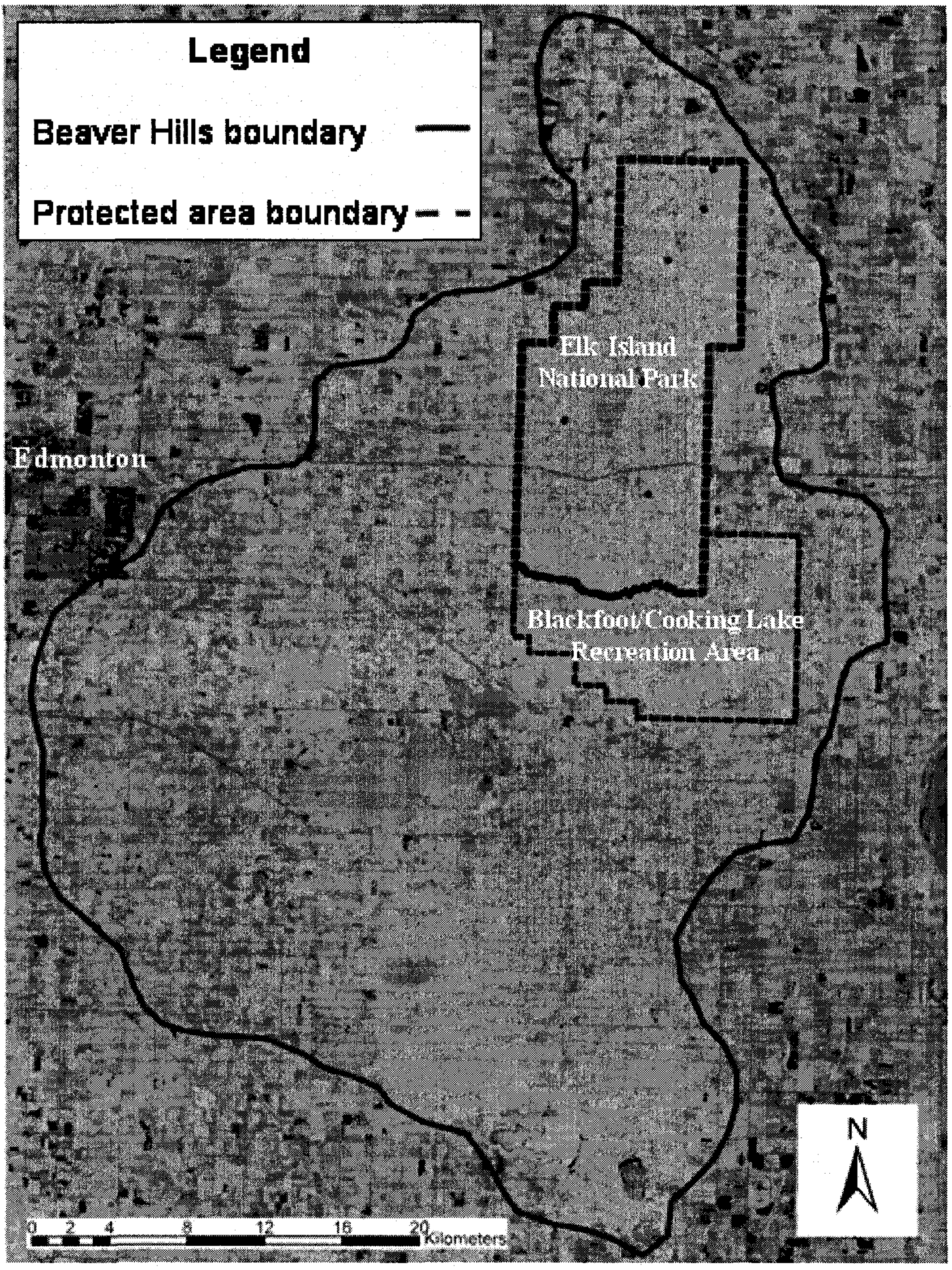

Figure 4.1. The Beaver Hills Region of east-central Alberta, Canada.

Poplar forests (*Populus tremuloides* and *P. balsamifera*) comprise the dominant upland vegetation, while white and black spruce (*Picea glauca* and *P. mariana*) occur in pockets throughout the area. Beaked hazel (*Corylus cornuta*) is the prominent shrub species, although willow (*Salix* spp.), rose (*Rosa acicularis* and *R. woodsii*), serviceberry (*Amelanchier alnifolia*), cherry (*Prunus virginiana* and *P. pennsylvanica*), red-osier dogwood (*Cornus stolonifera*), soapberry (*Shepherdia canadensis*), and snowberry (*Symphoricarpos albus* and *S. occidentalis*) are also common. Wild sarsaparilla (*Aralia nudicaulis*) and stinging nettle (*Urtica dioica*) are abundant herbaceous dicots at many sites. Major grass and sedge species include marsh reed grass (*Calamagrostis canadensis*), Kentucky bluegrass (*Poa pratensis*), creeping spike rush (*Eriophorum palustris*) and beaked sedge (*Carex utriculata*). Grey Luvisol soils dominate the upland areas while Humic Luvic and Rego Gleysols are present in moister areas (Crown 1977).

Beaver are found throughout the region, while the highest concentrations of ungulates are within Elk Island National Park. The park is completely fenced and, other than coyotes, lacks any resident species of large predators. This scenario has resulted in some of the highest concentrations of ungulates in North America (Blyth and Hudson 1987). Although both wood bison (*Bison bison athabascae*) and plains bison (*B. b. bison*) are free roaming inside EINP, there are no wild populations immediately outside the park. Elk, moose, whitetail deer, and mule deer occur within the park and, where suitable habitat exists, throughout the Beaver Hills.

The management of ungulate populations within EINP has evolved throughout the park's history. Ungulate populations peaked in the early 1990's after the park adopted an Ecological Carrying Capacity management model (Blyth and Hudson 1987). Although Parks Canada still removed some animals, populations were allowed to regulate themselves relative to natural carrying capacity levels within EINP. The park has since returned to an active live culling program to reduce the population. Park staff translocate elk and bison from the park every 2 years, to maintain a population density of ungulates in the park of approximately 13 ungulates per km^2.

Study design

To allow us to examine the effects of four different levels of beaver and ungulate herbivory, I used a stratified random sampling design to select 5 ponds for each of the 4 categories: 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). These four categories were referred to as "herbivory treatments". Each of the four herbivory treatments was classified as being either inside EINP or outside, and data were later analyzed using a nested design.

Staff at EINP have collected data on beaver lodge occupancy since beaver were successfully reintroduced in 1941. Since 1989 individual lodges were given unique codes that allowed their occupancy status to be consistently tracked over time. Using these data, I was able to determine beaver activity at individual sites within EINP. Outside the park I relied on local knowledge and aerial photo records to establish beaver activity at individual sites. A site was classified as "low beaver" if it had not been previously occupied by beaver over a >5 year period and as "high beaver" if the site had been occupied throughout the same period. Each site was then assessed to confirm the presence or absence of beaver at the pond by noting signs of current activity (e.g., cut stems, scent mounds, beaver presence, lodge maintenance). All sites were in areas that had not been burned by prescribed fire or wildfire in the history of the park to avoid the confounding effects of fire on vegetation response described in other studies (Vinton *et al.* 1993, Hobbs 1996, Bork *et al.* 1997).

I classified any pond site outside EINP as "low ungulate" relative to densities of ungulate pellet groups inside the park. During this study, there were no cattle grazing at any of these sites. Any pond within the park was classified as "high ungulate". This initial decision was based on findings in Blyth and Hudson (1987) and more recent work by Bork *et al.* (1997). To test this assumption, my field crew and I then conducted pellet group counts of all ungulate species to determine relative ungulate densities at each of the 20 pond sites (Figure 4.2). Pellet group surveys were conducted along four 2-m wide transects that extended 100 m from the pond edge at each of the locations. These transects were placed as close to the 4 cardinal directions as possible and were later used for corresponding vegetation surveys. Pellet groups were identified to species for all but deer, which were identified only to genus. All species were combined to determine an overall densities of ungulate pellet groups per m^2. Annual aerial census counts of ungulates in EINP determined ungulate densities to be approximately 13 ungulates per km^2. Similar data are not available for areas immediately adjacent to the park. Although some ungulates are categorized as browsers and others as grazers, I observed all species eating woody and non-woody vegetation as seasons changed. All ungulates were therefore included in my assessment of vegetation impacts.

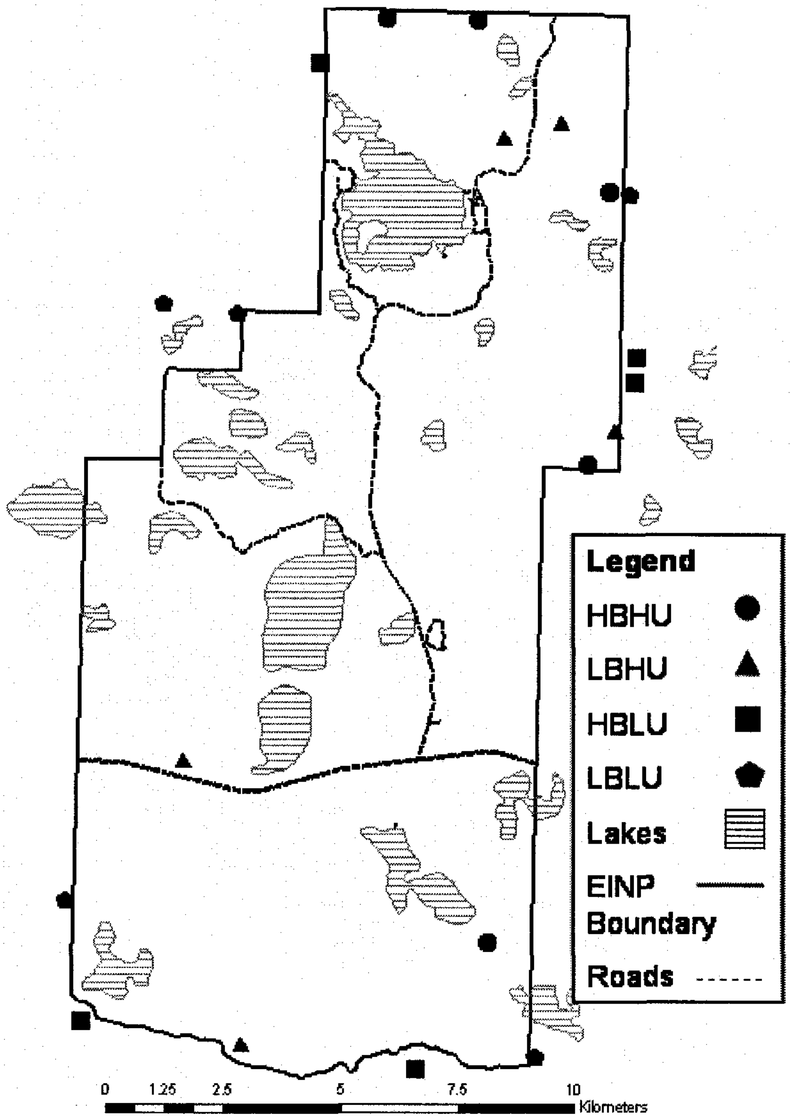

Figure 4.2. Study pond locations indicating 4 levels of herbivory relative to beaver and ungulate presence. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU).

Vegetation sampling

Using the same transects established for the pellet group surveys, my field crew and I sampled 12 plots (1 m^2) in the riparian zone from the pond (emergent) edge to the forested upland. Six plots were randomly selected within the lower sections of the transect that was dominated by shrubs, and 6 plots were selected in the treed areas that were generally further from the pond edge. The distinction between these 2 areas was not always apparent. I also randomly sampled six 1-m^2 plots in the emergent zone on each transect. All woody and aquatic plants were then identified to species. To facilitate data collection, other vegetation types were categorized as a herbaceous dicot, grass, sedge, moss, or horsetail. *P. tremuloides* and *P. balsamifera* were classified only as "*Populus* sp." for the analysis of shrubs due to the difficulty in distinguishing some of the heavily browsed plants. Although most other plants were identified to species; the broader classification (e.g., herbaceous dicot, grass) was used for expediency as the initial focus was mainly on the obvious forage species shared by both beaver and ungulates.

At all plots I estimated the percent cover within 1-m^2 plots for all plants (except trees), coarse woody debris (CWD), and unvegetated ground. Plots were used to measure canopy cover and stem height rather than a line intercept method to facilitate the measurement of canopy cover for smaller vegetation such as shrubs and herbaceous plants (Bork *et al.* 1997) on both terrestrial and semi-aquatic sites. Because the long-term effects of browsing are more apparent on woody plants, we visually estimated the overall percent cover of the area of the plot by species, average shrub height (cm), percent of stems browsed, and browse severity for those species following similar methods used in Yellowstone and Banff National Parks (Singer *et al.* 1994, Nietvelt 2001). If a shrub was browsed, the browser (ungulate or beaver) was noted. Current annual growth (CAG) was not measured as we lacked data for a retrospective comparison and required a rapid assessment technique that could be used to measure hundreds of plants along all 4 transects at all 20 sites. For our study a stem constitutes an axis off of the main shoot of a plant and is the structure that bears the leaves flowers and fruit. Estimates were recorded for the basal cover of trees rather than canopy cover. The percent of stems browsed for each shrub species was a categorical variable (0%, 1 – 5%, 5 – 20%, 20 – 50%, and 50 – 100%). For statistical analysis I then used a numerical classification to represent these categories, with "0" representing 0% browsed progressing to "4" to represent 50 – 100% browsed. Where possible, I also determined whether the shrub was browsed by beaver or an ungulate. I was not able to differentiate which ungulate species had browsed a particular plant.

Browse severity was a visual assessment of the morphological presentation of a stem or group of stems in the context of ungulate browsing (Figure 4.3). A stem that was browsed, but showed healthy leader growth and no dead wood was classed as "low" browse severity. A branch with some secondary branches and a small amount of dead wood was considered "medium" browse severity, while branch with several secondary branches (excessive hedging) and more than 50% dead material was given a "high" browse severity rating. As with the percent of stems browsed, I applied a numerical classification to these ratings, with "0" for "none" progressing to "3" for "high" browse severity.

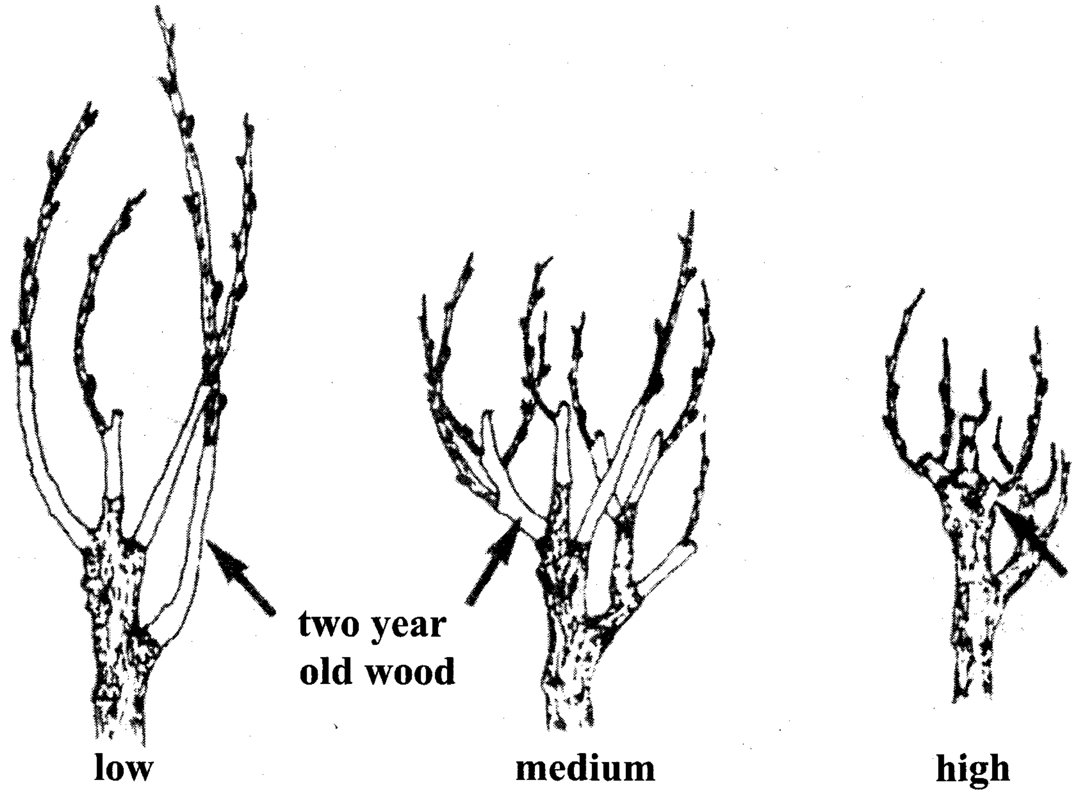

Figure 4.3. Browse severity guide for rating stems relative to ungulate herbivory (botanical illustration courtesy of Parks Canada).

I then took the product of the percent browsed and browse severity values to calculate a browse impact index (BI index). For example, a stem or group of stems that were 20 – 50% browsed (3 on the numerical scale) with a high browse severity (3 on the numerical scale) would have a browse impact index of 9. This index was used to assess initial site classifications (e.g., LBLU) and the effectiveness of pellet group counts in determining relative ungulate densities. It was also used to quantify the effects of browsing on various plant species in each of the 4 different herbivory treatments.

Data analysis

All data sets were analyzed using a mixed linear model that accommodated a double-nested analysis of variance (ANOVA) in SPSS (SPSS Inc. 2002). This procedure allows for the analysis of fixed and random factors and for experimental units (e.g., pond sites, transects) to be nested in a hierarchical order. In this study, each of the four transects were nested within pond site, which was then nested within one of the 4 different levels of beaver and ungulate herbivory (i.e., HBHU, LBHU, HBLU, and LBLU). Herbivory treatment and transect were considered fixed effects while individual lodges within an herbivory treatment were treated as a random effects. All results were considered significant at $\alpha = 0.05$.

To determine whether my initial assumption of ungulate densities inside EINP and outside the park was accurate, I used a nested ANOVA, to compare whether the pellet group data and the browse impact indices differed between each herbivory treatment. Then, to measure the strength of correlation between pellet counts and the browse impact indices, I calculated a Pearson product-moment correlation (SPSS Inc. 2002).

To assess the effects of differing combinations of beaver and ungulate densities on the composition of the vegetation community, I analyzed the total percent cover of all 10 cover classes (emergent, CWD, herbaceous dicots, grass, horsetail, moss, sedge, shrub, trees, and unvegetated) and the average percent cover of all aquatic and woody species. In addition the heights of the shrub layers were compared to assess structural differences between sites. Finally, I used the Shannon Index (Shannon 1948) to estimate diversity for the woody and emergent plant communities and compared the resultant diversity indices to the four herbivory treatments.

4.3 RESULTS

Pellet group counts and browse intensity

Pellet group counts were highest at sites classified *a priori* as "high ungulate" (HBHU and LBHU) and lowest at the sites classified as "low ungulate" (LBLU, HBLU; $F = 91.6$, $df = 3, 16$, $P = 0.01$). All "high ungulate" sites were inside EINP and all "low ungulate" sites were outside the park (Figure 4.4A). Pellet groups for elk were 6 times higher inside EINP than outside, while there were 3 times more moose pellet groups outside the park than inside. Despite the higher incidence of moose pellets outside EINP, the densities of ungulate pellet groups in the park were still almost 3 times higher than outside.

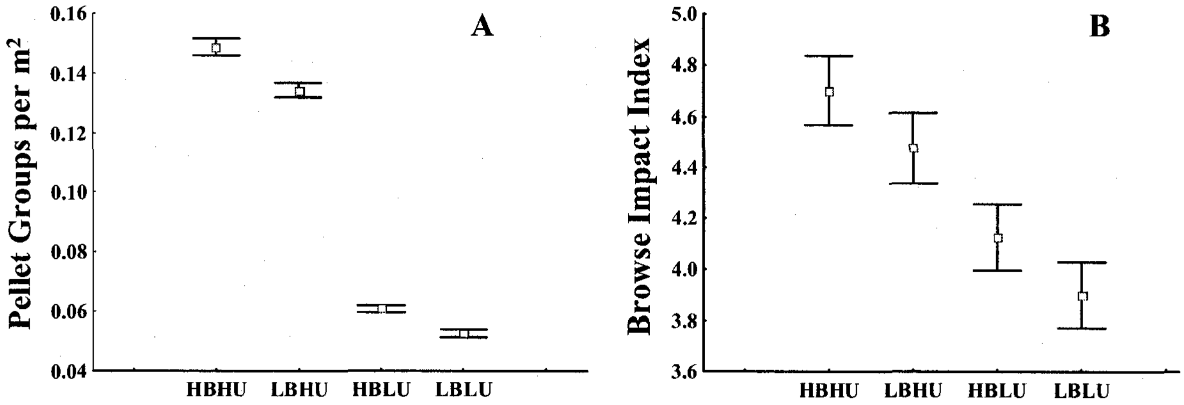

Figure 4.4. Pellet groups per m^2 of all species of ungulates (A) and Browse Impact Index values (B) relative to 4 levels of beaver and ungulate presence. Values given are means ± standard error. Browse Impact Index is derived from the product of the % of stems browsed X browse severity rating. The percent of stems browsed for each shrub species (0%, 0 – 5%, 5 – 20%, 20 – 50%, and 50 – 100%) was represented by a numerical classification ranging from "0" representing 0% browsed to "4" to represent 50 – 100% browsed. Browse severity ranged from "none", "low, "medium" and "high" with "0" representing "none" progressing to "3" for "high".

Although the BI index for shrubs did not follow the same pattern as pellet group counts exactly (Figure 4.4B), the order from highest to lowest was the same. As with the pellet group data, the highest and second highest BI index values were in the HBHU and LBHU areas respectively, and the lowest values were in the LBLU and HBLU sites ($F = 4.01$, $df = 1, 3497$, $P = 0.007$). There was a weak, but significant correlation between pellet counts and BI index values ($R = 0.05$, $P = 0.003$). Both measures of relative ungulate use of the sites confirmed my original assumption that sites within the park had significantly higher ungulate densities than sites outside EINP and that browse effects were more apparent inside the park.

Vegetation response

All species of shrubs were browsed to some degree and of these shrubs, 91 % were eaten exclusively by ungulates. Approximately 6% of shrubs were browsed by both beaver and ungulates: only 3% were browsed solely by beaver (Hood and Bayley, unpublished data). Snowshoe hare (*Lepus americanus*) are uncommon inside the park, but localized pellet groups were found on some sites outside the park. Certain shrub species exhibited less dramatic responses than others to higher levels of ungulate herbivory (Table 4.1). *Corylus cornuta* was heavily browsed in areas of high ungulate densities, regardless of the presence or absence of beaver. However percent cover was higher in high ungulate areas. *Prunus virginiana* was highly browsed in all sites except in those categorized as HBLU, while *Salix* spp. had the highest browse impact indices at sites with both beaver and high ungulates (HBHU). Those shrub species appeared less resistant to high ungulate herbivory and, for *Salix*, both beaver and ungulates. Browse impacts for other species of shrubs were not significantly different between treatments. A list of all species can be found in the Appendix.

Table 4.1. Results of mixed linear model nested ANOVA for differences in pellet group counts and browse impact indices with four different levels of beaver and ungulate herbivory. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). For individual variables, *P*-values at $\alpha = 0.05$ are statistically significant.

Response variable	*F*	*df*	*P*	Site comparisons
Pellet groups	4.89	3, 16	0.013	HBHU and LBHU > HBLU and LBLU
<u>Browse impact index</u>				
Shrubs (all species)	4.01	3, 3497	0.007	HBHU and LBHU > HBLU and LBLU
Corylus cornuta	34.02	3, 378	<0.001	HBHU and LBHU > HBLU and LBLU
Prunus virginiana	4.02	3, 62	0.011	HBLU < HBHU, LBHU, and LBLU
Salix spp.	4.07	3, 70	0.019	LBHU > than HBHU, HBLU, and LBLU

Among the 10 cover classes and several species of vegetation specifically examined, there were two distinct trends relative to percent cover and height of vegetation within the study sites: 1) depressed shrub heights for most shrubs and less percent cover of various vegetation classes (Figure 4.5) in areas with more ungulates regardless of the presence of beaver (HBHU and LBHU) and, 2) a dramatic increase in shrub heights and percent cover (Figure 4.6) in sites with low beaver and ungulate densities (LBLU). Percent cover was lowest for emergent vegetation and herbaceous dicots in areas with higher ungulate densities and, along with shrub cover, highest in LBLU areas (Table 4.2, $P < 0.01$). Heights of *Populus* shrubs and *Rosa acicularis* were significantly shorter at HBHU ungulate sites (Table 4.3, $P < 0.01$). Percent cover of *Salix* spp. and *Viburnum edule* increased significantly at LBLU sites (Table 4.2, $P < 0.01$). In areas with lower ungulate densities and no beaver (LBLU) *Salix* was over 4 times taller than in areas with HBHU. *Amelanchier alnifolia* only grew to tree height in areas with low ungulate herbivory (HBLU and LBLU), which were all outside of EINP.

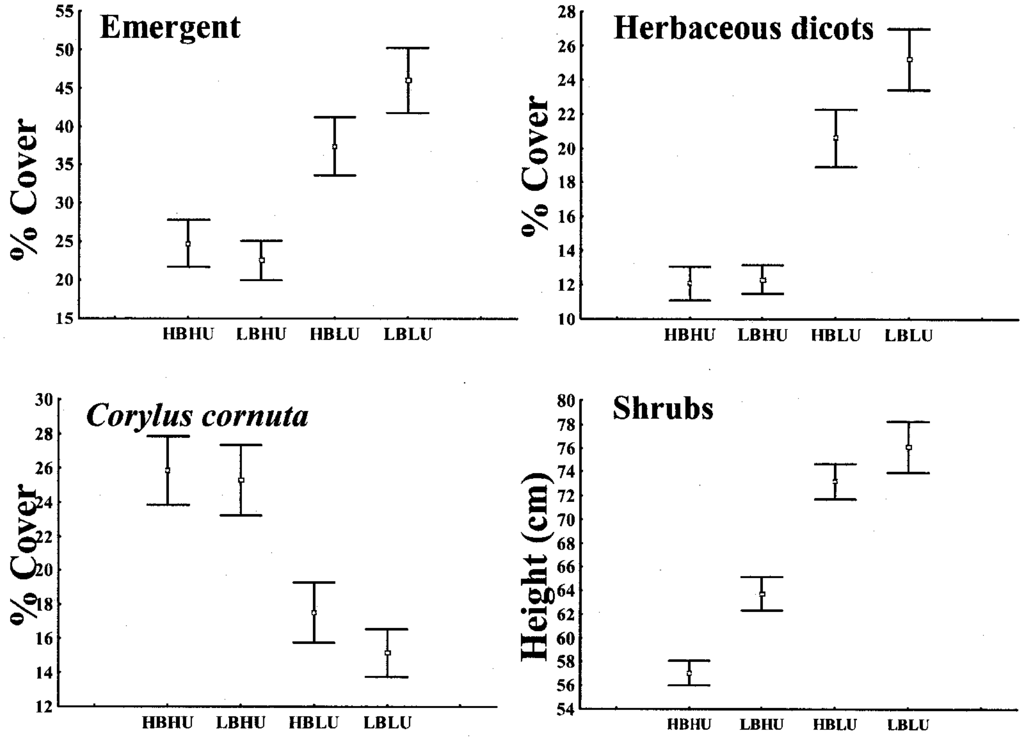

Figure 4.5. Effects of ungulate and beaver herbivory treatments on mean height of shrubs and percent cover of emergent vegetation, herbaceous dicots, trees, and *Corylus cornuta* relative to herbivory treatments. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). Vertical lines represent standard errors.

Table 4.2. Results of mixed linear model nested ANOVA testing response of vegetation cover and average heights under four different levels of beaver and ungulate herbivory. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). For individual variables, *P*-values at α = 0.05 are statistically significant. ND = no difference.

Response variable	*F*	*df*	*P*	Site comparisons
Percent cover by cover class				
Aquatic vegetation	4.66	3, 213	0.004	LBLU > LBHU
Coarse woody debris	1.46	3, 618	0.221	ND
Herbaceous dicots	14.56	3, 719	< 0.001	HBHU and LBHU < HBLU and LBLU
Grass	1.99	3, 823	0.113	ND
Horsetail	0.32	3, 32	0.812	ND
Moss	0.72	3, 59	0.544	ND
Sedge	25.39	3, 248	< 0.001	LBLU < HBHU and LBHU
Shrub	1.56	3, 896	0.197	ND
Trees	6.76	3, 41	0.001	HBHU and LBHU > HBLU and LBLU
Unvegetated	4.69	3, 530	0.003	LBHU < HBHU, HBLU, and LBLU
Shrub heights				
All species	35.60	3, 3442	< 0.001	HBHU and LBHU < HBLU and LBLU
Amelanchier alnifolia	1.44	3, 207	< 0.001	HBHU and LBHU < HBLU and LBLU
Betula papyrifera	6.15	3, 5	0.039	HBLU > HBHU, LBHU, and LBLU
Cornus stolonifera	1.39	3, 33	0.263	ND
Corylus cornuta	16.61	3, 368	< 0.001	HBHU and LBHU < HBLU and LBLU
Populus spp.	4.36	3, 292	0.006	HBHU < LBHU, HBLU, and LBLU
Prunus pensylvanica	1.33	3, 36	0.28	ND
Prunus virginiana	5.79	3, 62	0.001	LBLU > HBHU, LBHU, and HBLU
Rosa acicularis	17.37	3, 500	< 0.001	HBHU < LBHU, HBLU, and LBLU; HBLU > HBHU, LBHU, and LBLU
Rubus idaeus	3.50	3, 357	0.016	HBHU < LBLU
Salix spp.	1.96	3, 69	0.012	LHLU > HBHU, LBHU, and HBLU
Shepherdia canadensis	0.27	3, 31	0.85	ND
Symphoricarpos albus	4.58	3, 271	0.004	LBLU < HBHU and HBLU
Symphoricarpos occidentalis	3.86	3, 85	0.012	HBLU > LBHU
Viburnum edule	1.07	3, 121	0.364	ND
Viburnum opulus	2.95	3, 21	0.056	ND
Percent cover by species				
Amelanchier alnifolia	2.12	3, 209	0.098	ND
Betula papyrifera	1.59	3, 7	0.277	ND
Cornus stolonifera	1.74	3, 34	0.0177	ND
Corylus cornuta	4.99	3, 378	0.002	HBHU and LBHU > HBLU and LBLU
Populus spp. (shrubs)	2.23	3, 324	0.84	ND
Populus spp. (trees)	8.55	3, 33	< 0.001	LBHU > HBHU, HBLU and LBLU
Prunus pensylvanica	0.11	3, 36	0.952	ND
Prunus virginiana	1.85	3, 63	0.147	ND
Rosa acicularis	3.08	3, 515	0.027	HBLU > HBHU
Rubus idaeus	4.07	3, 377	0.007	HBLU > HBHU
Salix spp.	5.89	3, 98	0.001	LBLU > HBHU, HBLU, and LBHU
Shepherdia canadensis	1.36	3, 36	0.271	ND
Symphoricarpos albus	2.50	3, 277	0.06	ND
Symphoricarpos occidentalis	1.14	3, 94	0.338	ND
Typha latifolia	5.20	3, 159	0.002	LBHU < HBLU and LBLU
Viburnum edule	4.39	3, 126	0.006	LBLU > HBHU, HBLU, and LBHU
Viburnum opulus	3.19	3, 21	0.045	LBLU > LBHU

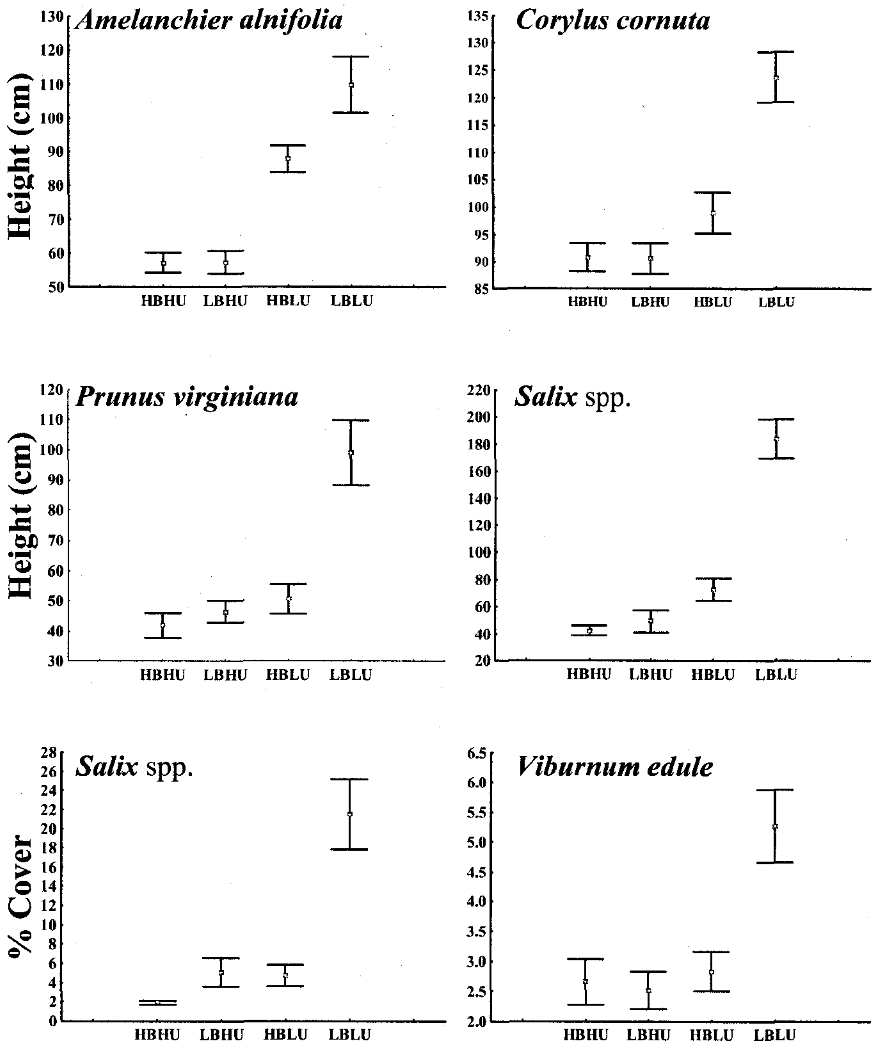

Figure 4.6. Effects of lower ungulate and beaver herbivory on mean heights of *A. alnifolia*, *C. cornuta*, *P. virginiana*, and *Salix* spp. and percent cover of *Salix* spp. and *V. edule* relative to herbivory treatments. These five species of shrubs increased in height and/or cover in areas with lower ungulate densities and no beaver. Significant differences are found in Table 4.2. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). Vertical lines represent standard errors.

Table 4.3. Mean heights (with SE in parenthesis) of shrubs subject to four different levels of beaver and ungulate herbivory. Heights are in centimeters. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU).

Species	HBHU	HBLU	LBHU	LBLU
All species combined	57.06 (1.12)	73.22 (1.56)	63.73 (1.47)	76.08 (2.27)
Amelanchier alnifolia	57.22 (3.16)	87.87 (4.14)	57.31 (3.54)	109.83 (8.87)
Betula papyrifera	73.17 (16.33)	218.50 (41.50)	92.71 (18.54)	33.50 (9.5)
Cornus stolonifera	55.07 (5.97)	62.63 (7.01)	84.71 (6.77)	68.17 (9.40)
Corylus cornuta	90.8 (2.79)	98.95 (3.94)	90.61 (3.01)	123.74 (4.89)
Populus spp.	82.02 (5.33)	113.98 (7.12)	111.16 (8.34)	108.58 (10.46)
Prunus pensylvanica	53.67 (4.81)	73.14 (18.97)	45.18 (4.36)	61.75 (10.09)
Prunus virginiana	41.96 (4.38)	50.64 (5.04)	46.37 (3.84)	99.04 (11.32)
Rosa acicularis	46.04 (1.62)	67.48 (1.94)	56.99 (2.38)	56.19 (2.70)
Rubus idaeus	49.46 (1.84)	60.14 (2.50)	55.00 (2.64)	49.68 (2.75)
Salix spp.	42.52 (3.68)	72.95 (8.54)	49.29 (8.61)	183.92 (14.96)
Shepherdia canadensis	92.57 (11.75)	89.00 (6.26)	81.20 (7.32)	84.57 (14.33)
Symphoricarpos albus	30.35 (0.96)	30.67 (1.11)	29.10 (1.31)	27.41 (1.13)
Symphoricarpos occidentalis	44.60 (3.68)	50.80 (3.40)	36.31 (2.45)	43.73 (3.07)
Viburnum edule	40.66 (4.28)	49.32 (3.95)	44.77 (4.70)	49.71 (3.04)
Viburnum opulus	37.88 (5.77)	62.00 (7.49)	50.96 (6.18)	63.80 (6.53)

At all sites, trembling aspen (*Populus tremuloides*) was the dominant tree species, however, I found that aspen density was highest in areas with no beaver but high densities of ungulates (LBHU; Table 4.4). When comparing all herbivory treatments, the presence of beaver and high densities of ungulates appeared to decrease height of aspen shrubs. Although sample sizes were small, other species of trees responded more dramatically than did aspen. In areas with higher densities of ungulates, mature forms of *Amelanchier alnifolia*, *Prunus virginiana*, and *Salix* spp. rarely grew to tree height (> 3 m) or were eliminated completely (Table 4.4). No coniferous species (e.g., *Picea glauca*) were found along transects in low ungulate sites.

Table 4.4. Mean % basal cover (with SE and *N* in parenthesis) of trees subject to four different levels of beaver and ungulate herbivory. *N* indicates number of transects. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU).

Species	Mean % cover (± SE) by herbivory treatment			
	HBHU	LBHU	HBLU	LBLU
Alnus rugosa	–	10.0 (*N* = 1)	–	–
Amelanchier alnifolia	–	–	30.0 (*N* = 1)	5.5 (2.5, *N* = 2)
Betula papyrifera	34.0 (18.2, *N* = 4)	–	–	5.0 (*N* = 1)
Picea glauca	30.7 (14.6, *N* = 3)	10.0 (*N* = 1)	–	–
Populus balsamifera	5.0 (2, *N* = 2)	31.3 (8.8, *N* = 4)	10.0 (3.5, *N* = 3)	6.2 (1.4, *N* = 5)
Populus tremuloides	10.1 (3.6, *N* = 10)	16.5 (3.9, *N* = 6)	7.6 (1.7, *N* = 16)	8.4 (1.0, *N* = 34)
Prunus virginiana	–	–	–	3.0 (*N* = 1)
Salix spp.	–	10 (*N* = 1)	3.0 (*N* = 1)	2.7 (1.3, *N* = 3)

Although diversity for emergent vegetation was greater at areas with higher ungulate use than with lower levels of ungulates (*F* = 10. 62, *df* = 3, 60, *P* = 0.00001, Figure 4.7), there was no difference in diversity for the shrub community (*F* = 0.70, *df* = 3, 60, *P* = 0.56). Diversity indices were not calculated for herbaceous dicots or other vegetation classes because not all plants were classified to species.

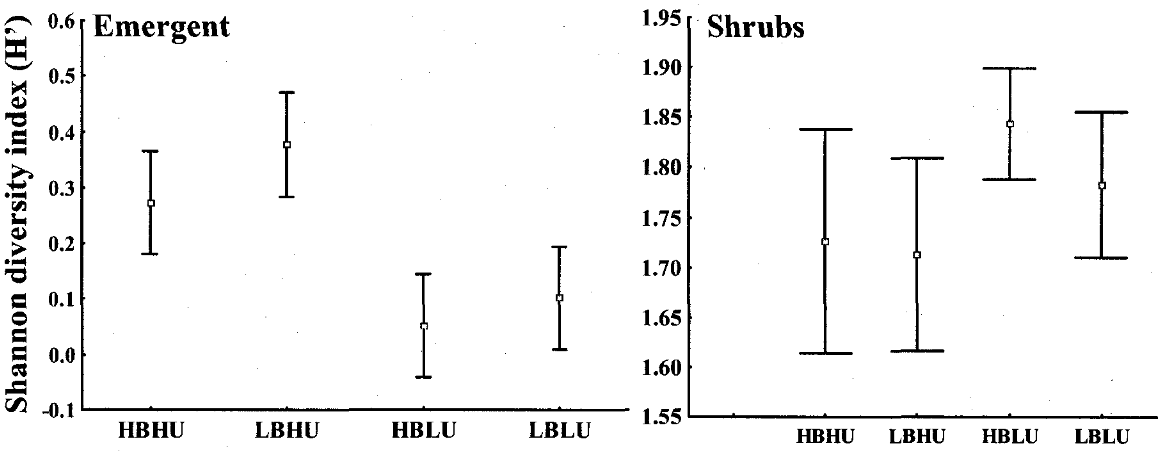

Figure 4.7. Mean species diversity for emergent vegetation and shrubs relative to 4 combinations of beaver and ungulate herbivory. Sites were classified as 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU).

4.4 DISCUSSION

There were 3 times more pellet groups per area inside EINP than on adjacent lands. Elk accounted for a high proportion of pellet groups in EINP, an area classified as "high ungulate" for the purpose of this study. Moose was the primary ungulate species represented by pellet group counts outside the park. Although pellet groups indicate the presence of an animal in an area (Rowland *et al.* 1984, Edge and Marcum 1989), they are not reliable indicators of actual resource use or true ungulate density (Leopold *et al.* 1984, Collins 1984). When pellet counts were compared with a measure of browse intensity and severity (browse impact index), both measures shared similar trends and confirmed my initial site classifications. Although pellet counts and aerial surveys provide some indication of the density of ungulates, only through an analysis of fecal deposits or examination of individual plants can the actual use of forage species be assessed. The use of the browse impact index and pellet counts is an attempt to account for both relative density and intensity and extent of use.

My findings also showed that high ungulate herbivory, regardless of the presence of beaver, reduced shrub height, but not cover, in many species and the percent cover of emergent plants and herbaceous dicots. Because *Salix* was not consistently identified to species, it was only analyzed to genus level, although different species of *Salix* show marked differences in form (Cooper *et al.* 2006). Ungulate use increased the total percent cover of trees and *Corylus cornuta.* In their work in Ontario, Canada, Donkor and Fryxell (1999) noticed an increase in the dominance of conifers over deciduous species of trees in areas under browsing pressure by beaver; however my study suggests the increase in conifers is possibly related to higher ungulate densities and active beaver colonies. Although still affected, *Corylus cornuta* appeared to be the most tolerant species of woody plant to browsing by ungulates. It comprised a large percentage of the shrub cover in high ungulate systems regardless of the presence of beaver. These findings are consistent with those of Best *et al.* (2003) who also noted its tolerance to extensive browsing. They also found that when stems of *Corylus cornuta* were protected from browsing pressures, they experienced significant increases in current annual growth (40% over 2 years) and stem production (26%). Although they used exclosures, a similar result was also observed in my study.

Emergent vegetation contributes to the diet of beaver and some ungulates (Belovsky 1984, Lodge 1991, Ray et al. 2001). Moose in particular rely on aquatic plants to increase sodium intake in summer (Lodge 1991). I found that emergent vegetation in the study ponds was dominated by *Typha latifolia* and, as such, the overall cover of emergent plants was lower as *Typha latifolia* decreased at sites classified as high ungulate. Concurrent with this reduction in cover, diversity of emergent vegetation increased in high ungulate sites, possibly due to a competitive release with declines in *Typha* cover. My results could not confirm the mechanism for the decline of *Typha*; however, it might be due to an indirect effect of ungulates on riparian vegetation communities or some hydrologic effect. *Typha latifolia* is not a preferred forage species of ungulates in the study area (Olson and Blyth 1986), however, beaver cut it at several sites and even included it in their winter food caches.

Cover by herbaceous dicots also decreased in high ungulate systems and possibly was grazed by several ungulate species. Elk typically spent much of their time grazing in summer, although they switch to browse species from late fall to early spring (Cairns and Telfer 1980, Blyth and Hudson 1987). Because of wallowing activities of bison and the extensive trails all ungulates create, ground cover can be significantly altered just by the movements of these animals (Vinton *et* al. 1993, Campbell *et al.* 1994, Hobbs 1996).

Where ungulate density was lower and beaver were absent for several years, there appeared to be a positive growth response in height and cover of several key forage plants. *Salix*, preferred forage for beaver and ungulates, showed some of the most dramatic results. Areas with lower ungulate densities and no beaver activity had shrub heights more than 4 times taller than in areas with higher foraging pressures. This result is consistent with findings by Baker *et al.* (2005) in Colorado, USA where high elk densities negatively impacted *Salix* stem regeneration and growth. Although not as dramatic, other key forage species (*Amelanchier alnifolia*, *Corylus cornuta*, and *Prunus virginiana*) showed similar trends at LBLU sites.

Following the assumptions of Connell's intermediate disturbance hypothesis (Connell 1978), I expected to find the highest diversity in areas predicted to have intermediate browsing pressures (e.g., LBHU or HBLU). My results did not support this assumption. There was no statistical difference in diversity (*H'*) in shrubs for any of the sites, despite the fact that structural complexity (e.g., vegetation height and cover), did vary. Diversity for emergent plants was highest in areas with the highest densities of ungulate pellet groups and beaver and the highest browse impact indices. The assumption that lack of beaver or lower densities of ungulates would bring disturbance to a lower level does not account for the temporal lag past beaver activities have had on their environment.

Several authors have presented evidence indicating long-term impacts of beaver activities on the landscape, even after lodge abandonment (Johnston *et al.* 1987, Naiman *et al.* 1988, Naiman and Rogers 1997). I was unable to find any pond sites that had not experienced some beaver activity at some point in their history and for that reason, considered recent occupancy only (i.e., in the past 5 to 10 years). It is possible that despite the classification of sites as "low beaver", the legacy effects of beaver activities were still influencing vegetation communities over and above the continued retention of water in the pond. Certainly areas that were no longer wetted would have altered soils due to extensive anaerobic inputs under past flooded conditions (Naiman *et al.* 1988). In addition, it was not possible to remove ungulates from the system and, despite their lower densities at sites considered "low density", they were still present and therefore still had some effect on the vegetation. A study that completely excludes the effects of beaver and ungulates in areas with low and high levels of these herbivores would further clarify the influence beaver and ungulates have on vegetation.

With geographically extensive plant communities, there is never just one influence that drives interactions and processes. Plants are directly linked to soils and microsite characteristics that cannot be easily controlled in natural experiments. I assumed that all sites represented equivalent soil types and other edaphic features, but accounted for any site-specific variation through the use of a nested design. In addition to abiotic factors, I was also limited in my ability to quantify the actual number of herbivores at each site. Despite these limitations, I found an overwhelming effect of ungulates on riparian vegetation, but the long-term effects of beaver foraging was less obvious. Beaver, as a keystone species, are instrumental in creating and maintaining wetlands (Chapter 3), which facilitates riparian habitat used by ungulates and other species. In that sense, the creation of wetland habitats by beaver likely has the greater effect on riparian plant communities than ungulates do through their foraging activities.

Regardless, ungulates also have the ability to dramatically alter vegetation communities, in turn affect other species and processes. Hobbs (1996) found that ungulates reduced forest understory heights, trampled vegetation, and increased available nitrogen through the deposition of fecal deposits. Through these activities they altered soil structures, fire behaviour (i.e., increased incidence of crown fires), and net primary production.

4.5 CONCLUSION

High levels of herbivory have dramatic and often immediate effects on vegetation composition and structure. In areas with higher numbers of pellet groups, shrub heights and, in many cases, percent cover of shrubs and herbaceous plants decreased to the point of less forage and reduced vigor in plants. In the Beaver Hills region of east-central Alberta, Elk Island National Park represents such a system, where high densities of ungulates have created plant communities with different composition and structure than areas immediately adjacent to the park boundary. As such, the Beaver Hills provides a comparative environment to examine the effects of varying levels of foraging disturbance on vegetation communities. The presence of a well-established beaver population adds to the complexity of these interactions due to the effects of foraging by beaver on riparian vegetation and offers further insight into the effects of multiple foragers on the very species they depend on to exist.

Previous studies examined foraging impacts of beaver and ungulate species in isolation. My study differs in that I examined the effects of foraging by these herbivores concurrently within a riparian system. Despite the very obvious effects of ungulate herbivory on shrub heights and cover, I was unable to find any effects on the overall composition and structure of vegetation communities that were exclusively related to beaver activities in the absence of ungulates. This finding is somewhat contrary to that found elsewhere in the boreal mixedwood forests further north of my study area where beaver were one of the primary disturbance agents structuring riparian zones on low order streams (Martell *et al.* 2006). In areas with no beaver and lower ungulate densities there was positive growth response in preferred species (e.g., *Salix* spp., *Prunus* spp.), which clearly demonstrated the degree of influence that these herbivores have in combination on riparian communities.

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5.0 THE EFFECTS OF HIGH UNGULATE DENSITIES ON FORAGING BY BEAVER

5.1 INTRODUCTION

Competition between consumers plays a key role in the form and function of ecological communities. When a shared resource is in limited supply, competition can range from coexistence to complete exclusion of the inferior competitor. The degree to which resources are limited and the unique characteristics of each consumer determines the severity of competition and the ability of consumers to coexist. Competitive exploitation occurs when the superior consumer depresses a shared resource to a level sufficient for its own maintenance, but limiting to the inferior consumer (Holt *et al.* 1994). Coexistence is possible, but it is at some cost to at least one competitor. Studies show that exploitative competition can manifest in altered foraging strategies, fitness levels, or forage selection (Richards *et al.* 2000, Wilson *et al.* 1999, Schmitt 1996, Holt *et al.* 1994). Increasingly some land managers suspect that past management policies such as the use of ecological carrying capacity models (Blyth 1995) have created competition between beaver and ungulates, resulting in significant declines in beaver populations in some areas (Kay 1994, Nietvelt 2001, Baker 2003, Baker *et al.* 2005, Hebblewhite *et al.* 2005). In most of these cases, the decline is thought to be the result of competitive exclusion due to overuse of forage resources by high elk populations (Kay 1994, Nietvelt 2001, Baker *et al.* 2005, Hebblewhite *et al.* 2005). In Elk Island National Park (EINP) in Alberta, Canada, beaver populations have been sustained in the face of high ungulate populations, and a highly managed ecosystem. This situation suggests that if competition between beaver and ungulates exists in this system, it is exploitative, but not to the extent of being exclusive.

Hardin (1960) proposed that the more niche overlap between competitors, the greater the potential for competition between them. Given this assumption, one would expect that beaver and ungulates could not compete to the point of either competitive exploitation or complete exclusion except in restricted habitats. Differing foraging behaviours and physical adaptations have allowed beaver (*Castor canadensis*) and various species of ungulates to co-exist in many ecosystems despite their reliance on common forage species (Skinner 1984). Beaver are a central place forager (Jenkins 1980); foraging away from their lodge to bring single prey items (e.g., branches or entire plants) back before processing them. In spring and summer, beaver will also forage on non-woody browse along pond edges, but always maintain access to water to facilitate escape from predators and reduce handling time. Ungulates are mobile terrestrial consumers that can forage over a wide area and forage on herbaceous as well as shrubby species, although their movements depend on spatial patterning of resources. Foraging behaviours, where resources are not limited, suggest little niche overlap.

Beaver foraging behaviour has been explained by the energy maximization model (Charnov 1976). Beaver adjust their feeding preferences to maximize energy intake (Fryxell and Doucet 1993), balancing the energetic expenditures of handling and processing of prey. These energetic costs vary with environmental constraints (Frxyell 1999), the profitability of prey (Jenkins 1979; Basey et al, 1988, 1990; Fryxell and Doucet 1993; Gallant *et al.* 2004), and predation risk (Basey and Jenkins 1995). Numerous studies have focused on foraging choices by beaver in the context of optimal foraging theory (Jenkins 1980; Belovsky 1984; Fryxell 1992, 1999; Fryxell and Doucet 1993; Gallant *et al.* 2004). All agree that beaver operate under an energy maximization foraging model.

Despite agreement with that model, some differences in foraging behaviour were noted in these studies where beaver lived in different types of habitats. These differences in behaviour appear to confirm the adaptability of beaver to a given environment, while operating under the energy-maximization model. Beaver in these studies lived in different habitat types. Habitat quality, shrub density, species composition of vegetation, and predation risk also influence choices beaver make while foraging (Jenkins 1979, Belovsky 1984, Fryxell 1999). Several of these studies found that the diameter of stems cut by beaver decreased with increasing distance from the lodge (Jenkins 1980, Belovsky 1984, Donkor and Fryxell 1999), while others determined that diameters of cut stems actually increased with increasing foraging distances (Fryxell and Doucet 1993, Gallant *et al.* 2004). During their study of beaver in west central Wisconsin, Barnes and Dibble (1988) found no effect of distance on the mean stem diameter cut by beaver. Given various scenarios within optimal foraging theory (Schoener 1979), all of these foraging strategies have merit within an energy-maximization framework when related to site-specific factors. The aim is for energy intake to exceed energy lost while searching for, cutting, provisioning, and digesting a prey item, which must necessarily vary with habitat-specific conditions. The apparent adaptability of beaver to resource availability has likely led resource managers to assume beaver will not be impacted by other management strategies for potential competing species such as ungulates.

Unlike central place foragers, animals that are not bound to a central place, such as moose (*Alces alces*) and elk (*Cervus elaphus*), do not face the additional energy expenditures required to transport food items back to a separate feeding area. They therefore have lower cropping time expenditures per item (Belovsky 1984). Wood bison (*Bison bison athabascae*) follow a time minimizing model (foraging only long enough to gain energy, leaving more time for other activities) while simultaneously meeting daily energy requirements (Bergman *et al.* 2001). Various studies have applied the marginal value theorem (Charnov 1976) to describe foraging behaviour in ungulate species. Ungulates are able to move from patch to patch as they forage and process food while looking for the next prey item. When the energetic cost of foraging in a patch falls below the mean of all patches, they move on to more profitable foraging locations, often covering large areas. This fundamental difference in foraging behaviour presents the possibility that beaver and ungulates would not compete for resources.

However, foraging strategies are not the only consideration when looking at potential resource competition between beaver and ungulates. Belovsky's allometric model of diet selection suggests that the degree of competition among herbivores depends on body sizes (Belovsky 1997). Body size will result in a partitioning of plant resources into exclusive and shared resources based on the herbivore's ability to access and process a given species or size class. Given their unique physical and physiological differences, the use of prey differs between beaver and ungulates. Beaver remove complete stems, from small shrubs to large trees; some stems provide food while others are used in the construction and maintenance of dams and lodges. Ungulates use browse strictly for food and generally leave the main stalk of woody plants intact (Cairns 1976, Cairns and Telfer 1980). Extensive browsing by ungulates however, can result in stems that are small, short and hedged in appearance (Bork *et al.* 1997, Baker *et al.* 2005) with altered palatability and concentration of secondary metabolites (Bryant *et al.* 1991).

Despite varied diet for both beaver and ungulates, most studies on the competitive interaction between these species have focused exclusively on willow (*Salix* sp.) as the main forage species (Kay 1994, Singer 1998, Nietvelt 2001, Baker 2003, Baker *et al.* 2005). Others have focused on aspen as the preferred food of beaver (Basey *et al.* 1988, Doucet *et al.* 1994, White *et al.* 2003). In addition, these studies mainly examined the effects of elk on shared forage species. The question of competition between beavers and ungulates has not been well examined in more productive and diverse systems offering multiple forage species and competitors.

Elk Island National Park (EINP) in east-central Alberta, Canada, provides a multi-herbivore system where beaver and ungulates share common resources. Various woody plant species are commonly browsed by beaver and ungulates at some point during the year, therefore providing an ideal scenario to assess how competition for food resources affects foraging behaviour by beaver.

In other studies, competitive exclusion between elk and beaver was quantified through decreases in beaver populations (Hebblewhite *et al.* 2005), forage species (Baker *et al.*

2005), or both (Nietvelt 2001). In EINP, beaver and several species of ungulates coexist, which suggests that if competition exists, it is exploitative, not exclusive. As such, there is a unique opportunity to measure differences in foraging behaviour of beaver relative to different levels of competition with ungulates. To explore the hypothesis that high ungulate densities are detrimental to beaver in managed systems, I assessed plant selection by beaver, foraging distances, and the diameters of stems cut by beaver to confirm and quantify the effects of ungulates on beaver.

In this chapter I examine whether competition exists between beaver and ungulates by comparing a system with high ungulate densities to a system with lower ungulate densities. Specifically, I examine how 2 different levels of ungulate herbivory influence vegetation availability, diameter classes, and beaver foraging activities relative to these parameters. To determine whether competitive exploitation exists between beavers and ungulates in this system I tested whether 1) densities of ungulate pellet groups in Elk Island National Park are significantly higher than those in the surrounding area ("relative ungulate abundance"), 2) shrub densities and diameters of key forage species differ in areas with higher levels of ungulates ("forage availability"), 3) beaver alter their forage selection to less preferred food plants to compensate for a potential decrease in preferred forage in areas with high levels of herbivory by ungulates ("species selection"), and 4) distances that beaver forage are farther from the pond edge in areas with higher pellet group densities than areas with lower densities ("foraging distances and size-distance relationship").

5.2 STUDY SITE AND METHODS

Study Area

Elk Island National Park (194 km^2) is located in the boreal mixed-wood forest region of east-central Alberta, but is surrounded largely by an agricultural landscape. EINP was fenced immediately after it was established in 1906 and has been completely fenced since that time. Consequently there are no large predators resident in the park except coyotes (*Canis latrans*). Currently EINP is home to 6 taxa of large ungulates including elk (*Cervus elaphus*), moose (*Alces alces*), plains bison (*Bison bison bison)*, wood bison (*Bison bison athabascae*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*). In addition, beaver have recolonized the park area after being successfully reintroduced in 1941. EINP has a long history of ungulate management ranging from prescribed fire to culling programs. Currently the park reports some of the highest year-round ungulate densities in Canada (approximately 13 ungulates per km^2).

In late 1985 the park adopted an ecological carrying capacity model for ungulate management (Blyth 1995). The herd reduction strategies previously used by the park were abandoned and fewer live animals were removed from EINP in hopes that populations would self-regulate around carrying capacity. By the late 1990's ungulate populations were at an all time high and it became obvious that vegetation communities could no longer sustain the associated foraging intensity. The park increased live culling of elk and bison to facilitate the recovery of plant communities.

Aspen (*Populus tremuloides*) is the dominant tree species and covers over 70% of the park. Balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh) occur in moist areas whereas black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* (Moench) Voss) are generally in pockets in the northern areas of the park. The park has a diverse shrub understory of beaked hazel (*Corylus cornuta*), serviceberry (*Amelanchier alnifolia*), choke cherry (*Prunus virginiana*), pin cherry (*Prunus pensylvanica* L.f), willow (*Salix* spp.), prickly and wild red rose (*Rosa acicularis* Lindl. and *R. woodsii* Lindl.), raspberry (*Rubus idaeus*), highbush cranberry (*Virburnum edule* Michx.), red osier dogwood (*Cornus stolonifera* Michx.), snowberry (*Symphoricarpos occidentalis* Hook.), currant (*Ribes* spp.) and honeysuckle (*Lonicera* spp.). In the park, beaver and all ungulate species forage on these tree and shrub species at some point during the year (Cairns 1976, Skinner 1984).

Due to its location in the Cooking Lake Moraine (Figure 5.1), most of EINP is hilly and has a variety of wetland types. Open water in the form of lakes, ponds and marshes covers 28% of the park. Other more vegetated wetlands (bogs, swamps, and fens) comprise 5% of the park. Grey Luvisols (covering 65% of the park) are the dominant soil type, while Humic Luvic Gleysols, Terric Mesisols, Eluviated Eutric Brunisols, Grey Solodized Solonetz, and Typic Fibrisols comprise the remaining soil classes (Hardy & Associates 1986). These soil and wetland characteristics are also typical for lands located immediately adjacent to the park. The entire area is known as the Beaver Hills, which to date has avoided large-scale agricultural and urban development due to its poor soils and hilly terrain. Immediately adjacent to the Beaver Hills are level plains with rich Chernozomic soils and productive croplands.

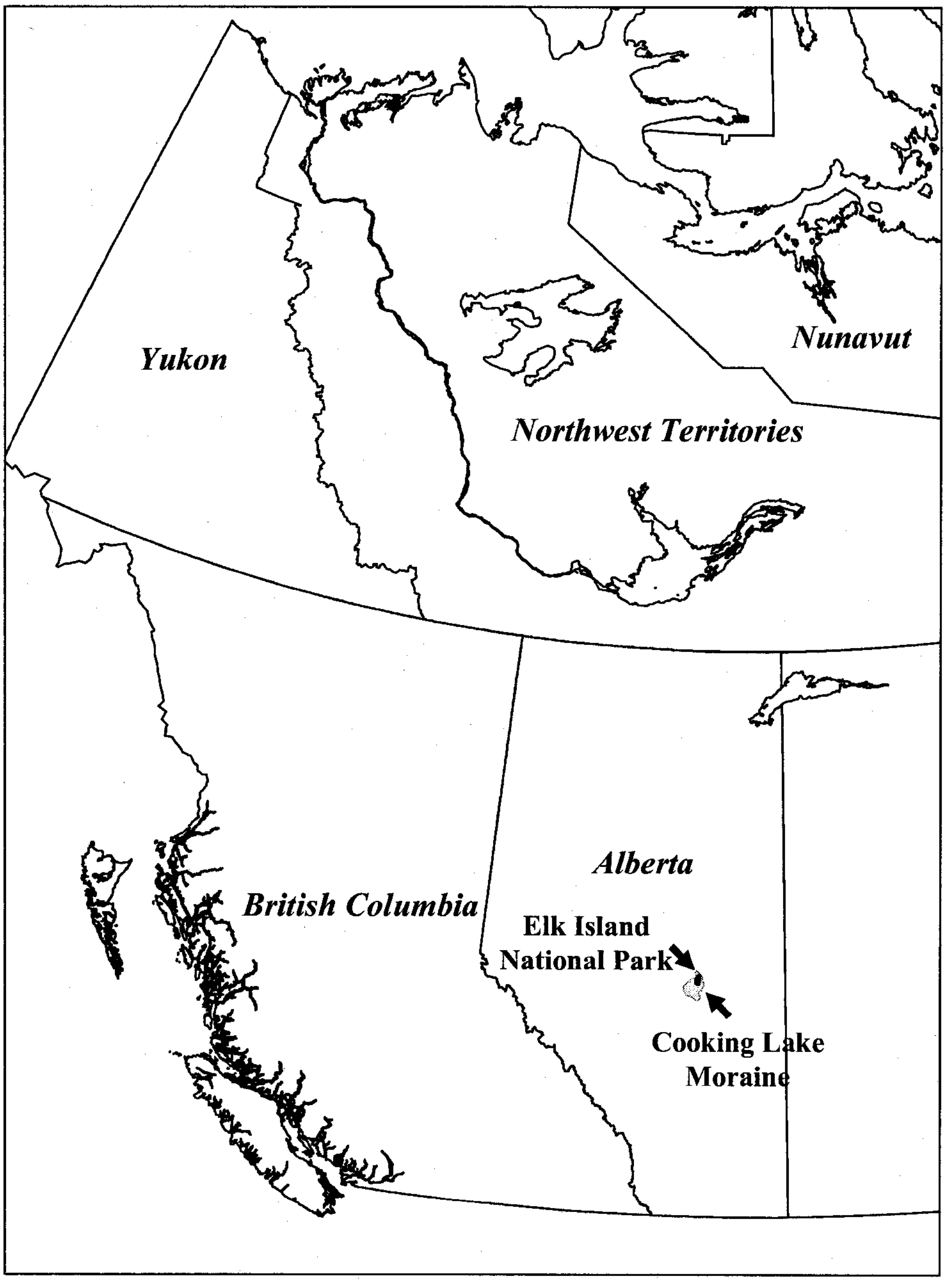

Figure 5.1. Elk Island National Park in Alberta, Canada lies within the Cooking Lake Moraine.

Beaver Population Surveys

Parks Canada has conducted regular beaver lodge occupancy surveys in EINP following their successful reintroduction in 1941. Since 1989, park staff have conducted regular aerial surveys during the late fall or early winter every 2 to 3 years. Surveys are done using a helicopter flying at approximately 30-m above ground. All known beaver lodges are visited during the survey as well as all water bodies in the park. Each lodge is assigned a unique number that is consistent throughout the survey years. Lodges are classified as either active or inactive and their location noted. All data are then entered into a Geographic Information System (GIS). New lodges are assigned a unique identifying number and are added to the existing dataset. In addition, ground surveys are conducted to validate or complement the aerial survey data. Beaver lodges are considered occupied in both survey types if a winter food cache is present. All data are entered into the park's Geographic Information System as a data layer. Each lodge is assigned a unique identifier to allow long-term occupancy to be tracked for each lodge.

Lodge Selection

Using the unique lodge numbers, a random number generator in Statistica (StatSoft Inc. 2003) was used to select 5 active beaver lodges inside the park that had been occupied at least 5 years. Active lodges outside the park are limited by land access (particularly on private lands). Through aerial photo interpretation and local knowledge I was able to identify 5 active beaver lodges comparable to those selected inside the park (i.e., similar pond size, lodge age, surrounding vegetation, and fire history), but distributed around the outer park boundary. My field crew and I then conducted vegetation, ungulate pellet counts, and lodge occupancy surveys around each of these ponds during the summer, late fall, and early spring of 2002, and 2003.

All beaver ponds utilized in this study were > 2 ha in size. The lodges were well established and none had been exposed to fire since the establishment of the park. In Chapter 2 I determined that lodges exposed to repeated burns have lower lodge occupancy rates than those never exposed to fire. Study sites located outside the park were within 1 km of the park boundary on private and provincial lands in areas free of cattle grazing and previous fires. Ungulates outside the park are free roaming and subject to predation and hunting pressures, while those inside the park are not. As a result, ungulate densities are higher inside, than outside the park.

Densities of ungulate pellet groups

To determine densities of ungulate pellet groups around each of the 10 lodges, my field crew and I conducted pellet group counts along four 2-m wide 100-m long transects perpendicular to the pond edge (the edge between the emergent and terrestrial zone). Edge and Marcum (1989) found the pellet group technique was useful for estimating relative elk densities when compared with telemetry data. Pellets were identified to species. Deer pellets cannot be differentiated to species; these were identified as "deer". A group of ≥ 5 pellets was considered an individual pellet group. A single fecal deposit for bison was considered to be equivalent to a pellet group because bison do not produce pellets. For an overall assessment of total ungulate densities, pellet groups for all species of ungulates were pooled to calculate an overall density of pellet groups per m^2 for each transect.

Beaver Browse

Using the edge of active beaver ponds as a starting location, we surveyed 60-m long transects in the riparian zone perpendicular to shore every 50 meters along the entire circumference of the pond. Transect length was based on previous studies, which determined that beaver in the study area rarely forage beyond 60 meters from the pond edge (Schwanke and Baker 1977, Skinner 1984). However, if the transect had obvious browsing by beaver beyond the 60-m mark, we continued to survey to the point last browsed. We identified to species all woody plants > 20 mm in diameter within the 2-m wide transect. Stem diameters were measured 10-cm above the ground or at the point where the stem had been completely cut by beaver. We then classified a stem as either "cut" (those stems cut by beaver) or "uncut" (those stems not cut by beaver) and noted its distance along the transect. Although we used the wood, pith, and bark characteristics to identify cut stems, there were stems (particularly older ones) that could only be classified to genera. This data set was completely independent from the data set used in Chapter 4.

We surveyed over 21,400 stems of woody plants along 106 transects. As a result we examined 9,594 stems over a 7,273 m^2 area inside EINP and 11,813 stems over a 5,380 m^2 area outside the park. A stem is considered to be the rooted stalk of the plant. Of the 37 species of woody plants found along the transects, we identified 15 species of *Salix* (Appendix), the stumps of which were difficult to differentiate when cut by beaver.

Identification to species also proved difficult for other genera once beaver had cut the stems. Therefore I pooled data by genera for *Populus* (*P. tremuloides* and *P. balsamifera*), *Salix*, *Rosa* (*R. acicularis* and *R. woodsii*), *Prunus* (*Prunus pensylvanica* and *P. virginiana*) and *Viburnum* (*V. opulus* and *V. edule*). The resulting ten species or genera that were consistently browsed by both beaver and ungulates provided a large enough sample size for analysis (*A. alnifolia*, *B. papyrifera*, *C. cornuta*, *C. stolonifera*, *Populus* spp., *Prunus* spp., *Rosa* spp., *Salix* spp., *S. canadensis* and *Viburnum* spp.). Because it has a large range of stem diameters, for some analyses I divided *Populus* spp. into three diameter classes (<120 mm, 120 to 300 mm, and > 300 mm).

Data analysis

To determine whether the data met the assumptions for parametric analyses, the *F*-test and the Brown and Forsythe test were used to assess homogeneity of variance and the Shapiro-Wilks *W* test to assess normality (Shapiro *et al.* 1968). Where necessary, data were log transformed to normalize the data prior to statistical analysis. Statistica (StatSoft Inc. 2003) and SPSS (SPSS Inc. 2002) were used for all analyses.

Densities of ungulate pellet groups

A nested analyses of variance (ANOVA) was used to compare differences in relative ungulate densities inside and outside the park. The location of the lodge (inside or outside the park) was a fixed factor and individual lodges were random factors nested within location (inside or outside the park). To differentiate between means I calculated least-squares means (LSM) and their standard errors (SE).

Forage availability

A nested analyses of variance (ANOVA) was used to compare differences in stem densities (stems per m^2) and stem diameters (cut + uncut and cut only). These two variables were then used as an assessment of forage availability. As with densities of ungulate pellet groups, the location of the lodge (inside or outside the park) was a fixed factor and individual lodges were random factors nested within location (inside or outside the park). I calculated least-squares means (LSM) and their standard errors (SE) to differentiate between means.

Species selection

To determine which species comprised the bulk of those harvested by beaver at each lodge ("species selection"), I divided the total number of stems of each plant species cut by beaver by the total number of stems of all species cut at each individual lodge. A tree was equivalent to one stem. I then determined whether there was any difference in species selection relative to the lodge and its location inside or outside of EINP. Each species was then ranked relative to its contribution to the total number of stems cut at each lodge. A simple linear regression was used to analyze whether species-specific density (stems per m^2) predicted whether a given species would comprise the bulk of stems browsed by beaver.

Foraging distances and size-distance relationship

A nested mixed model design was calculated using SPSS to determine whether mean foraging distances differed at lodges inside and outside the park. Individual lodges were nested within location (inside or outside the park). Location and stem status (cut or uncut by beaver) were fixed factors and individual lodges were treated as a nested random factor in the analysis. Distance of the stem from the pond edge was a continuous response variable.

I also used a general linear model to test the effect of distance away from the pond, location (inside or outside of EINP), lodge (nested within location), as well as the interaction between distance and location to determine whether there was a difference in the mean size of stems cut by beaver at increasing distances away from the pond at each location. If there was a plausible effect of location on the relationship between stem size and foraging distance, I then calculated a product-moment correlation to assess the relationship between distance and diameter.

5.3 RESULTS

Densities of ungulate pellet groups

The total number of ungulate pellet groups per m^2 was 2.9 times higher at lodges inside EINP than around lodges located outside the park. (Figure 5.2A, $F_{1,20} = 18.89$, $P = 0.0003$). The higher number of pellet groups per m^2 in the park was partly driven by bison and elk inside the park. Bison are not free-roaming outside EINP and the number of elk pellet groups per m^2 inside EINP was > 6 times higher than outside the park. The number of pellet groups per m^2 for moose was over 3 times higher outside the park than inside (Figure 5.2B). Densities of pellet counts for deer were identical in and outside the park at 0.01 pellet groups per m^2.

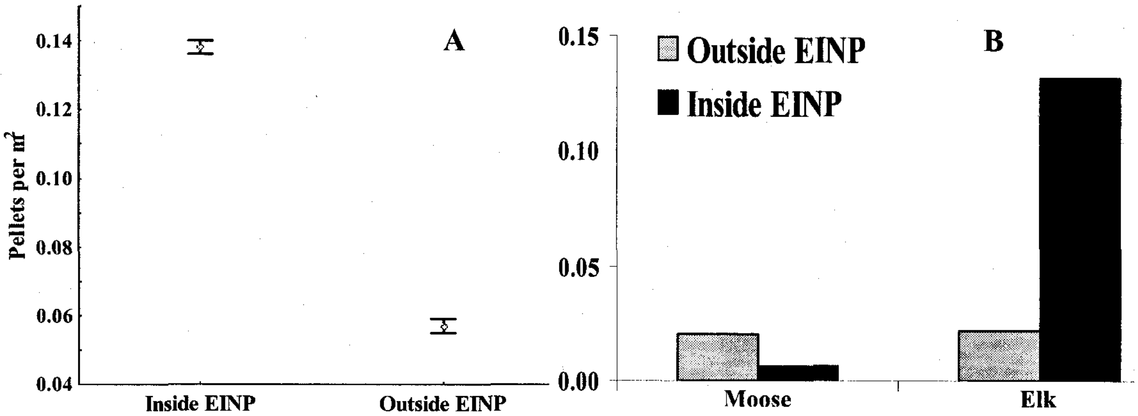

Figure 5.2. Number of ungulate pellet groups per m^2 inside and outside Elk Island National Park of (A) combined pellet groups for deer, elk, moose and bison, and (B) a comparative number of pellet groups per m^2 for moose and elk.

Forage availability

Although fewer stems were present over a larger area at lodges inside EINP (1.32 stems per m^2) than outside the park (2.2 stems per m^2), there was no statistically significant difference between overall stem densities inside and outside the park ($F_{1,46} = 1^{-10}$, $P = 0.29$). However, when I assessed stem densities of individual species or genera, there were significant differences for 4 of the 10 species and genera analyzed. The density of *Populus* spp. was lower inside the park than outside ($F_{1,96} = 33.59$, $P < 0.001$). There were similar trends with *Prunus* spp. ($F_{1,96} = 15.61$ $P = 0.0004$), *Viburnum* spp. ($F_{1,96} = 6.22$, $P = 0.014$) and *Rosa* spp. ($\mathrm{F}_{1,95} = 57.11$, $P < 0.0001$).

All shrub species at lodges inside the park tended to have smaller average stem diameters than those outside EINP (Table 5.1) and were often hedged in appearance (Chapter 4). Of the species analyzed, 5 species (including the < 120 mm diameter class for *Populus* spp.) had significantly smaller stem diameters than the same species outside the park. Despite the smaller stem diameters within the park, the diameter of stems cut by beaver for most shrub species was similar inside and outside the park (Table 5.1). Only *Amelanchier alnifolia* and the *Viburnum* spp. had cut stems that had significantly smaller diameters inside the park than those outside. Although not significant, there was also a trend for beaver to harvest more mature *Populus* trees inside the park than outside (Figure 5.3). In EINP there was a slightly higher proportion of *Populus* stems within the < 120 mm diameter class inside EINP (13%) than outside the park (9%, Hood and Bayley unpublished data). However, 10% of the *Populus* stems cut within the park were mature trees compared to 1% outside the park.

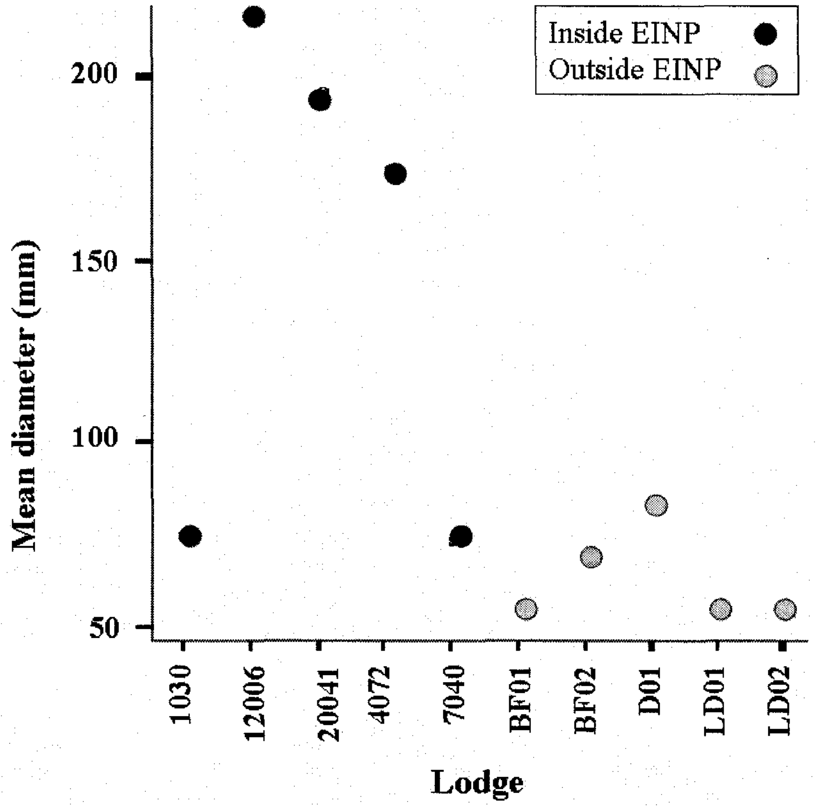

Figure 5.3. Mean diameters (mm) of *Populus* stems cut by beaver inside (•) and outside(◎) of Elk Island National Park for each of the 10 lodges surveyed.

Table 5.1. Mean diameters (mm) with standard errors in ( ) for 10 species of woody plants browsed by beaver inside and outside of Elk Island National Park (EINP). Both the diameters of all stems (cut+uncut) are included as well as the diameters of only those stems cut by beaver. Results from nested ANOVA are from log-transformed data to improve normality. *Populus* spp. was divided into 3 diameter classes (< 120 mm, 120 to 300 mm, and >300 mm) for the analysis of all stems (cut + uncut).

	Species/Genera	Inside EINP	Outside EINP	*F*-value	*P*
All diameters in (cut + uncut)	*Amelanchier alnifolia*	11.63 (0.28)	13.68 (0.16)	*F*(1, 1762) = 8.81	0.02*
	Betula papyrifera	29.23 (5.38)	46.88 (4.86)	*F*(1, 336) = 7.97	0.01*
	Cornus stolonifera	10.37 (0.42)	13.02 (0.46)	*F*(1, 75) = 9.57	0.01*
	Corylus cornuta	10.97 (0.11)	12.25 (0.06)	*F*(1, 11 304) = 3.28	0.11
	Populus spp. (< 120 mm)	16.73 (0.52)	27.51 (0.34)	*F*(1, 4786) = 10.05	0.01*
	Populus spp. (120 - 300 mm)	222.42 (5.69)	209.75 (3.56)	*F*(1, 404) = 0.75	0.41
	Populus spp. (> 300 mm)	430.93 (38.38)	568.44 (87.42)	*F*(1,132) = 0.38	0.55
	Prunus spp.	11.50 (1.30)	14.91 (0.49)	*F*(1, 326) = 6.87	0.01*
	Rosa spp.	11.14 (0.53)	11.38 (0.13)	*F*(1, 361) = 0.59	0.49
	Salix spp.	17.15 (1.35)	24.68 (1.07)	*F*(1, 649) = 7.36	0.03
	Shepherdia canadensis	15.61 (1.18)	16.25 (0.55)	*F*(1, 830) = 0.17	0.69
	Viburnum spp.	4.28 (1.08)	11.60 (0.73)	*F*(1, 51) = 35.26	0.00003*
Diameters of cut stems	*Amelanchier alnifolia*	9.10 (1.01)	11.86 (1.12)	*F*(1, 264) = 4.65	0.04*
	Betula papyrifera	36.67 (6.40)	36.62 (7.05)	*F*(1, 145) = 0.37	0.55
	Cornus stolonifera	---**	---	---	---
	Corylus cornuta	9.89 (0.71)	11.67 (0.12)	*F*(1, 2178) = 2.55	0.13
	Populus spp.	144.14 (5.54)	62.13 (5.28)	*F*(1,1720) = 2.93	0.12
	Prunus spp.	9.91 (2.87)	14.91 (0.49)	*F*(1, 56) = 2.17	0.18
	Rosa spp.	5.68 (0.55)	10.91 (1.01)	*F*(1, 62) = 454.95	0.85
	Salix spp.	28.99 (2.56)	22.34 (4.00)	*F*(1, 407) = 1.04	0.34
	Shepherdia canadensis	10.29 (1.21)	13.44 (1.13)	F(1, 172) = 1.69	0.23
	Viburnum spp.	4.28 (0.88)	10.27 (0.72)	*F*(1,13) = 27.53	0.0002*

*indicates a significant result

**--- inadequate sample size

Species selection

Although *Populus* and *Corylus cornuta* accounted for 65% to 92% of the total of stems harvested at all 10 lodges, beaver cut a broad spectrum of species throughout the study area (Table 5.2). Species-specific density explained 55% of the variability in the number of cut stems within a species relative to the overall number of stems of all species cut by beaver ($R^2 = 0.55$, $P < 0.001$).

Table 5.2. Stem selection for individual lodges, both inside and outside of Elk Island National Park (EINP). Percent of stems cut = (#stems cut of species$_i$ ÷ all cut stems of all species) x 100. Stem densities (#stems per m^2) for species$_i$ are in parentheses ( ). The two species most commonly selected by beaver at each lodge are in **bold**.

Species	**Lodges in EINP**					**Lodges outside EINP**			
	1030	**12006**	**20041**	**4072**	**7040**	**BF01**	**BF03**	**D01**	**LD01**
Alnus rugosa	—*	—	—	—	—	0.09% (0.006)	—	—	0.3% (0.002)
Amelanchier alnifolia	2% (0.08)	0% (0.02)	—	1% (0.03)	6% (0.08)	9% (0.16)	0.5% (0.07)	0% (0.08)	5% (0.31)
Betula papyrifera	3% (0.02)	10% (0.06)	2% (0.002)	2% (0.02)	5% (0.06)	2% (0.06)	0.5% (0.01)	0% (0.005)	1% (0.01)
Cornus stolonifera	0% (0.005)	0% (0.003)	2% (0.004)	0.4% (0.01)	0.2% (0.003)	0.4% (0.03)	0% (0.005)	—	0% (0.005)
Corylus cornuta	**30% (1.4)**	**24% (0.1)**	2% (0.02)	**63% (1.92)**	**47% (0.5)**	**47% (1.07)**	**59% (0.95)**	0% (0.07)	**47% (1.55)**
Lonicera diocia	0.2% (0.0006)	0% (0.0009)	0% (0.002)	—	—	0.09% (0.02)	—	—	0% (0.0008)
Lonicera involucrata	0% (0.002)	—	0% (0.0008)	—	0.07% (0.0005)	0% (0.004)	—	—	0.1% (0.002)
Picea glauca	—	—	—	0% (0.0008)	0.6% (0.01)	—	—	—	—
Populus spp.	**51% (0.6)**	**54% (0.2)**	**43% (0.07)**	**29% (0.33)**	**21% (0.28)**	**20% (0.51)**	**34% (0.54)**	**63% (0.36)**	**38% (0.67)**
Prunus spp.	1% (0.01)	0% (0.004)	0% (0.002)	0.8% (0.01)	1% (0.01)	3% (0.08)	0.5% (0.03)	0% (0.05)	0.4% (0.03)
Ribes lacustre	0.2% (0.002)	7% (0.008)	2% (0.0008)	0% (0.0008)	—	0.09% (0.002)	—	—	0.1% (0.0008)
Rosa spp.	0% (0.002)	0% (0.004)	0% (0.0008)	0% (0.005)	3% (0.02)	7% (0.04)	0.5% (0.06)	4% (0.06)	1% (0.07)
Rubus idaeus	—	—	—	0.4% (0.0008)	0.6% (0.004)	—	—	—	—
Salix spp	7% (0.04)	0% (0.02)	**49% (0.04)**	—	3% (0.03)	17% (0.29)	1% (0.03)	**32% (0.08)**	3% (0.03)
Shepherdia canadensis	2% (0.08)	4% (0.1)	0% (0.0008)	0% (0.01)	10% (0.14)	1% (0.03)	3% (0.02)	0% (0.02)	0.6% (0.05)
Symphoricarpus alba	0% (0.01)	—	—	—	—	—	—	—	—
Symphoricarpus occidentalis	4% (0.01)	0% (0.005)	0% (0.002)	4% (0.009)	1% (0.009)	—	0% (0.02)	—	0.5% (0.008)
Viburnum spp.	—	—	—	—	0.4% (0.003)	0.09% (0.02)	0% (0.002)	—	0.8% (0.02)

*____ indicates the species was not present at that lodge.

Where present, *Salix* was harvested at all but one lodge. At 3 lodges *Salix* was one of the principal species cut by beaver. Several species were either avoided by beaver or were in such low densities that they did not comprise a large number of the stems (Table 5.2). Although not common adjacent to my study ponds, *Picea glauca* was harvested by beaver at one lodge (# 7040), but was completely avoided at the other 2 lodges where present. *Rosa* spp. was cut at all 5 lodges outside the park, but only at one lodge within EINP, despite being present at all pond locations in the study area.

Foraging distances and size-distance relationship

Beaver cut most stems closer to the pond edges inside EINP than beaver outside of the park (Figure 5.4, $F_{1,8} = 85.73$, $P < 0.001$), despite a relatively equal distribution of stems between 10 and 60 meters from shore (Figure 5.5). When forage data were divided into 10 meter distance categories, I found that more than 80% of the stems cut by beaver inside the park were cut within 30 meters from the pond edge (Figure 5.4A), while outside of EINP only 67% of stems were cut within the same distance (Figure 5.4B). In both areas, beaver harvested the greatest numbers of stems 10 to 20 m away from the pond edge. Maximum foraging distances inside and outside the park were 66 m and 73 m, respectively.

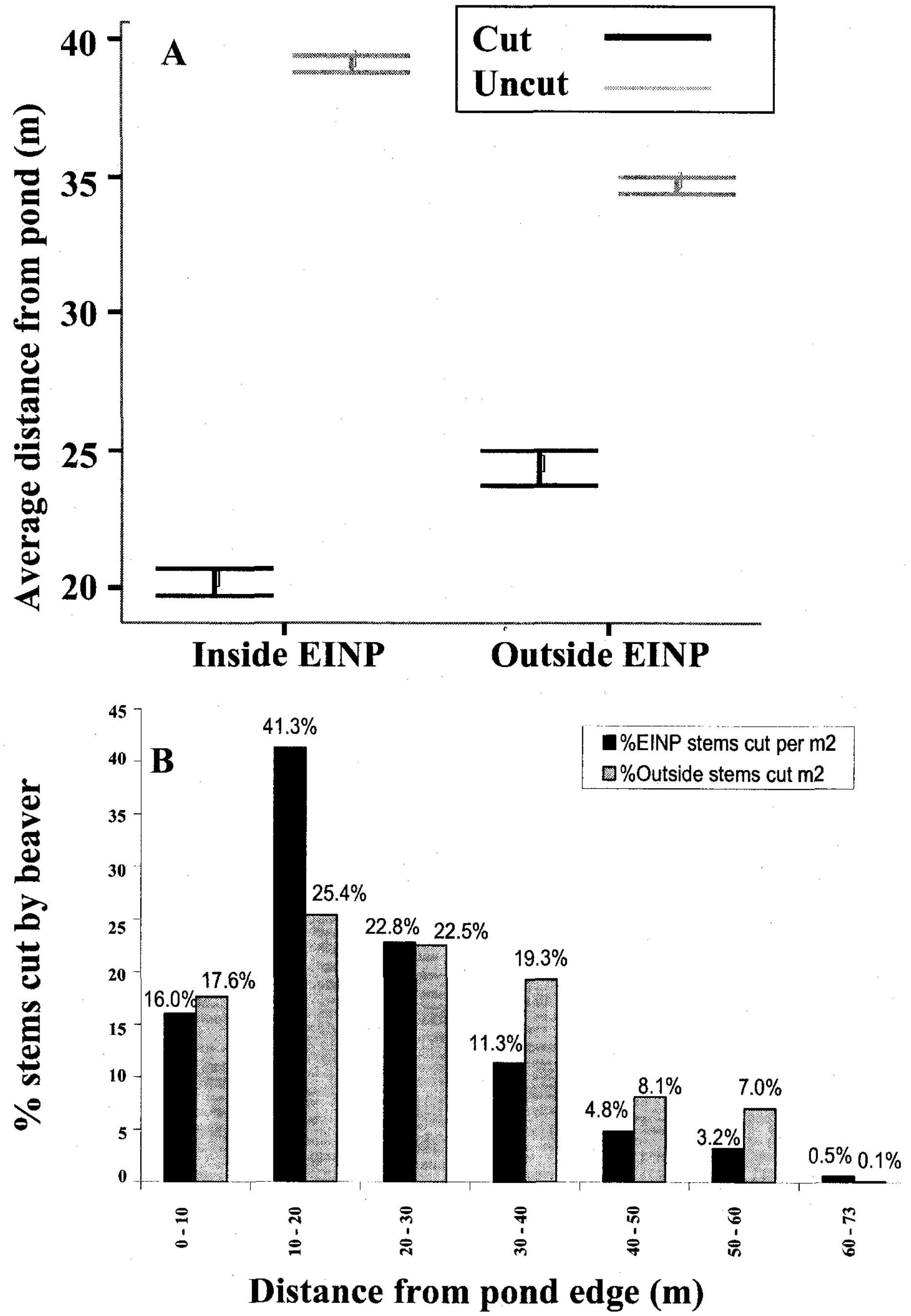

Figure 5.4. Mean browse distances (± 2 standard error) for cut and uncut stems inside and outside of Elk Island National Park relative to the distance from the edge of the study pond (A), and the percent of all stems cut by beaver in10 m distance classes from the pond edge for each location (B).

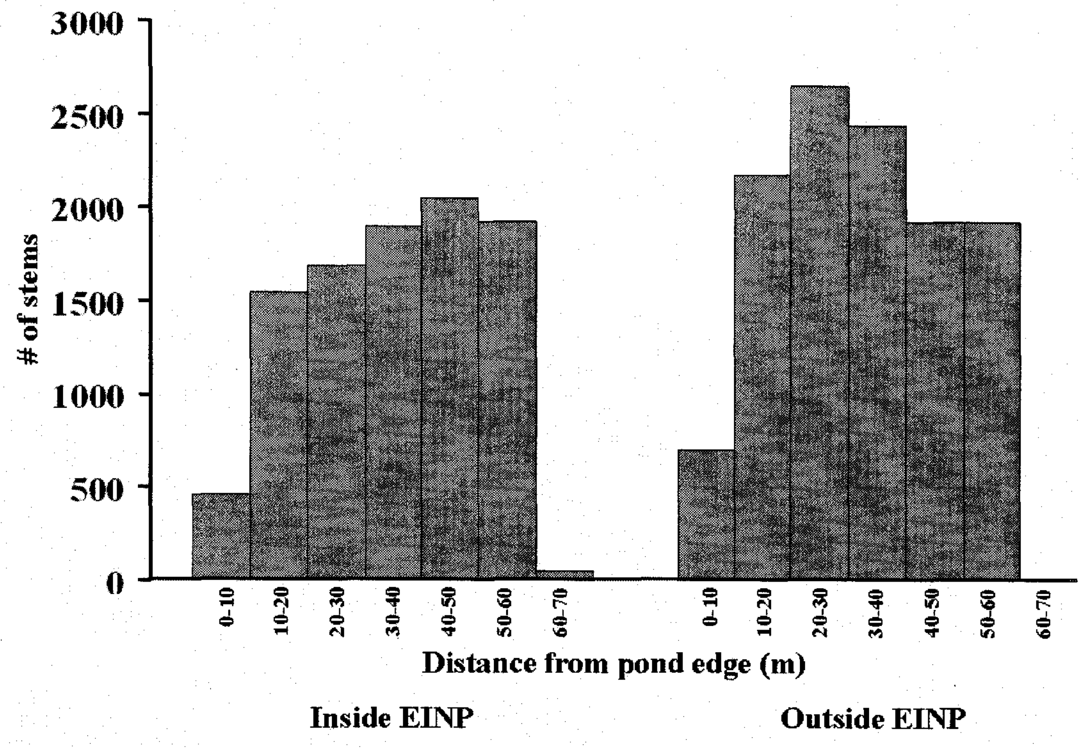

Figure 5.5. Number of total stems (cut and uncut) relative to the distance from the edge (m) of ponds inside and outside of Elk Island National Park (EINP).

There was also a significant difference in the size-distance relationship between the two locations ($F_{1,21371} = 85.73$, $P < 0.001$). Inside EINP, beaver cut larger diameter stems as foraging distances increased ($R = 0.15$, $P < 0.001$). There was no detectable difference in the diameter of stems cut by beaver relative to foraging distances outside the park ($R = 0.03$, $P = 0.11$).

5.4 DISCUSSION

Forage availability for beaver in areas with high densities of ungulates

My results suggest that intense browsing by ungulates within EINP results in lower stem densities and smaller diameters in several riparian shrub species also utilized by beaver (Table 5.1). Bork *et al* (1997) in their examination of upland terrestrial vegetation structure in EINP found similar results. As such, ungulate herbivory may potentially have exploited the resources in a way that negatively impacted forage availability for beaver. In my study, *Populus*, *Virburnum*, *Rosa*, and *Prunus* all had fewer stems per m^2 inside the park than outside, where densities of ungulate pellet groups were almost 3 times lower. As with previous research, I also found that stems in EINP were often hedged and heavily browsed (Blyth and Hudson 1987, Bork *et al.* 1997).

Average stem diameters were lower within EINP for several species. Adult forms of *Amelanchier alnifolia* and *Prunus spp.* were almost non-existent inside the park and, along with *Betula papyrifera*, *Cornus stolonifera*, and *Viburnum* spp., had significantly smaller diameters than those same species outside EINP. Where present, however, only the larger stems of these species were regularly browsed by beaver. Fryxell and Doucet (1993) suggested that larger food items are more profitable. Other research found that smaller stem classes of some species had lower digestibility for beaver (Basey et al. 1988, Fryxell 1999). Several studies have also found a strong relationship between stem diameter and biomass (Fryxell and Doucet 1991, Baker and Cade 1995, Nietvelt 2001, Bond-Lamberty *et al.* 2002). Using diameter and stem density as a general indicator of biomass, I would predict that total available biomass is lower within the park; however beaver seem to maximize their energy intake by choosing larger diameter stems for most species (with the exception of *A. alnifolia* and *Viburnum*) to counteract lower stem densities and the availability of smaller diameter classes.

Species selection by beaver

Despite lower densities of key forage species (e.g., *Populus*), in general, beaver still cut stems relative to their overall densities (Table 5.2). As in Belovsky's study (1984), I found beaver chose species relative to their availability. *Populus* spp. and *Corylus cornuta* comprised the bulk of stems harvested throughout the study area, and these 2 species often had the highest relative densities (Table 5.2). Choosing more common species serves to reduce search time and increase energy intake, which is consistent with an energy-maximization model.

Selection of *Populus* spp. and *C. cornuta* is consistent with other research (Fryxell and Doucet 1993, Gallant *et al.* 2004, Martell *et al.* 2005). *Populus* is commonly identified as a dominant food item used by beaver due to its palatability and nutritional content (Jenkins 1979, Basey et al 1988, Fryxell and Doucet 1993, Fryxell 1999, 2001). In my study area, *Populus* was the preferred species at almost all lodges sampled. *Corylus cornuta* was also highly represented, but *Salix*, a shrub commonly preferred by beaver in many areas (Baker *et al.*2005), was selected as a dominant stem in only 2 of the 10 ponds, despite being present (but not abundant) at all but one pond. As a generalist herbivore, beaver have a broad diet (Roberts and Amer 1984, Belovsky 1984, Fryxell and Doucet 1993), which can change both annually and seasonally (Jenkins 1979). Beaver can also adjust their diet relative to palatability (Basey et al. 1988, 1990; Fryxell 1999), availability (Belovsky 1984, Fryxell 1999), and stem size (Basey *et al.* 1988, Fryxell 1999, Gallant *et al.* 2004). Despite documented preference for certain species, my results suggest that beaver forage selection is driven by availability.

A key response to the impacts of ungulate foraging on vegetation was that beaver tended to cut more mature trees within EINP than outside the park. Although cutting larger trees increases cutting time, search time subsequent to cutting is dramatically reduced because of the additional amount of available forage once the tree is felled. Many of the branches are of equivalent size to saplings cut by beaver within the foraging area. Foraging at a consistent location, however, requires a balance between energy maximization (through reduced search time and access to a highly palatable species) and predation risk. Larger trees also take more time to be sectioned and, therefore, might increase both predation risk and energy expenditures.

Predators are likely quick to recognize travel routes and feeding locations of prey and would therefore focus their hunting pressures accordingly. Beaver, in particular, leave ample evidence of foraging areas and access routes. Basey and Jenkins (1995) found that beavers minimized predation risk by depending on the relative distances of large and small aspen in areas with a higher risk of predation (i.e., higher coyote densities). During her research in EINP, Pruss (2002) reported some of the highest recorded densities of coyotes in North America (0.87 to 1.05 coyotes per km*2*). She also found that coyotes in EINP predated on beaver. Given these numbers, by selecting larger trees with predicable profitability and location while foraging closer to the pond edge, beaver behaviour within EINP supports an optimal foraging model as suggested by Basey and Jenkins (1995).

Foraging distances and size-distance relationship

Foraging distances are a key factor in evaluating energy expenditures and predation risk. Extensive research has been conducted on the relationship between foraging distances and the selection of specific sizes or species of food as beaver range further from their lodge (Jenkins 1980, Fryxell 1991, Basey and Jenkins 1995, Donker and Fryxell 1999). In optimal foraging models for beaver, foraging distances are often found to be related to stem density and diameter of cut stems. Fryxell (1999) predicted that a depletion of resources closer to the central place would result in longer foraging distances, which supports my original hypothesis. However, I found that in habitats with lower stem densities and smaller stem sizes, beaver actually foraged closer to the pond than beaver outside the park where stem densities were higher (Figures 5.4 and 5.5). It is possible that in an environment with significantly higher levels of competition with other herbivores, beaver in EINP are maximizing energy intake by foraging closer to their central place and maintaining shorter escape distances. Security cover is generally lower in the park due to lower stem densities and predators (coyotes) are more numerous. Also, because of the positive relationship between diameters of cut stems and foraging distance, maintaining shorter foraging distances would decrease handling time.

These findings were based on the assumption that each colony has equivalent population numbers, but these numbers were based only on observational data and not on strict mark–recapture methods. The park monitors lodge occupancy, but not exact population numbers, therefore, I was unable to determine forage effort relative to colony size. In addition, it is difficult to determine whether all stems cut by beaver were used as food. As with other studies (e.g. Jenkins 1980, Belovsky 1984, Gallant *et al.* 2004), I assumed that all stems cut by beaver were directly related to energy intake. However, in the course of my research I observed beaver cutting non-food items (e.g., wooden transect posts, plastic culvert markers) and using cut stems for lodge and dam construction. In many of the natural experiments done relative to central place foraging and beaver there is no differentiation between a stem cut for construction purposes and that cut for food. It is this inability to fully determine the fate of a particular stem that discouraged me from using common electivity indices (Ivlev 1961, Jacobs 1974) to determine diet preference.

Along with the inability to determine the exact number of stems used specifically for food, I was also not able to establish exact density measurements for ungulates outside the study area and had to rely on pellet counts to establish relative densities. A true controlled experiment would be the only way to determine exact use of shared resources by each species.

Despite these limitations, my findings indicate that beaver within EINP are able to adapt their foraging behaviour to accommodate differences in resources due to higher ungulate densities and the consequent competition for shared resources. Vegetation in the park showed several impacts of browsing by ungulates. Lower stem densities, smaller diameters, and hedged stems likely resulted in lower available biomass. Regardless, beaver were still able to access adequate resources as indicated by the long-term occupancy of the study lodges. We do not know, however, where the threshold lies between coexistence between ungulates and beaver in EINP and competitive exclusion as seen in other areas (Baker *et al.* 2005, Baker 2003, Nietvelt 2001, Singer 1998, Kay 1994). We also do not know how major landscape perturbations such as drought and fire would affect the availability of forage for beaver in environments of intense ungulate herbivory.

Research in other areas, where *Salix* is the key forage species for beaver, showed marked reductions in beaver when exposed to high elk densities (Baker *et al.* 2005, Baker 2003, Nietvelt 2001, Singer 1998, Kay 1994). In the boreal mixed-wood conditions of my study, perhaps the very productive riparian areas created by beaver allow them to accommodate decades of competition with larger herbivores. In this sense, beaver might be the superior consumer, as it can modify both behaviour and habitat to its own advantage.

A logical extension of this research would be to determine whether there are predictable thresholds for competition between beaver and other herbivores and whether this competition could be incorporated into existing optimal foraging models for beaver. In addition, it is often noted that beaver enhance forage species for other herbivores (Naiman et al. 1986, 1988, Grover and Baldassarre 1995), yet there is little known about whether, given the right circumstance, beaver has the potential to be the superior competitor.

5.5 CONCLUSION

Although other studies have found competitive exclusion of beaver in managed areas with high densities of elk, I have shown competitive exploitation in an area with high densities of multiple ungulate species. The study area, a highly productive mixed-wood boreal forest, supported a suite of forage species, which may have allowed beaver to adapt to ungulate competition, unlike other study areas where these forage species are centralized in limited montane habitats. EINP and areas surrounding the park provide an ideal location to compare how differing ungulate densities and their associated impacts on vegetation influence foraging by beaver. Some notable changes in foraging decisions by beaver (e.g., shorter forage distances, increased use of mature *Populus* trees), indicated competitive exploitation by ungulates on food resources for beaver. However, despite lower stem densities and smaller diameters for many species within EINP, beaver were still able to select preferred foods and maintain a diet breadth equivalent to beaver in areas with lower ungulate densities.

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6.0 SYNTHESIS AND CONCLUSION

6.1 BACKGROUND AND RATIONALE

Riparian habitats represent a transition between aquatic and upland ecosystems and, as such, possess high levels of biodiversity and increased nutrient exchange derived from the two adjacent ecosystems (Gregory *et al.* 1991, Naiman *et al.* 1993). Beaver (*Castor canadensis*) play an important role in riparian habitats, as they create and maintain wetlands and, in turn, riparian zones (Naiman *et al.* 1988). They impound water through the construction of dams and thus modify riparian vegetation communities through changes in soil moisture and chemistry and they also impact vegetation through the removal of select species during their foraging activities. For that reason, they have been called ecosystem engineers (Wright *et al.* 2002). These changes in vegetation and soils create habitats for numerous species. Along with beaver activities, other processes such as fire and herbivory can significantly affect riparian habitats. Though their combined effects have not often been examined.

Fire is a natural process and plays a key role in nutrient exchange in soils and water (Bayley *et al.* 1992, Neary *et al.* 1999, Naiman *et al.* 2000, Bisson *et al.* 2003). It also contributes to the regeneration of plant communities in terrestrial and aquatic ecosystems (Bartos and Mueggler 1979, Bailey *et al.* 1990, Bisson *et al.* 2003). It can affect vegetation directly by removing older stems and promoting suckering from surviving roots in existing plants (Bork *et al.* 1997, White *et al.* 1998). As well as prompting releases of nutrients into soil, fire can also open up forest canopies and facilitate the growth of more fire tolerant species such as *Rubus idaeus* and *Corylus cornuta* (Anderson and Bailey 1979, Bork *et al.* 1997).

In many areas subject to decades of fire suppression activities, fire has been reintroduced as a tool to re-establish forage species such as grass (Bailey *et al.* 1990) or aspen (White *et al.* 1998, Bailey and Whitham 2002). This practice is true in areas supporting large herbivores such as elk and bison (Blyth and Hudson 1987, Vinton *et al.* 1993). Although fire is also often assumed to benefit smaller herbivores such as beaver (Kellyhouse 1979, Naiman *et al.* 1988), very little empirical research exists to confirm these assumptions. Given the ecological importance of beaver, the effect of fire on beaver populations warrants more investigation. This issue is examined in Chapter 2.

The modification of ecosystems by beaver and to some degree, ungulates, can influence both fire behaviour and severity. In their study of the effects of fire, topography, and herbivory by ungulates on *Populus* forests in Elk Island National Park (EINP), Bork *et al.* (1997) found that herbivory reduced the regeneration of *Populus* forests more than did burning alone. Romme *et al.* (1995) found similar results following the fires in Yellowstone National Park where browsing was so intense as to inhibit aspen regeneration in burned stands. By foraging shrubs, ungulates can inadvertently reduce mid-layer fuels and increase the potential of crown fires (Hobbs 1996). Through their flooding and foraging activities, beaver create aquatic and vegetative patches throughout the landscape (Johnston and Naiman 1987, Donkor and Fryxell 1999), which can alter the intensity and movements of fire. In times of drought, when fire severity and frequency are predicted to increase (Camill and Clark 2000, Hogg and Bernier 2005), wetland creation and retention due to beaver activities has important implications in sustaining hydrologic regimes that support riparian vegetation communities and mitigating large scale losses of wetlands. This issue is examined in Chapter 3.

Herbivory can also affect plants at landscape scales (Hobbs 1996). Many studies have examined the effects of ruminants (e.g., ungulates) and hindgut fermenters (e.g., hare and beaver) on vegetation, but rarely are the two studied in combination. From individual studies, we know that mammalian herbivores can alter forest structure through selective foraging (Risenhoover and Maass 1987, Donkor and Fryxell 1999) and induce metabolic and morphological defenses in plants such as the output of increased secondary metabolites (Basey *et al.* 1990) or the production of defensive structures such as thorns. Foraging can also encourage compensatory growth in some species of plants, such as willow (*Salix* spp.) through increased annual net primary production by means of additional branching (Hobbs 1996, Baker *et al.* 2005). Foraging can also open up areas where less palatable species can thrive (Donkor and Fryxell 1999). Multiple herbivore systems present unique challenges given the differing foraging strategies and the degree to which individual plant species are altered by herbivores. Beaver, as central place foragers (Orions and Pearson 1979), cut entire stems and transport them to their lodge or feeding platforms, while ungulates are able to move from patch to patch and remove only select parts of a stem (e.g., new stem growth and leaves). The effects of foraging by these species on the composition and structure of vegetation communities can be dramatically different, given the marked differences in foraging behaviour between them. The effect of foraging on riparian vegetation communities is examined in Chapter 4. Having evolved together, some plant-herbivore interactions are described as mutualistic, such as the relationship between beaver and willow (Baker *et al.* 2005). There are some who argue, however, that even mutualistic relationships can deteriorate within multi-herbivore systems where the foraging activities of one species compromise the resource to the detriment of other herbivores. Competition between herbivores can result in altered foraging strategies, reduced fitness or, ultimately, the complete exclusion of one or more of the competitors. In some areas of the Rocky Mountains, competition between ungulates and beaver has been implicated in a decrease in beaver populations due to extremely high levels of herbivory by elk on willow and aspen, key forage species for both elk and beaver (Kay 1994, Nietvelt 2001, Baker *et al.* 2005). Kay (1994) maintained that beaver were extirpated from the northern range of Yellowstone National Park due to repeated browsing of willow and aspen by ungulates. Nietvelt (2001) found similar trends in Banff National Park, Canada where he determined that elk had excluded beaver from wetland sites in the Vermilion Lakes area. Ultimately, the degree to which two or more species can compete depends on the amount of niche overlap (Hardin 1960), resource availability, and the adaptability of competitors. In a natural context, where fires and drought can limit beaver survival, how does herbivory by ungulates, who use similar woody forage, affect beaver? This question is examined in Chapter 5.

Fire, flooding by beaver, and herbivory, are important ecological processes in Elk Island National Park. The effects of one process can directly and indirectly impact the others through a complex web of interactions. Fire and flooding directly influence habitat. Fire alters vegetation structure and composition, thereby impacting the available habitat for beaver and ungulates. Flooding creates habitat for beaver and enhances riparian vegetation communities used by both beaver and ungulates. The degree to which water is available is also controlled by climate and, ultimately the relationship between these biotic and abiotic factors. Fire and flooding in turn affect patterns of herbivory. Multiple herbivores not only shape the resource itself; their use of these critical resources also can indirectly affect the foraging activities of other herbivores through competition.

The impact of fire on beaver is poorly understood and, until now, unsupported by empirical evidence; however, its effects on vegetation communities are well documented (Bartos and Mueggler 1979, Bailey *et al.* 1990, Bisson *et al.* 2003). I examined the impact of fire on beaver first to clarify the role of this ecological process due to the extensive use of fire in Elk Island National Park. Based on my findings, the remainder of this study was confined to unburned areas. The chapters in this dissertation presented a sequential examination of the interactions described above, beginning with fire, then water, then landscape scale herbivory, and ending with competition.

6.2 THE EFFECTS OF PRESCRIBED FIRE ON BEAVER (Chapter 2)

I examined the effects of prescribed burning on beaver lodge occupancy in the mixed-wood boreal forests of Elk Island National Park (Chapter 2). My objectives were to determine 1) whether beaver lodge occupancy was lower in areas that had been burned than in unburned areas over and above differences in wetland availability, 2) whether a decrease in beaver lodge occupancy in burned areas resulted in a predictable reoccupation of these areas over time, 3) whether the frequency of burning and the time since the last fire affected lodge abandonment, and 4) whether distances between abandoned and active lodges differed between burned and unburned habitats (such increases in distance could have implications for the re-colonization of abandoned areas through juvenile dispersal and dispersal of beaver from burned habitats to more suitable habitats).

A total of 734 lodges were categorized as to their location within areas of Elk Island National Park. Lodges were classified as "burned" if they had been exposed to fire at least once between 1979 to 2002 and "unburned" if they had never been exposed to fire. I then used long-term data on occupancy of the beaver lodges to assess the effects of burn frequency, time since the lodge area was last exposed to fire, and the distance of each lodge to the nearest active lodge on lodge occupancy by beaver. I also assessed wetland availability in both burned and unburned areas to determine whether wetlands might be driving the differences in lodge occupancy rather than fire.

Although the total area of wetland coverage did not differ significantly between burned and unburned areas, beaver lodge occupancy in areas that were exposed to fire was almost 16% lower. The number of times an area was burned accounted for 68% of the AIC weight in a model that included both burn frequency and the distance to the nearest active lodge (time since last burn was highly correlated to burn frequency and was removed from the model). According to this model, the odds of a lodge being active decrease by 0.58 for each additional burn. I determined that there was a decrease in lodge occupancy after more than one burn and after 3 burns, lodges were often permanently abandoned. In areas burned prior to green-up, some lodges and dams were completely destroyed by fire and the area was promptly abandoned.

In an area of the park that had been intensely burned during a severe drought (2000 to 2002), I found a dramatic decrease in lodge occupancy with very little recovery (from 15 active lodges to 3 following the burn). In addition, EINP has some of the highest densities of ungulates in North America (Blyth and Hudson 1987), which Bork *et al.* (1997) found to be drawn to burned areas. It is possible that due to the high levels of herbivory in the park, even moderate fire does not benefit beaver in this highly grazed system. The interactive effects of high levels of herbivory, an increasingly warming climate, and fire on beaver lodge occupancy warrants further research due to the important role of beaver in the creation and maintenance of wetlands and associated riparian habitat.

6.3 BEAVER REGULATE WETLANDS DURING DROUGHT

The objective of Chapter 3 was to examine whether beaver, climate or some combination thereof drives retention of open water areas in wetlands. Specifically, I determined 1) whether beaver increased the area of open water in wetlands, 2) whether beaver maintained areas of open water during drought, 3) the importance of precipitation and temperature in creating and maintaining open water wetlands in the presence of beaver, and 4) the effects of precipitation and temperature on open water in wetlands when beaver were absent from the models.

I analyzed 12 separate years of aerial photographs between 1948 and 2002 to measure the area of open water in Elk Island National Park. Photographs were scanned and then georectified in a geographic information system (GIS) to make them spatial relevant. All open water (excluding all burned areas) was digitized and areas calculated to determine the total area of open water area for each year. When compared to the number of active beaver lodges and various precipitation and temperature variables, I determined that the presence of beaver explained over 80% of the variability in the area of open water over the 54-year period. The best combined model that explained the greatest amount of variability in the area of open water in EINP included active beaver lodges, mean maximum annual temperature, and mean 2-year precipitation ($R^2 = 0.87$, $P = 0.00075$). Within this model, the presence of active beaver lodges was the strongest predictor of open water coverage in the park (relative Pratt index $d_j = 0.8492$). Neither mean maximum temperature (relative Pratt index $d_j = 0.0784$), 2-year mean annual precipitation (relative Pratt index $d_j = 0.0733$), nor any other climatic variable, significantly affected the amount of open water in wetlands.

Beaver were not present in the area of interest in 1950 (the 2nd driest year of the study), so I was able to determine how the presence of beaver were able to affect open water areas by contrasting drought periods without beaver (1950) with drought periods with beaver (2002). In 1950, when beaver were not present, wetlands held 61% less open water than in 2002 (the driest year on record and when beaver were well established), despite the fact that 1950 had 47% more precipitation.

The ability of beaver to create and maintain wetlands is well documented (Johnston and Naiman 1987, Naiman *et al.* 1988); however there is little data to illustrate the importance of beaver during periods of drought or in non-riverine landscapes. Given the ability for beaver to mitigate wetland loss even during periods of extreme drought, the removal of beaver from aquatic systems should be recognized as a wetland disturbance equivalent to in-filling, draining, groundwater withdrawal, and other common wetland disturbances.

6.4 RIPARIAN PLANT COMMUNITY RESPONSE TO HERBIVORY BY BEAVER AND UNGULATES

The objective of Chapter 4 was to quantify the effects of four levels of ungulate and beaver herbivory on the composition and structure of riparian vegetation. Specifically, I tested the hypotheses that 1) vegetation cover would decrease in areas with high levels of beaver and ungulate densities, 2) stem heights would be lowest in areas with the highest densities of beaver and ungulates, 3) species diversity would be highest at intermediate levels of herbivory (areas lacking either beaver or high densities of ungulates), and 4) species diversity would be lowest at sites with no beaver and low densities of ungulate.

I used a stratified random sampling design to select 5 ponds for each of 4 combinations of herbivores: 1) low beaver + low ungulate densities (LBLU), 2) low beaver + high ungulate densities (LBHU), 3) high beaver + low ungulate densities (HBLU), and 4) high beaver + high ungulate densities (HBHU). Through the use of pellet group counts and assessment of the severity and degree of browsing on plants, I confirmed that ponds classified as "high ungulate" had more than 3 times the number of pellet groups than those classified as "low ungulate". The number of pellet groups deposited by elk was 6 times that of areas outside the park. The percent of stems browsed and the browse severity (determined by morphological changes of the stems due to browsing) were also higher in areas classified as "high ungulate". All "high ungulate" sites were within EINP, while all "low ungulate" sites were outside the park. I was also able to develop a new measure that was the product of the percent of a stem that was browsed and the browse severity rating. This index of browse effects is called the Browse Impact Index and had a positive linear relationship to ungulate pellet group densities.

My results showed two main trends. In areas of high ungulate pellet group densities (HBHU and LBHU), vegetation exhibited significant responses to high levels of ungulate herbivory by producing shorter shrub heights and decreased cover by herbaceous dicots and emergent vegetation. In addition, disturbance tolerant species such as *Corylus cornuta*, though stunted, had significantly higher cover values in heavily browsed areas than in areas with lower ungulate densities. Although diversity for emergent vegetation was greater at areas with higher densities of ungulates than those with lower densities, there was no difference in diversity for the shrub community.

In areas with no beaver and lower densities of ungulates, I found that some species responded to decreased herbivory through a dramatic increase in shrub heights and percent cover. In particular *Salix* spp. were 4 times taller in LBLU areas than elsewhere and they were the only sites where *Amelanchier alnifolia* grew to tree height.

The Beaver Hills Region, of which Elk Island National Park is a major component, provides a unique opportunity to examine the effects of high ungulate herbivory and beaver on the composition and structure of riparian vegetation communities in mixed-wood boreal forests. Ungulates have been maintained at high levels within the park, while neighboring lands have significantly lower densities. I found that herbivory by ungulates represented the dominant effect of foraging on riparian vegetation. Over 91% of the plants examined in this study were browsed by ungulates, while only 3% were browsed only by beaver. The dramatic impacts ungulates have on shrub heights and vegetation cover could translate in reduced available biomass for themselves and other species. In addition, the vigor of the plants themselves is also compromised.

It was impossible to find any ponds within the area that had never been inhabited by beaver at some time; therefore residual effects of abandoned ponds could still have been influencing riparian vegetation. Although areas outside EINP had lower densities of ungulates, these animals were still present and as such, their foraging activities had an obvious impact on vegetation. Further research is required to determine the exact degree to which ungulates and beaver, in combination or individually, affect riparian vegetation. To accomplish this objective, additional categories would be required that completely exclude the effects of either beaver or ungulates, or both.

6.5 THE EFFECTS OF HIGH UNGULATE DENSITIES ON FORAGING BY BEAVER

The objective of Chapter 5 was to examine whether competitive exploitation exists between beaver and ungulates by comparing a system with high ungulate densities to a system with lower ungulate densities. Specifically, I tested whether 1) ungulate pellet group densities in Elk Island National Park are significantly higher than those in the surrounding area, 2) stem densities and diameters of key forage species differ in areas with higher levels of competition, 3) beaver alter their forage selection to less preferred food plants to compensate for a potential decrease in preferred forage in areas with high levels of competition with ungulates, and 4) beaver forage farther from the pond edge in areas with higher ungulate densities than areas with lower densities.

I determined that in areas with high levels of ungulate herbivory (EINP) there was a general, but not significant, trend toward lower densities of woody stems than in the areas with significantly fewer ungulates immediately adjacent to the park. Select genera, including *Populus*, *Prunus*, *Viburnum*, and *Rosa* had significantly lower stem densities inside the park than outside. In addition to differences in stem densities, stem diameters were also smaller inside the park where ungulate herbivory was more intense. Despite these differences, beaver in EINP still selected stems within the same size classes as beaver outside the park except for *Amelanchier alnifolia* and *Viburnum* spp., which were of smaller diameter inside the park. *Populus* spp. and *Corylus cornuta* accounted for 65% to 92% of the stems cut by beaver, although in both areas, beaver cut a broad spectrum of woody shrubs. The amount of *Populus* spp. and *C. cornuta* cut by beaver reflected the relative densities of these two common shrub species. Overall species-specific density explained 55% of the variability in the amount of stems beaver cut of each species.

There were two notable differences in the foraging choices by beaver within EINP in the context of high ungulate herbivory. Beaver inside the park harvested more mature *Populus* trees relative to their availability than beaver outside the park (10% versus 1% of the total number of *Populus* stems cut by beaver). By cutting larger trees, it is plausible that beaver inside EINP were compensating for the lower densities of smaller sized *Populus* stems. Cutting large trees allows beaver to access numerous stems (branches) that are of equivalent size to single stems cut within the foraging areas. However, this access comes at a considerable effort and risk of predation, due to the increased time required to fell these larger trees.

Secondly, beaver inside the park had shorter foraging distances from the pond than beaver outside EINP. Over 80% of the stems cut by beaver inside the park were within 30 m of the pond edge, while only 67% of the stems outside the park were cut within this same distance. The diameter of cut stems also increased with foraging distance for beaver within the park, but not outside EINP. It is possible that beaver in EINP are maximizing energy intake by foraging closer to their central place and maintaining shorter escape distances. Security cover is generally lower in the park due to lower stem densities and predators (coyotes) are more numerous (Pruss 2002). Also, because of the positive relationship between diameters of cut stems and foraging distance, maintaining shorter foraging distances would decrease handling time and energy expenditures.

Beaver in EINP appear to adapt their foraging strategies to accommodate high levels of herbivory and competition for food by ungulates. Competition for food resources exists between beaver and ungulates; however, neither beaver nor ungulates were excluded from the study area. The ability for beaver to adapt there behaviour and choices to lower levels of forage availability suggests that competition is exploitative, not exclusive. The riparian areas in the mixed-wood boreal forest provide numerous forage species to a broad range of herbivores. It is likely because of this diversity, multiple herbivores are able to co-exist in this ecosystem, despite high levels of herbivory. Future research is warranted, however, to determine whether there are predictable thresholds for competition between beaver and other herbivores and whether this aspect of competition could be incorporated into existing optimal foraging models for beaver.

6.6 DISCUSSION

In ecology, almost nothing occurs in isolation. A benefit to one organism could pose a loss to another, or facilitate access to resources for numerous species. In my research, I examined the impacts of four major ecological processes (fire, flooding by beaver, climate, and herbivory) on the configuration of riparian vegetation and the maintenance of beaver ponds in Elk Island National Park (EINP). Although examined as relatively distinct topics, their inter-relationships were immediately apparent (Figure 6.1) and it was easy to recognize that one process influenced the intensity or effects of other processes.

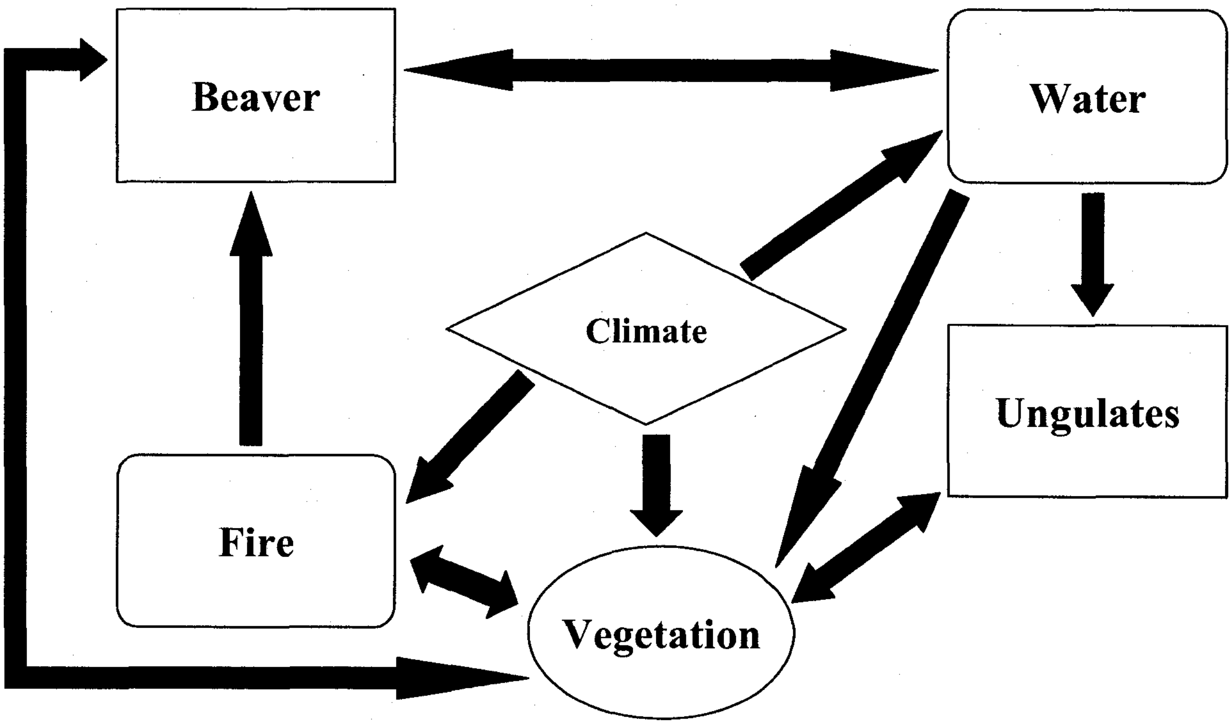

Figure 6.1. A generalized model of biotic and abiotic interactions in riparian communities shared by beaver and ungulates.

Climate is a central influence in all ecosystems, whether they are dominated by ice flows in the high Arctic or thick vegetation of the tropical rainforests. Such is the case with the forests of the mixed-wood boreal region. Increasingly, predictions of global warming and increased incidents of drought have brought the anticipated impacts of wildfires into the forefront in the boreal forest (Camill and Clark 2000, Hogg and Bernier 2005). With warmer and drier climates, fires are expected to burn larger areas at higher frequencies and greater intensities. As shown in my research, higher burn frequencies could negatively impact long-term occupancy of areas by beaver. In addition, vegetation and fire are intimately related: although vegetation feeds the fire and is thus altered, the structure and composition of the vegetation community also influence how fire moves across landscapes and the intensity at which it burns. As with fire, climate plays a role in vegetation community composition and structure, as plant productivity changes relative to temperature and moisture availability.

Flooding by beaver naturally regulates the amount of water available to riparian plant communities, even during drought. Beaver activities increase riparian and aquatic habitats, which in turn attract species that seek water and the diverse array of riparian vegetation. Following the establishment of a beaver colony, beaver modify the structure and composition of vegetation communities through the removal of shrubs and trees during their foraging activities. Beaver impoundments also increase soil moisture due to flooding and the creation of dendritic channels that radiate out from the pond edge. In addition, flooding causes alterations in soil chemistry by increasing the amount of reduced nitrogen and available forms of nitrogen in soil solutions (Naiman *et al.* 1988). The excavation and the constant movement of large quantities of mud during construction activities by beaver create large areas of soil disturbance suitable for seed propagation.

The use of riparian systems by other mammalian herbivores such as ungulates can also have dramatic effects at the ecosystem level (Risenhoover and Maass 1987, Hobbs 1996, Naiman and Rogers 1997). Intense herbivory resulting from high densities of ungulates within riparian areas can affect shrub heights and the density of select species. Average shrub heights within EINP were 15 cm shorter than shrub heights immediately adjacent to the park and stems were often hedged from heavy browsing by ungulates. In addition, mature forms of favored forage species for ungulates such as *Amelanchier alnifolia* were not present inside EINP, but grew to mature form in reference areas outside the park.

The influence of multiple foragers on the same resource can dramatically influence the quality or availability of the resource. Intense herbivory by a dominant competitor can lead to reduced biomass for other herbivores. Such is the case in many national parks in the Rocky Mountains, where high densities of elk have reduced the availability of willow and aspen for beaver (Kay 1994, Nietvelt 2001, Baker *et al.* 2005). Such exploitive competition, where species interact indirectly through the use of a shared resource, can result in reduced fitness of one or both competitors (Holt *et al.* 1994).

With ungulates and beaver, riparian vegetation is a shared resource. Although beaver are bound to a central place (their lodge), their foraging behaviour differs dramatically from ungulates. They are able to remove stems completely and bring them to their lodge or feeding platforms for further processing. This behaviour prevents ungulates from having further access to these resources and allows beaver to consume or store their food with minimal interference. In areas such as the mixed-wood boreal where there are highly productive vegetation communities, the combination of forage availability and diversity appears to allow beaver and ungulates to coexist, even in areas with high levels of herbivory.

Studying one aspect of ecology in isolation can neglect important relationships within ecosystems. Beaver can dramatically alter riparian communities, both to the benefit and detriment of other species. However, beaver are not impervious to the influences of other ecosystem processes such as climate, fire and herbivory. It is within these intimate relationships that one truly begins to appreciate the overwhelming complexity and the importance of beaver in the ecosystem. Their adaptability and ability to thrive in highly competitive and variable environments is testament to their resourcefulness. Their ability to mitigate even large scale disturbances, such as drought, underscores their importance in a world of changing climates and uncertain ecological change.

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Appendix

Species list by vegetation class for all plants identified in study area

Aquatics

Calla palustris
Ceratophyllum demersum
Hippuris vulgaris
Juncus spp.
Lemna minor
Menyanthes trifoliata
Polygonum sp.
Potamogeton sp.
Potentilla palustris
Ranunculus aquatilis
Sagittaria cuneata
Scirpus hudsonianus
Scirpus lacustris
Typha latifolia
Utricularia vulgaris

Horsetail

Equisetum arvense
Equisetum hyemale
Equisetum pratense
Equisetum sylvaticum

Herbaceous dicots

Achillea millefolium
Achillea sibirica
Adoxa moschatellina
Agastache foeniculum
Agrimonia striata
Anemone canadensis
Aralia nudicaulis
Aster borealis
Aster conspicuus
Aster puniceus
Aster umbellatus
Astragalus americanus
Bidens cernua
Brassica kaber
Chenopodium album
Cicuta bulbifera
Cicuta mackenzieana
Cicuta maculata
Cirsium arvense
Cornus canadensis
Epilobium angustifolium
Epilobium glandulosum
Epilobium latifolium
Erysimum cheiranthoides
Fragaria vesca
Fragaria virginiana
Galeopsis tetrahit
Galium boreale
Galium trifidum
Galium triflorum
Geum aleppicum
Geum macrophyllum
Geum rivale
Geum triflorum
Hieracium umbellatum
Lactuca tatarica
Lycopus asper
Lycopus uniflorus
Lysimachia thyrsiflora
Mentha arvensis
Mertensia paniculata
Petasites palmatus
Petasites sagittatus
Plantago major
Potentilla gracillis
Potentilla norvegica
Potentilla tridenta
Pyrola sp.
Ranunculus acris
Ranunculus lapponicus
Ranunculus macounii
Ranunculus sceleratus
Rorippa islandica
Rumex crispus
Rumex maritimus
Rumex occidentalis
Rumex salicifolius
Scutellaria galericulata
Senecio congestus
Sium sauve
Smilacina stellata
Smilacina trifolia
Solidago canadensis
Sonchus arvensis
Sonchus oleraceus
Stachys palustris
Stellaria longifolia
Stellaria longipes
Taraxacum officinale
Trifolium hybridum
Urtica dioica
Utricularia vulgaris
Veronica scutellata
Vicia americana
Viola canadensis

Moss

Aulacomnium palustre
Brachytecium rivulae
Sparganium angustifolium
Sparganium eurycarpum
Sphagnum angustifolium

Sedge

Carex aquatilis
Carex atherodes
Carex bebbii
Carex canadensis
Carex canescens
Carex diandra
Carex lasiocarpa
Carex scirpoidea
Carex utriculata
Eleocharis acicularis
Eleocharis palustris
Eriophorum angustifolium
Eriophorum vaginatum

Trees

Alnus rugosa
Amelanchier alnifolia
Betula papyrifera
Picea glauca
Populus balsamifera
Populus tremuloides
Prunus virginiana
Salix bebbiana
Salix planifolia

Shrubs

Alnus rugosa
Amelanchier alnifolia
Betula glandulosa
Betula papyrifera
Cornus stolonifera
Corylus cornuta
Kalmia polifolia
Lonicera dioica
Lonicera involucrata
Myrica gale
Populus balsamifera
Populus tremuloides
Prunus pensylvanica
Prunus virginiana
Ribes americanum
Ribes glandulosum
Ribes hudsonianum
Ribes lacustre
Ribes oxyacanthoides
Ribes triste
Rosa acicularis
Rosa woodsii
Rubus idaeus
Rubus parviflorus
Rubus pubescens
Salix arbusculoides
Salix bebbiana
Salix discolor
Salix glauca
Salix lasiandra
Salix maccalliana
Salix mackenzieana
Salix monticola
Salix myrtillifolia
Salix pedicellaris
Salix petiolaris
Salix planifolia
Salix pyrifolia
Salix scouleriana
Salix serissima
Salix sitchensis
Shepherdia canadensis
Spiraea alba
Symphoricarpos albus
Symphoricarpos occidentalis
Viburnum edule
Viburnum opulus