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HERBIVORY INTERACTIONS BETWEEN BEAVER (*CASTOR CANADENSIS*) AND ELK (*CERVUS ELAPHUS*) ON WILLOW (*SALIX* SPP.) IN BANFF NATIONAL PARK, ALBERTA

by

Clifford G. Nietvelt ©

A thesis submitted to the Faculty of Graduate Studies and research in partial fulfillment
of the requirements for the degree of Master of Science.

in

Environmental Biology and Ecology
Department of Biological Sciences

Edmonton, Alberta
Spring 2001

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Dr. Suzanne E. Bayley

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Dr. J. Brad Stelfox

Date: Dec 13, 2000

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DEDICATION

This thesis is dedicated to the loving memory of my mother, Thérèse Philomenia Johanna Spoorenberg Nietvelt, who sadly passed away before the completion of this thesis.

ABSTRACT

I examined the herbivory interactions between beavers (*Castor canadensis*), elk (*Cervus elaphus*), and willow (*Salix* spp.) in the Bow Valley in Banff National Park, Alberta. I found that beavers foraged selectively on willow, selecting larger than average stems of tall (≥ 250 cm) willow. The amount of willow food biomass within 30 m of the shoreline of the Vermilion Lakes Wetland (VLW) is substantially lower than what was present near active beaver lodges in other areas, suggesting that there is insufficient food in the VLW for beavers at present time.

The combined effects of beaver cutting followed by elk browsing eliminated tall willow communities in the Vermilion Lakes Wetland. Willows that had been cut by beavers and browsed by high densities of elk were in shorter height classes (< 100 cm), than willow communities affected by either beaver or elk alone. These beaver-elk interactions may be an example of exploitative competition, where elk have excluded beaver from the Vermilion Lakes Wetland by browsing on willow.

I compared two areas of the Bow Valley, the central zone and the western zone. The central zone is characterized by high elk densities, few beaver, few wolves, heavy human presence, short heavily browsed willow, and low songbird diversity and abundance, while the western zone is characterized by low elk densities, beaver with adequate food resources, wolves, lower human presence, tall lightly browsed willow, and higher songbird diversity and abundance. These interactions were consistent with a top-down (predator driven), trophic cascade ecosystem, where the presence or absence of large predators, in this case wolves, has had a dramatic effect on lower trophic levels.

ACKNOWLEDGMENTS

I wish to thank the many people involved with this project. Firstly I would like to extend a huge thanks to Parks Canada Conservation Biologist Cliff White who was entirely responsible for initiating this project and brought to me Banff National Park. I especially thank Cliff for allowing me the freedom to design and conduct this project, ensured that funding was in place, encouraged me to pursue graduate studies, and his enthusiasm throughout; words cannot describe how grateful I am. I also wish to thank my graduate supervisor, Dr. Suzanne Bayley who helped with study design, her patience with me as I butchered the English language, and her continued support and understanding throughout this entire project, which were at times "difficult." I wish to thank Aquatics Specialist Charlie Pacas (Parks Canada), Faunal Specialist Tom Hurd (Parks Canada), Fire and Vegetation Specialist Ian Pengelly (Parks Canada), who provided critical feedback on reports and for their generally enthusiasm throughout. Extended thanks to Tom Hurd and Cliff White for providing accommodation and office space. I wish to thank my committee members whom, Dr. Stan Boutin and Dr. Brad Stelfox, for critical comments on sampling design, for without, this thesis would have suffered greatly. I would also like to thank Dr. John Spence, who agreed to be my external examiner on very short notice.

Many big thanks to my invaluable field assistant Eoghan Debarra, who's hard work, sense of humor, and being able to put up with me day in and day out made the first field season a success. Thanks to others who have helped with my field work: field assistant Kim Barry, for volunteering many hours under less than ideal conditions; Gosia Bryja Sylvia Wood and Rob Serrouya for helping with beaver foraging and browse

surveys; Mark Hebblewhite for conducting the songbird surveys; Joanne Hatalcik, Barb Wilson, Shelly Bird for help with ungulate pellet counts and browse surveys. I would like to thank the staff at the Department of Botany, University of Calgary, for use of their drying ovens.

Huge thanks to the many friends and colleagues that have made the writing of this thesis less painful: Victor Delac, Adam Henwood, Rob Serrouya, Pete Smillie, Mark Hebblewhite, Cliff White, Tom Hurd, Charlie Pacas, Ian Pengelly, Kjerstin Gustafson, Sheena Majewski, Stephanie Zyvatkauskas, Joe Jazvac, Danah Duke, Timm Kaminski, Brian Chruszcz,...all apologies to those who I have forgotten!

Last, but not least, I would like to thank my family, Myra, Gary, Ken and Marika for their support throughout. I especially thank my mother, for without her love and support, this thesis would not have been possible.

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CHAPTER 1

GENERAL INTRODUCTION

"The ordinary citizen today assumes that science knows what makes the community clock tick; the scientist is equally sure that he does not. He knows that the biotic mechanism is so complex that its workings may never be fully understood."

--Leopold (1949)

"Like blind men touching different parts of the elephant and disagreeing about its form, those engaged in the debate about deer management in parks are viewing different parts of the ecological system. None has seen the entire system, and consequently, there is neither common agreement on the nature of the problem nor on the solutions."

--Porter and Underwood (1999)

INTRODUCTION

Due to their size, longevity, food and habitat requirements, large mammals tend to have a substantial impact on ecosystems (McNaughton et al. 1988, Naiman 1988). Activities such as browsing and grazing by large herbivores can have substantial impacts on the vegetation (Gerresheim 1970, Laws 1970, Kay 1990, Singer et al. 1994).

In North America, there has been great concern about the effects of ungulates on ecosystem structure and function, especially in national parks where high densities of ungulates greatly impact the vegetation (Kay 1990, Porter and Underwood 1999). In Yellowstone National Park (YNP) in Wyoming for example, elk (*Cervus elaphus*) on the northern range are present in very high densities, with approximately 15-20 elk per km^2

(Coughenour and Singer 1996). They have had a large impact on woody vegetation, including willow (*Salix* spp.), aspen (*Populus tremuloides*) and cottonwood (*Populus* spp.) (Kay 1990, Chadde and Kay 1991, Singer 1996). Browsing has caused height suppression and elimination of willow, prevented aspen and cottonwood from regenerating, and may have caused a significant decline in these species (Kay 1990, White et al. 1998). The impact of elk on woody vegetation may have been detrimental to other wildlife such as beavers (*Castor canadensis*), white-tailed deer (*Odocoileus virginianus*), and songbirds (Kay 1990).

One major concern in YNP is the decline of tall willow and beaver (Jonas 1955, Kay 1990, Singer et al. 1994). Jonas (1955) and Kay (1990) proposed a hypothesis that the interactive effect of elk and beaver caused the decline of tall willow communities. They suggested that beaver cutting of large willow stems, followed by browsing by high densities of elk could cause a decline of tall willow, as well as a decline of beavers. However no data to support this claim were presented. Kay (1990) suggested that beavers have been competitively excluded by elk on the Northern Range of YNP, but did not present data on willow to support this concept of exploitative competition (as defined by Holt et al. 1994). Exploitative competition occurs when two species have no direct interactions, but interact through a third species or resource (Krebs 1994: 258-259). When exploitative competition occurs, the species that will persist (the winner) is one that depresses the resource to the lowest level consistent with its own maintenance, relative to the needs of the competing species. This is known as the R* rule (Holt et al. 1994, Tilman 1990).

The loss of beavers, a keystone species, could have significant ecosystem impacts due to their dam building activities (Naiman et al. 1986, Mills et al. 1993). Beavers create and maintain riparian and wetland habitats, both of which are critical habitat to many animal and plants species (Naiman et al. 1988).

Some ecologists have stated that ungulates have become too abundant in parks due to the absence of large predators, such as wolves (*Canis lupus*) (Kay 1990, Peterson 1999, Porter and Underwood 1999). The major debate about ungulates in national parks and their role in the ecosystem is whether or not these ecosystems are structured from the top-down (predator driven) or the bottom-up (resource driven) (Hunter and Price 1992, Estes 1996, White et al. 1998, Peterson 1999). In a top-down ecosystem, predators and top consumers influence lower trophic forms (a trophic cascade), as opposed to a bottom-up ecosystem where herbivores are regulated by food supply (resource driven) (Hunter and Price 1992, Estes 1996). Since the late 1960's, the National Park system in the United States has adopted a natural regulation policy, whereby ungulates were regulated by food supply, and predators were not considered essential (a bottom-up view) (Cole 1971, Porter and Underwood 1999). However, there is mounting evidence that predators can have a substantial impacts on prey populations and ecosystem dynamics in studies on sea otters (*Enhydra lutris*), sea urchins (*Strongylocentrotus* spp.), and kelp forests on the Pacific coast of North America (Estes and Palmisano 1974), gray wolves, moose (*Alces alces*), and balsam fir (*Abies balsamea*) on Isle Royale, Michigan (McLaren and Peterson 1994), and coyotes (*Canis latrans*) in a shortgrass prairie ecosystem in western Texas (Henke and Bryant 1999).

BACKGROUND, PURPOSE AND OBJECTIVES

The primary focus of this thesis was to examine the interactions between beavers, elk, and willow in the Bow River Valley (BRV) (51° 07' N, 116° 30' W) of Banff National Park (BNP), Alberta (Figure 1.1). My goals were to examine the hypothesis proposed by Jonas (1955) and Kay (1990) (mentioned earlier) that cutting of large willow stems by beavers followed by browsing by elk at high densities could cause a decline of tall (≥ 250 cm) willow, as well as a decline of beavers. The concern in BNP was that there have been large declines in the number of active beaver lodges in the Vermilion Lakes Wetland since the early 1980's (see Chapter 3 in this thesis). I hypothesized that the decline in the number of active beaver lodges was attributable to the increase in elk numbers in the Vermilion Lakes Wetland (VLW). Associated with this increase in elk numbers would be the potential for herbivory interactions between beavers, elk, and willow. These interactions between beavers, elk and willow, which may have resulted from an increase in elk numbers, have been attributed to different patterns in human use and responses by wolves in the Bow Valley (Paquet et al. 1996, Woods et al. 1996). Thus, this thesis addressed willow-beaver-elk interactions at different spatial scales.

In Chapter 2, "Assessing Suitable Beaver Habitat Based on Foraging Patterns in the Vermilion Lakes Wetland, Banff National Park, Alberta," I investigated the foraging patterns of beavers for both willow and aspen food types, and used these data to evaluate beaver habitat in the VLW. My hypothesis was that beavers have declined in the VLW due to an inadequate food supply, namely tall willow. The objectives of this chapter were to:

1) Quantify and describe the differences in the foraging patterns of beavers for aspen and willow, the two main food types in the Central Canadian Rockies (Holroyd and Van Tighem 1983). I predict that there should be differences in the foraging strategies by beavers for these two species.
2) Quantify stem selection by beavers for willow. This is important since the size of willow that beavers select will be important in assessing beaver habitat.
3) Compare the available willow biomass (based on stem diameter) in areas of low beaver numbers to areas with high beaver numbers.

After determining the ecological relationship between beaver and willow, I investigated the effect of elk on beaver and willow interactions. In Chapter 3, "Herbivory on Willow by Elk and Beaver in Banff National Park, Alberta," the objective was to evaluate how the willow community structure may change with herbivory by elk alone, by beaver, and elk *and* beaver. My hypothesis is that beaver cutting of willow stems followed by heavy browsing by high densities of elk may reduce or eliminate tall willow communities. Beaver stem cutting of tall willow followed by heavy browsing by high densities of elk will result in willows in short height classes, which may be detrimental to beaver populations in the VLW.

If the above hypothesis is true, I predict the following:

1) Beaver harvesting of willow in areas of low elk densities with low browsing will have willows in many height classes.
2) Conversely, in areas with no beaver and both low and high elk densities, the willow community will have tall height classes.

3) In areas of high elk densities, elk will remove more of the twig biomass than will be produced by the willow each year. Combined with beaver stem cutting, this will suppress the height the of willow. Similarly, in areas of low elk densities, elk will remove less twig biomass than will be produced by the willow.

After documenting the effect of beaver and elk on willows, I wanted to quantify the broader ecological processes that may be occurring in the Bow River Valley. In Chapter 4, "Interactions Between Beaver, Elk and Willow in Banff National Park, Alberta: Evidence for a Trophic Cascade in a Wetland Ecosystem," the objective was to examine the potential top-down, trophic interactions between beavers, elk, willow, wolves, humans and biodiversity in the Bow River Valley of Banff National Park, Alberta, summarizing data from Chapters 2 and 3 with some additional data. I attempt to quantify ecological processes in two treatment areas of the BRV: the central zone (with high elk densities, few predators, heavily browsed willow, and few beaver); and the western zone (with low elk densities, presence of predators, lightly browsed willow, and active beaver lodges). I will present data on:

1) The condition of willow in the central and western zone summarized from Chapter 3;
2) Populations trends of wolves and elk in the central and western zones, and how the populations trends of wolves and elk relate to anthropogenic influences;
3) Population trends of beavers in the VLW (central zone) and how they relate to the populations trends of elk;
4) Brief documentation of songbird diversity and abundance in tall and short willow communities. Short willow communities with heavy browsing should support low bird species diversity and abundance;

5) Use these data to present conceptual models of these interactions.

Chapter 4 summarizes the data in Chapters 2 and 3 and places it in context of the ecological and human forces in Banff National Park.

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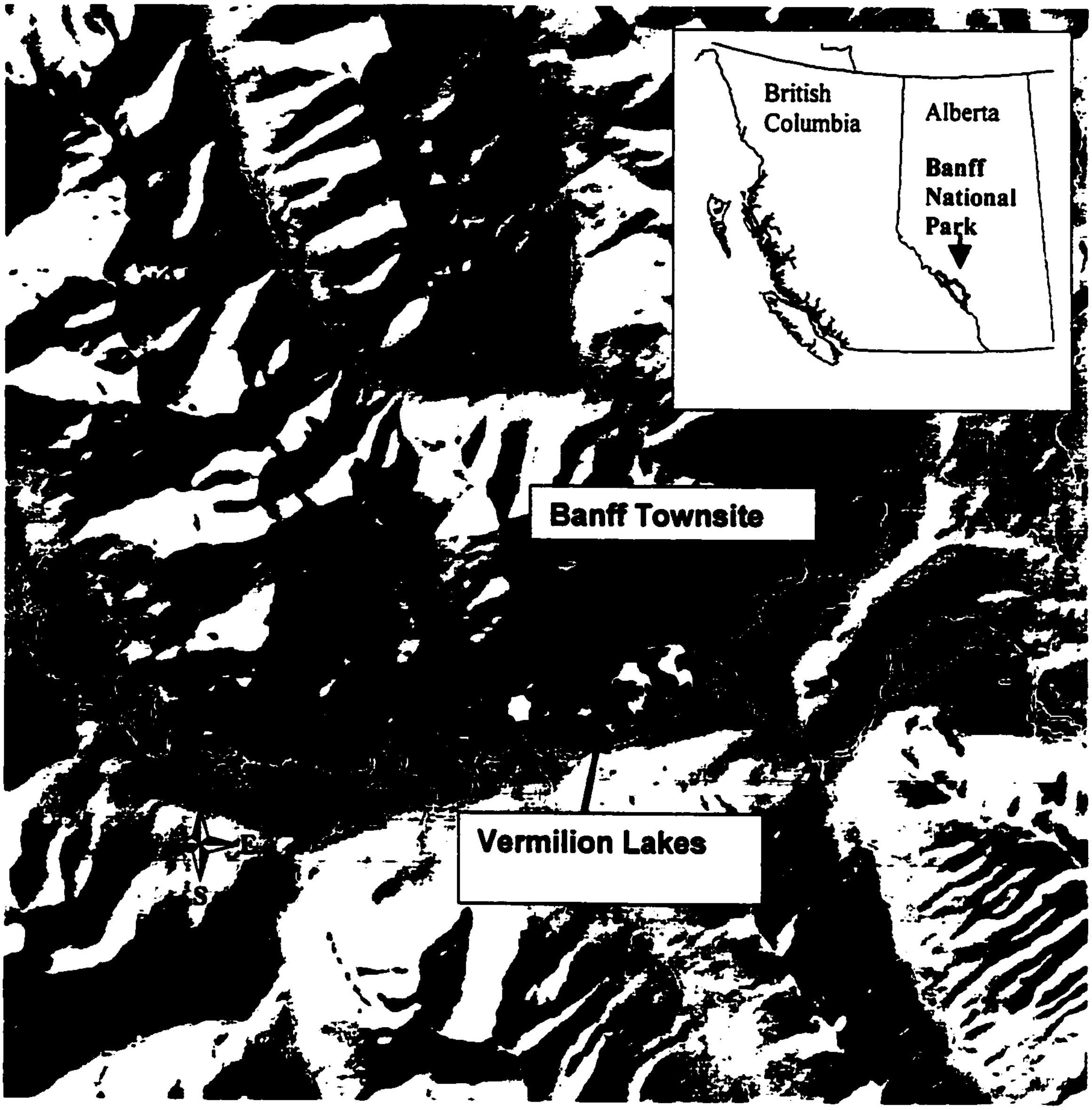

Figure 1.1: The Vermilion Lakes Wetland and Bow River Valley, Banff National Park, Alberta.

CHAPTER 2

ASSESSING SUITABLE BEAVER HABITAT BASED ON FORAGING PATTERNS IN THE VERMILION LAKES WETLAND, BANFF NATIONAL PARK, ALBERTA

INTRODUCTION

Beavers (*Castor canadensis*) feed primarily on woody vegetation, and are considered "choosy" generalist herbivores (Jenkins 1980). This implies that while beavers may feed on many different species of woody vegetation, they exhibit a strong preference within and among species (Jenkins 1979, 1980, Belovsky 1984, Fryxell and Doucet 1993). Generally, to obtain woody vegetation, beavers make forays onto land, cut a tree or stem and bring it back to the water or lodge for consumption, or to be placed onto the dam or lodge (as building material) (Jenkins and Busher 1979). Since beavers are aquatic mammals that require woody vegetation, restricted to riparian environments along streams, rivers, and lakes, although they typically dam streams to create ponds (Jenkins and Busher 1979, Howard and Larson 1985). Adequate amounts of woody vegetation must be present and accessible in order for beavers to construct lodges (Howard and Larson 1985).

Few studies have attempted to assess suitable beaver habitat. Howard and Larson (1985) developed a stream classification system for beaver, whereby habitat variables were quantified from aerial photographs to estimate the number of active beaver colonies. Likewise, Slough and Sadleir (1977) quantified beaver habitat factors and related them to beaver colony density in northern British Columbia. They calculated the number of beaver colonies an area could sustain given the amount of aspen forest that was accessible to beavers. However, these studies were not based on actual observed foraging patterns of beavers in their study area. The foraging behaviour of beavers may influence or determine suitable habitat (Howard and Larson 1985, Basey and Jenkins 1995). Factors such as distance from the water to woody vegetation, the density or biomass of woody vegetation and the presence of predators may be critical.

In the Vermilion Lakes Wetland (VLW) of Banff National Park (BNP), the number of active beavers lodges has declined substantially in recent years, and I hypothesize that there is inadequate woody vegetation, namely willow (*Salix* spp.) and aspen (*Populus tremuloides*), to support beavers.

The purpose of this study was to:

1) Quantify and describe the differences in the foraging patterns of beavers for aspen and willow, the two main food types in the Central Canadian Rockies. I hypothesize that there should be differences in the foraging strategies for these two species, where beavers will travel longer distances for aspen.
2) Quantify stem selection by beavers for willow. I hypothesise that beavers preferentially select tall, large-stemmed plants, which is a very important component of beaver habitat.
3) Calculate the willow biomass in the VLW based on stem diameter.

Assessing suitable beaver habitat based on a shrub species such as willow has not been attempted. Previous research efforts to assess beaver habitat have been for tree species such as aspen. Willow is a very important food resource for beavers in western North

America (Baker and Cade 1995), and information is needed to assess the quality of beaver habitat for this food resource.

METHODS

Study Area

Beaver habitat in two watersheds were sampled: the Bow River Valley (BRV) (51° 07' N, 116° 30' W) inside and outside of Banff National Park, Alberta, and the Kananaskis Valley, near the front ranges of the Canadian Rockies. All beaver lodges were located in the low elevation (1300 to 1400 m) valley bottoms. Sampling took place between July 1996 and September 1997. Three of the four willow foraging sites were measured in BNP, with the Lac Des Arcs site measured just outside of BNP. Since aspen is generally lacking within BNP, aspen foraging sites were located outside of BNP (either in the Kananaskis or Bow Valley).

The VLW (in BNP) is a relatively small area (4.4 km^2), with three lakes, dominated by willows (*Salix* spp.), sedges (*Carex* spp.), and some white spruce (*Picea glauca*) aspen, balsam poplar (*P. balsamifera*), lodgepole pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*) around the shorelines (Holroyd and Van Tighem 1983). Sedges and willow are the dominant vegetation along most of the shoreline (Holroyd and Van Tighem 1983). Aspen is only located along the north shore of VLW, usually >50 m from the shore.

Aspen Foraging

Four beaver lodges near aspen stands were sampled: Wasootch Creek in Kananaskis Country, and three (Loon Lake, White Gate, and Yamnuska 96) in the Yamnuska area (outside of BNP in the BRV). Each beaver lodge was located near a large homogeneous stand of aspen. Using the lodge as a starting point, transects 2 m wide were established perpendicular to the shoreline of the pond. Each transect began at the shoreline and ended where no more aspen trees were cut. Transects were spaced 10 m apart, following the contour of the shoreline. The diameter (cut and uncut) of all trees (cm) were measured within 1 m on either side of the transect line. Distance from the water (m) for each tree was recorded.

For each site, the number of transects varied due to differences in stand size. At the Wasootch Creek site, a total of 10 transects were sampled, and at the three sites in Yamnuska, 4, 16, and 28 transects were measured respectively.

To determine if beavers forage selectively, cutting larger than average trees at shorter distances from the shore, the diameter of cut versus uncut trees for each lodge site was compared at each distance category (10 cm intervals) using a t-test (Pinkowski 1983). Regression analysis was used to examine trends in the percent of trees cut as a function of distance from shore (Jenkins 1980, Pinkowski 1983). I predicted that beavers would cut fewer trees further away from the shore.

The diameters of cut trees and uncut trees were compared (separately) for each lodge using a one-way ANOVA to determine if there was any difference in the diameters of trees that beavers selected regardless of distance. To determine if there was any difference in tree density (trees per ha, cut and uncut), tree densities were compared for each lodge using a one-way ANOVA.

Willow Foraging

A total of four beaver lodges in the Bow River Valley were sampled: Sawback, Backswamp and 3rd Lake (all in BNP), and Lac Des Arcs (outside of BNP in the BRV). Each beaver lodge was near a relatively large, homogeneous stand of willow. Using the lodge as a starting point, four 100 m randomly chosen transects were established. The transect length of 100 m was selected because that is the maximum distance generally reported that beavers will travel from their lodge to obtain food (Jenkins 1980, Howard and Larson 1985). At the Backswamp site, a 100 m transect could not be accommodated, therefore six 30 m to 40 m random transects were established, radiating from the lodge. On each transect, one meter radius plots were established 10 m apart, for a total of 10 plots. At each plot, diameter of cut stem (cm), diameter of uncut stem (cm), willow height (cm), species, distance from lodge (m), and the distance from water (m) were measured.

A one-way ANOVA was performed to determine any difference in the diameter of cut willow stems between lodges (Sokal and Rohlf 1995). A t-test was performed to determine if beavers were cutting larger than average stems (cut versus uncut) at each lodge. To further test if beavers were selecting for larger than average diameter stems, a linear forage selection index was calculated for each site (Strauss 1979). The linear forage index (L) was calculated as follows (modified from Strauss 1979): $L = r_i - p_i$, where r_i is the relative abundance of cut willows stems for each diameter class (i) (as a proportion of the total number of cut stems), and p_i is the relative abundance of uncut willow stems for the same diameter classes (i) (as a proportion of the total of uncut stems). The forage index L, ranges from -1 to 1, where values -1 to <0 indicates avoidance or inaccessibility; 0 means random selection; and values >0 to 1 indicates strong preference and active selection (Strauss 1979, Johnson 1980). To verify the validity linear forage index, the proportion of willow stems cut in each diameter class versus what was available was calculated. A z-test was used to test for significance in the proportion of cut and uncut in each diameter class (Sokal and Rohlf 1995).

For each lodge, the percent of willow cut by beavers (of the total available), was calculated. By counting the fresh cut willow stems, I was able to estimate the annual cutting rates of beavers. I also estimated the amount of biomass in g/m^2 beavers remove annually using measured stem diameters (see the next section). I used this to determine the willow biomass in the VLW.

To assess if beavers cut stems from tall willow (to use for building material) (≅ 250-300 cm in height), the stem diameter of several willow species (*Salix maccalliana, S. planifolia, S. myrtillifolia, S. bebbiana, S. pyrifolia, S. pedicellaris, S. scouleriana, S. prolixa, S. lanatra,* and *S. drummondiana*), was regressed against willow height (n = 158 stems) (Sokal and Rohlf 1995). To calculate willow height from stem diameter, stem diameter was regressed against willow height.

Assessing Willow Biomass

The biomass (g) (wet and dry) of 13 willow stems (*Salix maccalliana* and *S. planifolia*) of various diameters were measured. Thirteen stems were selected since most stem classes were represented and an equation with adequate predictive capability (an $r^2 \geq 0.80$) was obtained. Willow stems were cut at the base of the shrub, and were divided into four components: 1) leaves, 2) twigs, 3) bark (bark, phloem, and cambium layers), and 4) wood (anything underneath the cambium layer was considered wood). The leaves, twigs, and bark were considered beaver food (Fryxell and Doucet 1991, Baker and Cade 1995). These components were air dried at room temperature (21°C) until the masses stabilised.

The basal diameter (cm) was regressed against the mass (g) of the leaves, twigs and bark (beaver food) (Baker and Cade 1995). A predictive equation was obtained to estimate total beaver food (in dry weight) from stem diameters.

Assessing Beaver Habitat

Willow biomass and aspen density were measured in all major water bodies in the VLW: 1st, 2nd, and 3rd lakes, and the channel between 2nd and 3rd lake. A series of 30 m transects, stratified 100 m apart from a random starting point, and were placed along the perimeter of the shoreline of each water body, perpendicular to the shore. Beginning at the shoreline, 2 m radius plots were placed at 0, 10, 20 and 30 m. At each plot, the diameters (cm) of willow stems were measured. Using the regression equation previously obtained for estimating food biomass the amount of willow, biomass (g/m^2) was calculated for each water body. A maximum distance of 30 m was used because beavers often dig channels to obtain willow, increasing their access to willow (Howard and Larson 1985). Total willow biomass for each water body within 30 m of the shore was compared using a one-way ANOVA (Sokal and Rohlf 1995).

Willow biomass (g/m^2) near active beaver lodges was calculated using data collected on beaver foraging (measured stem diameters in each plot). These data were then used to compare willow biomass near active beaver lodges to willow biomass available in the VLW using a one-way ANOVA (Sokal and Rohlf 1995).

Aspen is present along the north shoreline of the VLW. Transects (100 m long by 2 m wide) were made perpendicular to the shoreline to the nearest aspen stand and the diameter (cm), and the number of trees per ha and stand size (m^2) was calculated. A distance of 100 m was selected because other studies (e.g. Smith et al. 1994) found that beavers may travel as far as 100 m from the water to obtain aspen.

All statistical calculations were made at the 95% confidence level. All variables were first tested for equality of variance and normality. If either of these criteria failed, an equivalent non-parametric test was performed (Sokal and Rohlf 1995, Sigma Stat Software, © Jandel Scientific).

RESULTS

Aspen Foraging

Beavers at the four lodges sampled showed similar trends in their foraging behaviour with more trees cut closer to the shore. The percent of trees cut decreased as distance from the water increased: Loon Lake, $r = -0.92$, $F = 23.79$, $P < 0.01$; White Gate, $r = -0.90$, $F = 13.45$, $P < 0.05$; Wasootch Creek, $r = -0.77$, $F = 5.74$, $P = 0.075$;

Yamnuska, r = -0.77, F = 2.89, P = 0.23 (Figures 2.1a, b, c, d). Though very strong correlations between percent of trees cut and distance from water were obtained for all sites, due to low sample size the Wasootch Creek and Yamnuska sites were not statistically significant. Beavers foraged on aspen out of the water at all sites sampled.

The distance that beavers travelled from the water varied at each site: Loon Lake: 52.0 m; White Gate: 38.3 m; Wasootch Creek: 45.8 m; Yamnuska: 23.7 m (Figures 2.1a, b, c, d). This was due to the availability of aspen at each site, and different stages of tree depletion.

Beavers at each of the four lodges cut larger than average trees (P < 0.001, non-parametric t-test). At the Yamnuska lodge, statistical analysis could not be applied since these beavers had cut almost all of the trees when this lodge was sampled. In terms of size selectivity of trees, beavers selectively foraged on aspen (i.e. cut larger than average trees) at certain distances from the water at the Wasootch Creek, Loon Lake, and White Gate lodges. At the Loon Lake, Wasootch Creek, and White Gate lodges, beavers cut larger than average trees at 0-10 m from the water (P < 0.01, 0.001, and 0.01, non-parametric t-test), while at the Wasootch Creek and White Gate Lodges beavers also cut larger than average diameter stems at 10.1-20 m distance from the water (P < 0.001, non-parametric t-test). At distances > 20.1 m from the water, there was no difference between cut and uncut tree diameters at the Loon Lake and White Gate lodges, while at the Wasootch Creek lodge, beavers cut smaller than average trees 30.1-40 m distance from the water (P < 0.01, T = 1312.0, non-parametric t-test).

Overall, there were no differences in diameter of cut trees among lodges (P = 0.23, H = 4.32, Kruskal-Wallis one-way ANOVA). Mean diameters of cut trees were:

Wasootch Creek = 6.5 cm, Yamnuska = 6.8 cm, Loon Lake = 8.5 cm, and White Gate = 7.7 cm. The diameter of the remaining uncut trees were significantly smaller at the White Gate and Loon Lake lodges than the Wasootch Creek lodge ($P < 0.01$, $H = 13.36$, Kruskal-Wallis one-way ANOVA).

The density of trees near lodges were similar (3500 to 3990 trees per ha) except for the Wasootch Creek (5720.0 ± 644.3 trees per ha) and the Yamnuska (3660.0 ± 520.2 trees per ha) lodges, where the Wasootch Creek had significantly greater tree density than the Yamnuska lodge ($P < 0.05$, parametric one-way ANOVA).

Willow Foraging

Beavers selected willow stems from 2.5 cm to 3.2 cm at all four lodges, and they cut significantly larger than average diameter willow stems compared to what was available at all lodges ($P < 0.001$; non-parametric t-test) (Table 2.1). Willow stem diameter differed significantly among lodges, except Backswamp and 3rd Lake ($P < 0.001$, $H = 53.49$; Kruskal-Wallis one-way ANOVA) (Table 2.1).

At each lodge site sampled, beavers foraged very selectively on willow stems. The linear forage index suggests that the Lac Des Arcs and Sawback beavers showed strong preference for willow stem diameters in the 2.1 to 5.0 cm size ranges and generally beavers had very similar forage preferences (Figure 2.2). Similarly, beavers at the Backswamp and 3rd Lake lodges showed strong preference for willow stem diameters in the 3.1 to 5.0 cm size ranges (Figure 2.2).

The results from the linear forage index compared favourably with another measure of beaver preference, (the proportion (%) of willow stems cut versus available)

(Figures 2.3a, b, c, d). Where the linear index indicates strong preference (as indicated by a positive value), beavers cut stems in those diameter categories significantly more than what was available. Significant differences in the proportion of willow stem diameters cut versus available in each category were found in the 3.1-4.0 cm class (Backswamp) ($P < 0.05$, $z = 2.023$), 1.1-2.0 cm and 2.1-3.0 cm classes (Lac Des Arcs) ($P < 0.001$, $z = 3.310$, $P < 0.02$, $z = 2.51$), 1.1-2.0 cm and 2.1-3.0 cm classes (Sawback) ($P < 0.01$, $z = 3.25$, $P < 0.001$, $z = 4.49$), and 3.1-4.0 cm and >6.0 cm classes (3rd Lake) ($P < 0.01$, $z = 3.20$, $P < 0.01$, $z = -3.16$) (z-test). Each of these corresponded with the peaks in the linear forage indices (Figure 2.2).

A strong positive correlation between willow height and stem diameter was obtained ($r^2 = 0.94$, $F = 1216.81$, $P < 0.001$). The shape of the curve is non-linear, and is defined by the power function, $Y = mX^c + b$ where,
$\text{height (cm)} = 425.77668(\text{diameter[cm]})^{0.39442861} - 349.9404$. (Figure 2.4). Using this equation, beavers at all lodge sites selected for tall (≥ 250 cm) willow (Table 2.1). Using the mean stem diameters from each lodge to estimate height indicates that beavers cut willow stems that were 264.8 cm to 325.8 cm (on average).

Beavers had cut 22.1% to 28.8% of the willow stems available at each of the four lodge sites sampled. Using the total stems that were cut in one year, I calculated that beavers removed approximately 10-15% of the total amount of willow stems each year.

At the 3rd Lake beaver lodge, beavers travelled from the water to cut willow stems. At all other lodge sites, beavers foraged exclusively on willow stands immersed in water and dammed by the beavers. Beavers at the 3rd lake lodge crossed the railway tracks (a distance of 11.5 m) at two locations accessing willow via a small channel and a small pond. The maximum distances that beavers travelled from the water to obtain willow was 10 m and 10.7 m. The percent of willow stems cut sharply decreased with distance (past 8 m). The percent of cut willow stems, however, did not decline significantly 0 m to 10 m from the water ($r = -0.63$, $F = 2.71$, $P = 0.18$ (Across 3rd Lake); $r = -0.47$, $F = 1.11$, $P = 0.35$ (Pond East).

Willow Biomass

The diameter of willow stems and the food biomass were significantly correlated ($r^2 = 0.99$, $F = 872.66$, $P < 0.001$). The shape of the curve is defined by the power function, $Y = mX^b$ where,

Biomass (food [leaves, twigs, bark]) = 24.261041(diameter[cm])$^{2.34632 15}$ (Figure 2.5).

Using the stem diameters of cut willow near active lodges, beavers removed approximately 299.6 g/m^2 (3rd Lake) to 375.9 g/m^2 (Muleshoe) or 12.5% to 17.4% of the food biomass each year (mean of 346.0 ± 16.5 g/m^2).

There was no significant difference in the willow food biomass per unit area available around the four active beaver lodges ($P = 0.60$, $H = 1.87$, Kruskal-Wallis one-way ANOVA). All lodges have very similar biomass per unit area (Figure 2.6a). Food biomass per unit area ranged from 2123.4 g / m^2 (Lac Des Arcs) to 2481.1 g / m^2 (Backswamp), a range of 357.6 g / m^2 respectively. Willow food biomass near active beaver lodges was significantly greater than the major water bodies in the VLW ($P < 0.001$, $H = 349.084$, Kruskal-Wallis one-way ANOVA) (Figure 2.6a and b).

The amount of willow food biomass available per unit area (g/m^2) for the four major water bodies in the VLW show an increase in biomass moving from the shore to 30 m, except for the channel plot (data not shown). Generally, there is more food biomass farther away from the shore. The total willow biomass within 30 m of the shore in the four water bodies differed significantly from each other, except for the channel and 3rd Lake ($P < 0.001$, $H = 105.45$, Kruskal-Wallis one-way ANOVA). The channel plot had the highest overall biomass per unit area at 319.0 g / m^2, with the 1st Lake having the lowest at only 11.2 g / m^2 (Figure 2.6b).

Availability of Aspen in the VLW

In addition to very low willow biomass around the lakes in the VLW there was very little aspen. Only one aspen stand near 3rd lake fell within the 100 m x 2 m transect. The distance to the stand was 43.0 m. Stand size was 28 m x 38 m, with a tree density of 3888.9 trees per ha. Mean tree diameter was 13.0 ± 1.5 cm.

DISCUSSION

Foraging Patterns

Beavers clearly exhibited different foraging patterns for aspen and willow. While beavers travelled up to 60 m from the water to forage on aspen, beavers only travelled about 10 m from the water to forage on willow. Generally, beavers cut fewer trees farther from the water. Similarly, for the one lodge where beavers foraged on willow out of the water (3rd Lake), the percent of willow stems cut decreased as distance from the water increased. However, at the other three lodges where beavers foraged exclusively on willow, all of the foraging was done in the water. These beavers appeared to have dammed these willow stands, possibly to increase access for foraging. Nolet et al. (1994)

also found that willows appeared to be exclusively cut close to the water's edge, whereas non-willow species were cut away from the water. This concurs with the findings from our study, where the beavers both flooded the willow stand and foraged in the water, or only ventured a very short distance from the water.

Unlike willow, beaver foraging of aspen and other large hardwood trees has been well studied. Pinkowski (1983) found that beavers harvested aspen intensively from 0-19.9 m (93.3% of the tress cut), but harvesting declined to 10%, 40-55 m from the shore. Also, he found that beavers selected for smaller trees at increasing distances from the pond. Similarly, Jenkins (1980) found that beavers foraging on hardwood trees in Massachusetts generally cut greater amounts of smaller trees as distances from the shore increased. Belovsky (1984) also found that beavers deleted larger trees and stems from their diet as distance from the shore increased in Isle Royal National Park, Michigan. However, McGinley and Thomas (1985) found that beavers foraging on cottonwoods cut fewer branches and deleted small branches from their diet at increasing distances from the pond. In my study. I found that beavers cut larger than average aspen trees closer to shore, but at greater distances they had no distinct size preference.

Factors Influencing Foraging Patterns

Beaver may forage differently on aspen and willow for two reasons. First, the food benefits (energy return) may be higher in aspen than willow relative to the time spent foraging (provisioning time) (Fryxell and Doucet 1991). Second, Basey and Jenkins (1995) suggested that beavers may opt for a strategy to minimise the ratio of predation risk to energy return, and hence the longer time beavers require for provisioning, the greater their risk of being eaten. Thus, willow may not be as profitable a food item as aspen. The food energy return from aspen may be greater than the risk of predation of foraging greater distances from the water. Also, it appears that willow is a water stress tolerant plant, and can survive in shallow water. Therefore, at willow sites beavers can avoid venturing from the water by damming stands of willow and reduce the risk of predation. Damming of willow was observed at the Sawback, Backswamp, and Lac Des Arc lodges.

Predators may have a substantial impact of the foraging behaviour of beavers. The beaver pond itself acts as a refuge for beavers from predators, where beavers feed on woody vegetation in the water (Jenkins and Busher 1979, Basey and Jenkins 1995). In all of the lodges sampled as part of this study, coyotes (*Canis latrans*) are a common predator, and predation by coyotes has been documented in the park (Park Files, Banff National Park).

Other major predators found in the study area include wolves (*Canis lupus*), black and grizzly bears (*Ursus americanus, and U. arctos*), mountain lions (*Felis concolor*), lynx (*Felis lynx*), and wolverines (*Gulo gulo*) (Jenkins and Busher 1979, Fuller and Keith 1980, Smith et al. 1994). This large predator base in our study area may have a substantial influence on the foraging patterns observed in this study. Smith et al. (1994) found that black bear predation on beavers on an island in Lake Superior had a significant influence on beaver foraging behaviour. Under the threat of black bear predation, beavers only ventured 25 m from the shore for aspen trees (versus up to 100 m with no black bears present), and shrub use was intensive within 5 m from the shore.

Forage Selectivity

Beavers are selective foragers of both aspen and willow. In willow, beavers preferentially cut willow in certain diameter classes (2.1-5.0 cm based on the linear forage index). These findings were confirmed using the second approach (comparison of the proportion of willow cut in each size class versus the proportion available). Beavers took a disproportionate amount of willow in the 2.1-5.0 cm size classes.

Beaver foraged selectively on aspen, generally selecting for larger than average stems at closer distances to the shore. The size of the aspen stand may also have an influence on beaver foraging patterns. It appears that beavers tend to harvest small stands of aspen more intensively than larger stands. In larger stands (> 100 m in width, and >30 m in depth), beavers tend to be more selective, and cut fewer trees per unit area. In the smaller aspen stands [≤ 60 m wide and ≤ 30 m in depth (Loon Lake and the 1996 Yamnuska sites)], beavers harvested aspen very intensively. Fryxell and Doucet (1993) suggested that the functional response (i.e. the number of trees cut per beaver varies with tree density) of beavers at high sapling densities is to feed selectively, choosing larger than average saplings. At low sapling densities however, beavers may cut more small saplings and cut more intensively.

Willow Food Biomass and Beaver Habitat

I found that beavers remove approximately 12.5% to 17.4% of the willow biomass each year or 299.6 g/m^2 to 375.9 g/m^2 food biomass per unit area near active beaver lodges. Given these figures, the amount of willow food biomass near 1st Lake is only 11.17 g/m^2, 2nd Lake is 67.92 g/m^2, and the Channel is 319.78 g/m^2, while 3rd Lake is only 113.12 g/m^2. Clearly, beavers remove more willow biomass at active beaver lodge sites per unit area (g/m^2) than is available in the water bodies in the VLW. The amount of willow food biomass per unit area in the VLW was substantially lower compared to the area around active beaver lodges. Willow food biomass near active beaver lodges did not differ between sites, suggesting that beavers were very selective when establishing a lodge site location. Moreover, aspen was not available as food near the shorelines of the VLW; there was only one stand west of 3rd lake.

Hall (1960) studied beaver foraging on aspen and willow on Sagehen Creek California and found that beavers harvested as much as 44% of the available willow, and willow generally showed good vigour despite heavy use by these beavers. In a related study, Beier and Barrett (1987) found that willow showed good vigour despite heavy use by beavers in the Truckee River Basin, California. Nolet et al. (1994) studied the impacts of beavers (European beaver, *C. fiber*) on a riparian willow forest in Biesbosch, Netherlands. These authors found that willows formed the staple of the beavers' diet, but they only removed 1-4% of the standing crop.

With regards to the energetic and nutritional requirements of beavers, Belovsky (1984) estimated that beavers consume 551 g dry weight per day of hardwood leaves, bark and twigs, as well as 69 g per day of herbaceous aquatic plants, based on foraging observations during the summer months. Moreover, Nolet et al. (1994) suggested that a mixed diet might be important to a generalist herbivore like the beaver in order to detoxify or avoid large quantities of secondary metabolites. Alternate food sources such as aquatic plants are rich in Na and P, which are important for animals (Nolet et al. 1994).

However, the energetic and nutritional benefits beavers get from woody vegetation are not the only important aspects. Beavers also use woody vegetation for building material, namely for lodge and dam building (Jenkins and Busher 1979). I found that at active beaver lodges, beavers selected for larger diameter tall willow (≥ 250 cm in height). It appeared that all of the active beaver lodges and dams were constructed from tall willow, from which the twigs and leaves have been removed, and in some cases bark stripped (Nietvelt per. obs.). This structural component in relation to beaver foraging has generally been ignored, and should be explored further when evaluating suitable beaver habitat in other areas (Baker and Cade 1995).

Other Factors Relevant to Beaver Habitat

Though this study only looked at available beaver food, other factors may be important when assessing beaver habitat. Howard and Larson (1985) suggest that sufficient year round water supply is important. Beavers rely on a food cache to survive the winter and if the water is not deep enough, the pond could freeze to the bottom, preventing beavers from accessing the food cache. Howard and Larson (1985) also suggested that there is also a relationship between water and food availability. If water levels decrease, less food is available within an appropriate distance. In the VLW, much of the aspen and willow is well away for the water (>100 m for aspen, and >30 m for willow), making it difficult for beavers to access.

Little is known about how diet choice and size class preference of beavers' shifts when facing a dwindling food resource (Fryxell and Doucet 1993). Though I found distinct patterns in size preference, as these size classes become depleted, beavers may switch to smaller, less profitable size classes. Careful monitoring of active lodges and food choice over long periods is needed to fully understand the relationship between beaver lodge abandonment and vegetation succession.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

I found that foraging patterns between aspen and willow differed. While beavers travelled as far as 60 m from the water to forage on aspen, they only travelled up to 10 m from the water to forage on willow. I also found that beavers flooded stands of willow to increase access. Beavers foraged selectively on both aspen and willow, selecting larger than average aspen closer to the shore, and exhibiting a strong preference for willow in the 2.1 cm to 5.0 cm stem diameter range. I found that the amount of willow food biomass (g/m^2) within 30 m of the shoreline in the VLW was substantially less than what was present near active beaver lodges. I also found that beavers were removing more willow biomass (g/m^2) at active beaver lodges than was present along the shorelines in the VLW. Aspen was inaccessible to beaver (> 100 m from the shore). Hence the VLW is no longer suitable beaver habitat.

Due to their of their damming activities, beavers are regarded as a keystone species (Naiman et al. 1986, Naiman et al. 1988, Mills et al. 1993). They affect the hydrology, nutrient cycling, productivity, and help maintain wetland and riparian habitats (Naiman 1986). Wildlife managers have realised this, and throughout western North America, there has been interest in restoring beavers to areas that have been degraded by livestock (Munther 1981, 1982). In order to assess potential habitat for beaver reintroduction, ecologists must consider variables such as the availability of willow within 30 m of the shoreline, and the availability of aspen within 100 m of the shoreline (as in this study), but also variables such as bank slope angle, an adequate water supply, obstructions such as roads and railways, and predators.

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Table 2.1: A comparison of mean cut willow stem diameter (mm), and associated willow heights (cm) measured at four active beaver lodges. Willow stem diameters were significantly different in size for all lodges (Kruskal-Wallis one-way ANOVA, $P<0.001$, $H = 53.49$), except the Backswamp and 3rd Vermilion Lake lodges. At each lodge, beavers on average cut significantly larger diameter stems than what was available (non-parametric t-test; $P<0.001$). In general, beavers cut tall (>250 cm) willow stems at all lodge sites sampled.

Beaver Lodge Location	**Cut Willow Stem Diameter (cm)**	**Uncut Willow Stem Diameter (cm)**	**Height (cm)*** (of Cut Willow)**
Backswamp	3.2* (n = 90)	2.7** (n = 279)	325.8
Lac Des Arcs	2.9 (n = 274)	2.3** (n = 677)	295.04
Sawback	2.6 (n = 256)	1.4** (n = 871)	264.8
3rd Vermilion Lake	3.06* (n = 172)	2.6** (n = 611)	311.8

*not significantly different ($P>0.05$)

**significantly smaller than cut willow stems ($P<0.001$)

*****Using the equation:** $\text{height (cm)} = 425.77668(\text{diameter[cm]})^{0.39442861} - 349.9404$

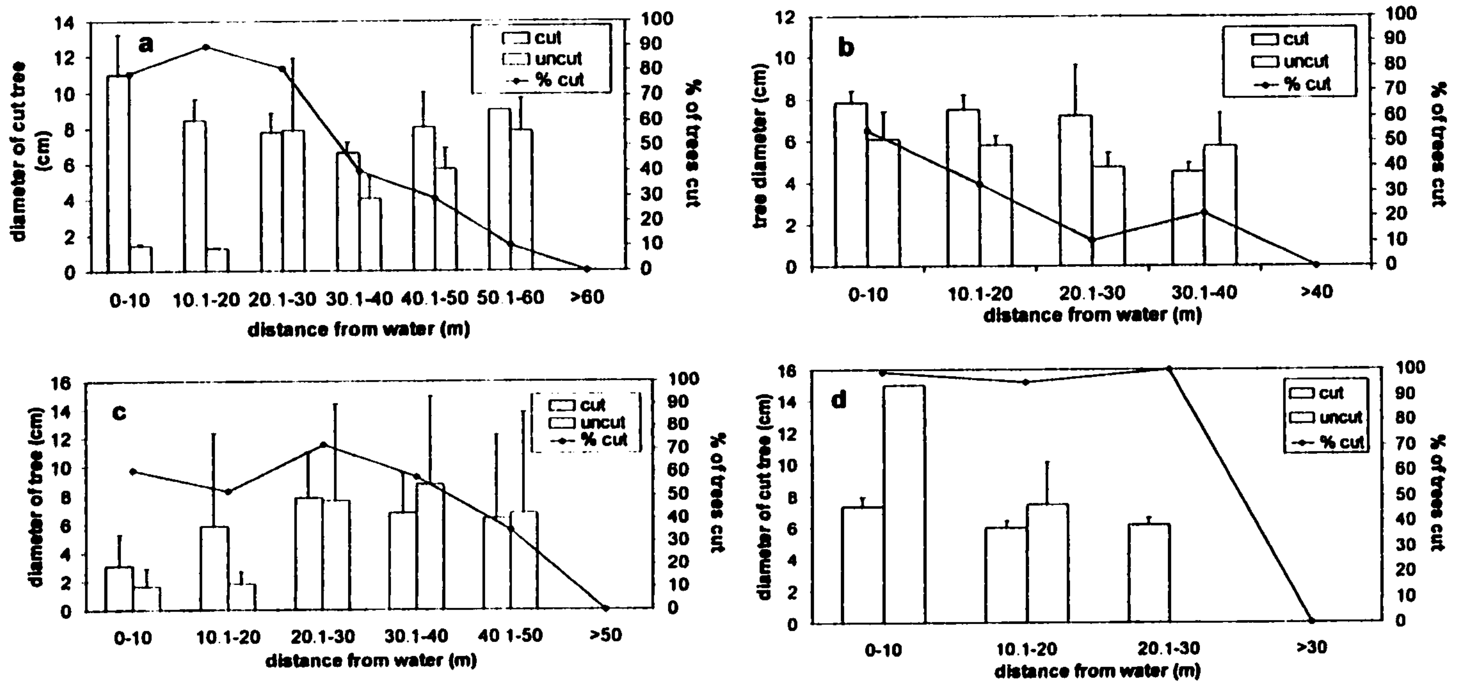

Figure 2.1: Diameter of aspen trees cut by beavers as a function of distance from shore. Beavers at the four lodges sampled showed similar trends in their foraging behaviour with more trees cut closer to the shore. The percent of trees cut decreases as distance from the water increased: Loon Lake (a), $r = -0.92$, $F = 23.79$, $P < 0.01$; White Gate (b), $r = -0.90$, $F = 13.45$, $P < 0.05$; Wasootch Creek (c), $r = -0.77$, $F = 5.74$, $P = 0.075$; Yamnuska (d), $r = -0.77$, $F = 2.89$, $P = 0.231$.

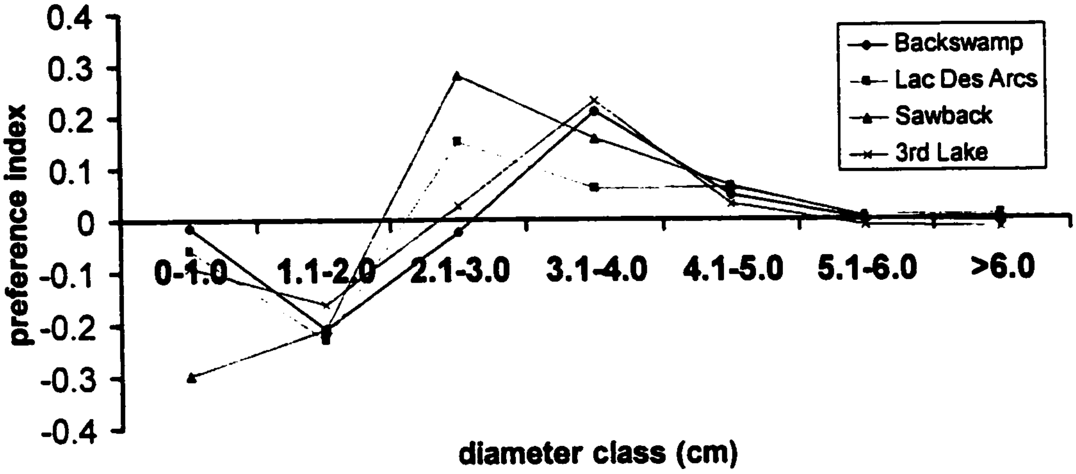

Figure 2.2: The diameter of willow stems preferred by beavers in the Bow River Valley, Alberta. This is expressed as a preference index (linear forage index), where positive values indicate preference, and negative values indicate avoidance or inaccessibility.

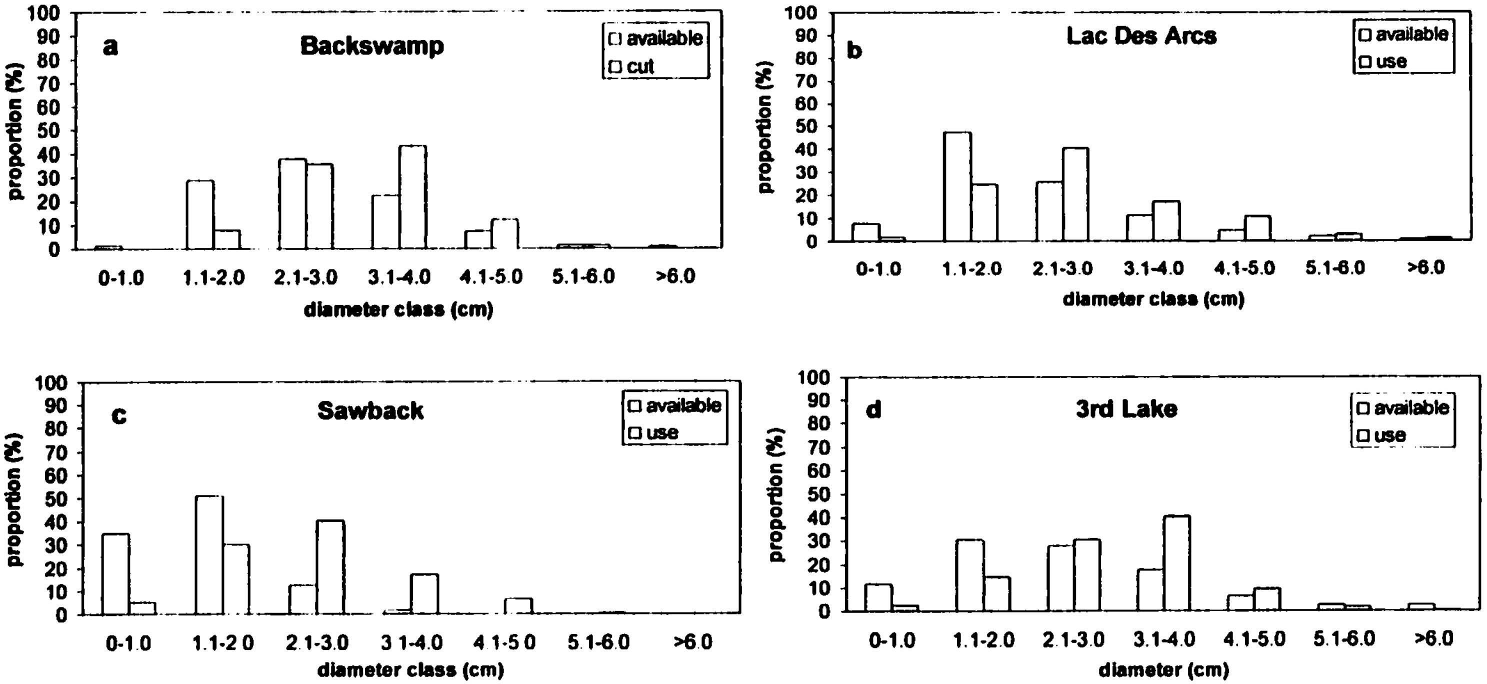

Figure 2.3: The proportion (%) of willow stems cut by beaver versus the % available. Generally, beavers cut disproportionately more of the larger diameter stem classes (> 2.1 cm). The sum of the cut and uncut stems in all diameter classes make up 100 % of the willow stems at each site.

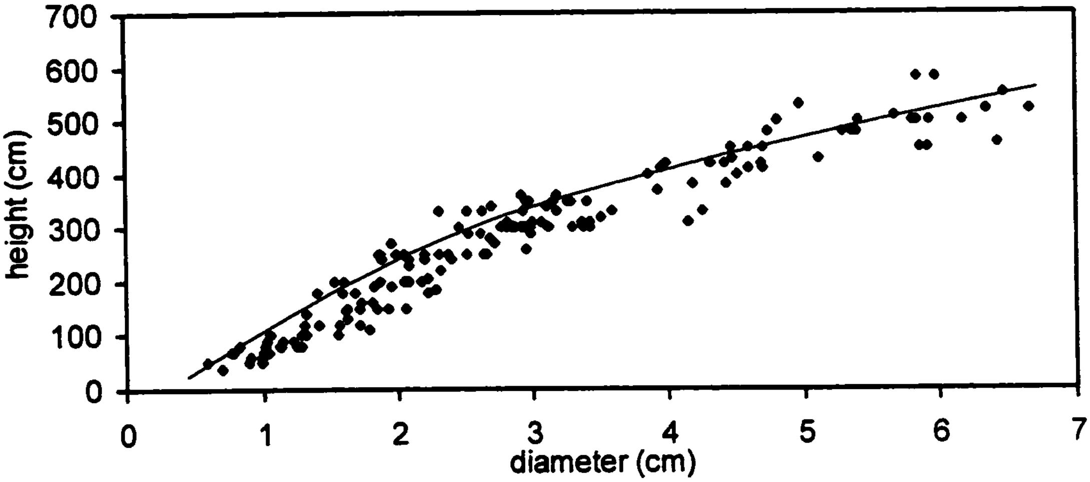

Figure 2.4: Willow height versus stem diameter. A strong positive correlation between willow height and stem diameter was obtained ($r^2 = 0.94$, F = 1216.81, $P < 0.001$, n = 158). The shape of the curve is nonlinear, and is defined by the power function, $Y = mX^c + b$ where height (cm) = 425.77668(diameter[cm])$^{0.39442861}$ - 349.9404.

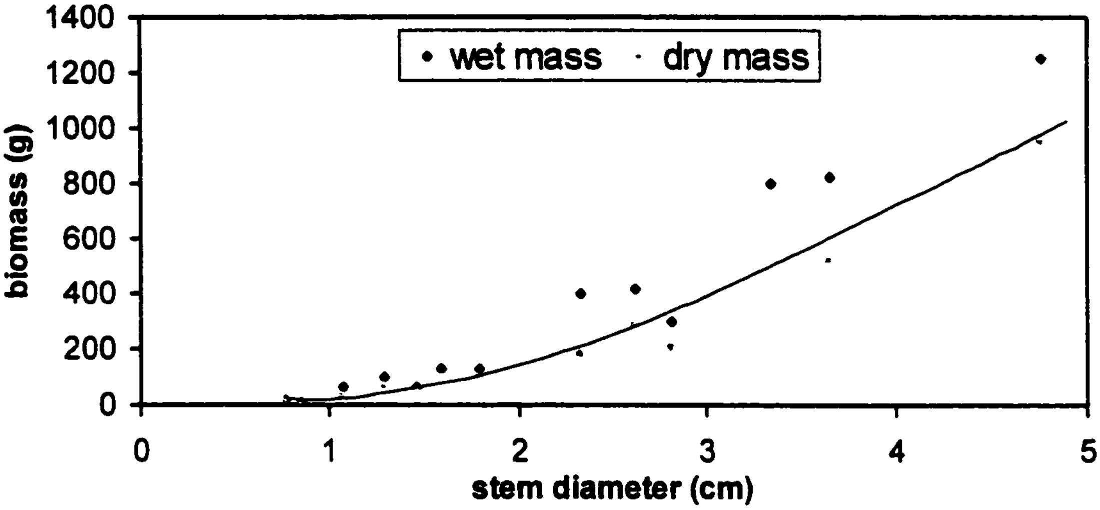

Figure 2.5: Willow food biomass as a function of stem diameter, for both wet and dry mass. A strong correlation was obtained between stem diameter and food biomass (dry) ($r^2 = 0.99$, $F = 872.66$, $P < 0.001$). The shape of the curve is defined by the power function, $Y = mX^b$ where, Biomass (food) = $24.261041(\text{diameter[cm]})^{2.3463215}$.

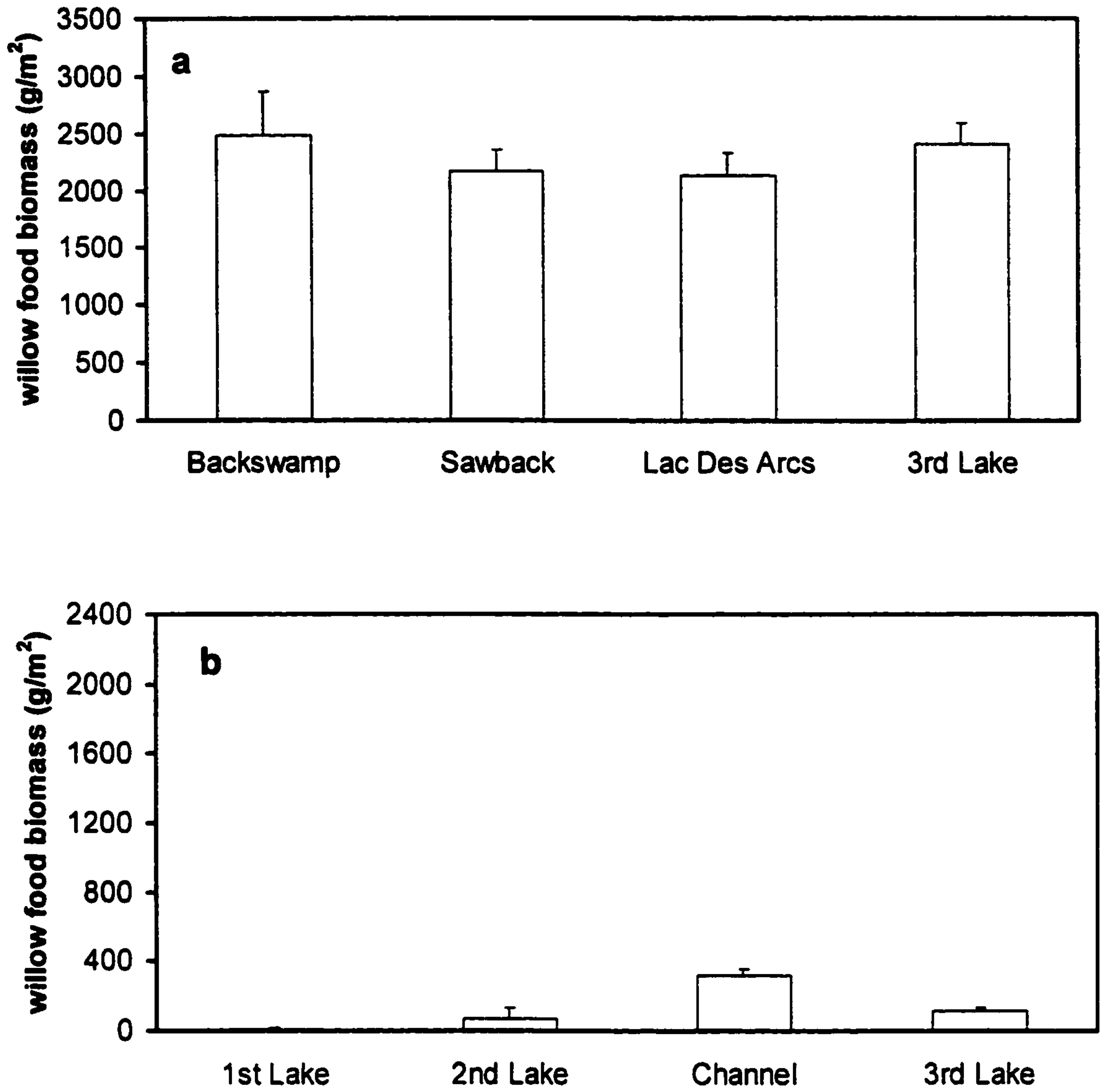

Figure 2.6: A comparison of willow food biomass (g/m^2) around active beaver lodges (a) versus the Vermilion Lakes Wetland (b). The willow biomass near active beaver lodges was significantly higher than the Vermilion Lakes Wetland ($P < 0.001$, $H = 349.084$, Kruskal-Wallis one-way ANOVA).

CHAPTER 3

HERBIVORY ON WILLOW BY ELK AND BEAVER IN BANFF NATIONAL PARK, ALBERTA

INTRODUCTION

Due to their size, longevity, food and habitat requirements, large mammals tend to have a substantial impact on ecosystems (McNaughton et al. 1988, Naiman 1988). Activities such as browsing and grazing by ungulates can have substantial impacts on the vegetation (Kay 1990, Singer et al. 1994). One of the better known examples is the effect of bush elephants (*Loxodontia africana*) and giraffes (*Giraffa camelopardalis*) on trees and shrubs in the Serengeti (Gerresheim 1970, Laws 1970). After the appearance of elephants in 1951, elephants reduced the abundance of large trees by pushing them over and stripping the bark (Gerresheim 1970). Giraffes browsed the regrowth (samplings) preventing them from maturing into trees (Laws 1970, McNaughton et al. 1988). The combined effects of elephants killing larger trees, browsers inhibiting recruitment of seedlings and saplings, and frequent fires, woodlands were converted into open grasslands in a couple of decades (Gerresheim 1970, Laws 1970, McNaughton et al. 1988). Since elephants are strong modifiers of the environment, they are regarded as a keystone species (Paine 1969, Mills et al. 1993).

In North America, there has been great concern about the effects of ungulates on ecosystem structure and function, especially in national parks where high densities of ungulates greatly impact the vegetation (Kay 1990, Porter and Underwood 1999). In Yellowstone National Park (YNP) in Wyoming, for example, elk (*Cervus elaphus*) on the

Northern Range are present in very high densities, (approximately 15-20 elk per km^2) (Coughenour and Singer 1996), and have had a large impact on woody vegetation, such as willow (*Salix* spp.), aspen (*Populus tremuloides*) and cottonwood (*Populus* spp.) (Kay 1990, Chadde and Kay 1991, Singer 1996). Browsing has caused height suppression and elimination of willow, prevented aspen and cottonwood from regenerating, and may have caused a significant decline in these species (Kay 1990, White et al. 1998). The impact of elk on woody vegetation may have been detrimental to some wildlife species such as beavers (*Castor canadensis*), white-tailed deer (*Odocoileus virginianus*), and songbirds (Kay 1990). Singer (1996) has proposed two main hypotheses for the decline of willow in YNP: 1) Heavy browsing by high densities of elk that developed in the park due to the elimination of wolves (*Canis lupus*) and disrupted elk migrations, may have resulted in significantly higher concentrations of elk wintering on the northern range than in historic times; 2) Reduced water tables due to a warmer and drier climate and a drastic decline of beavers, with the subsequent loss of beaver impoundments. Willows are reduced to sites that are drier and less productive, and are less apt to tolerate high levels of herbivory.

Banff National Park (BNP) in Alberta may be experiencing similar ecosystem disruptions. Elk densities have increased greatly in the Vermilion Lakes Wetland (VLW) of BNP since the mid-1980's (Woods et al. 1996). At the same time the number of active beaver lodges has declined in the VLW (Chapter 4). This increase in elk numbers coincided with the recolonization of wolves in the early 1980's, and the fencing of the Trans Canada Highway (TCH) at approximately the same time (Woods 1991, Paquet 1993, Paquet et al. 1996, Woods et al. 1996). Woods et al. (1996) suggested that elk in the central part of the valley bottom (central zone) have increased due to reduced human caused mortality (highway fencing) and the fact that these elk experience little predation from their principal predator, wolves.

One hypothesis for the decline of tall willow and beaver that was not considered by Singer (1996), [proposed by Jonas (1955) and Kay (1990)] is the interactive effect of elk and beaver on willow communities. They suggested that beaver cutting of large willow stems followed by browsing by high densities of elk could cause a decline of tall willow, as well as a decline of beavers. Kay (1990) suggested that beavers have been competitively excluded by elk on the Northern Range of YNP, but did not present data on willow to support this concept of exploitative competition (defined by Holt et al. 1994). Exploitative competition occurs when two species have no direct interactions, but interact through a third species or resource (Krebs 1994: 258-259). When exploitative competition occurs, the species that will persist (the winner) is one that depresses the resource to the lowest level consistent to its own maintenance, relative to the needs of the competing species. This is known as the R* rule (Holt et al. 1994, Tilman 1990).

The purpose of this study is to evaluate how the willow community structure may change with herbivory by elk, by beaver, and elk *and* beaver. My hypothesis is that beaver cutting of willow stems followed by heavy browsing by high densities of elk may reduce or eliminate tall willow communities.

If the above hypothesis is true, I predict the following:

1) Beaver stem cutting of tall willow followed by heavy browsing by high densities of elk will result in willows in short height classes.

2) Beaver harvesting of willow in areas of low elk densities (with low browsing) will have willows in many height classes.

3) Conversely, in areas with no beaver and both low and high elk densities, the willow community will have tall height classes.

4) In areas of high elk densities, elk will remove more of the twig biomass than will be produced by the willow each year. Combined with beaver stem cutting, this will suppress the height the of willow. Conversely, in areas of low elk densities, elk will remove less twig biomass than will be produced by the willow each year.

STUDY AREA

All sampling sites were located in the lower elevation (1400 m) montane (valley bottom) ecoregion in the Bow River Valley (BRV) (51° 07' N, 116° 30' W), of Banff National Park, Alberta Canada (Holroyd and Van Tighem 1983). The montane ecoregion is a mosaic of willow, white spruce (*Picea glauca*), aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*) (Holland and Coen 1983). Plots were located in wetland-willow communities, which are relatively rare in BNP (Holland and Coen 1983, Achuff et al. 1986).

The Vermilion Lakes Wetland, is located immediately west of the Banff Townsite. It is a relatively small area (4.4 km^2), with three lakes, dominated by willows, sedges (*Carex* spp.), and some spruce around the shorelines, with some aspen, balsam poplar, pine, and Douglas fir (Bow Valley Naturalists 1978, Holroyd and Van Tighem 1983, Sentar 1992).

METHODS

Experimental Design and Treatments

I used four treatments to test the effects of elk and beavers on willow (Krebs 1989):

1) High Number of Beaver Lodges (recently abandoned) and High Elk (Treatment 1)
2) High Number of Active Beaver Lodges and Low Elk Densities (Treatment 2)
3) No Beaver Lodges and High Elk Densities (Treatment 3)
4) No Beaver Lodges and Low Elk Densities (Treatment 4)

At least three sites were sampled for each treatment. Treatment 1, with high numbers of *active* beaver lodges and high densities of elk could no longer be located in BNP. Hence, I located sites where beaver lodges were active within approximately the last 5 years and the lodges were recently abandoned. Willow cut by beavers was clearly evident near these lodges.

In treatments 2 and 4, where elk were considered to be in relatively low density, elk densities were approximately ≤ 1 elk per km^2, or 0-200 pellet-groups per hectare (Hurd 1999). In Treatments 1 and 3, where elk were considered to be in relatively high densities, elk densities were 10 to 20 elk per km^2 or >400 pellet-groups per hectare (Hurd 1999) (pellet-group measures are described below).

Due to the limited study area (montane wetland willow habitat type is only 2.6 % of the park area), pseudo-replication was unavoidable, thus each site is not independent (Hurlbert 1984, Krebs 1989).

Measures of Willow Browse

Measurements of browsing were made in May 1996 and May 1997. Each site was located in a stand of exclusively willow, where two random 90 m transects were established. A total of 10 plots (1 m radius) were stratified 10 m apart in each transect for a total of 20 plots per site. In each plot, the diameter (mm) at the point of browsing was measured for 12 twigs (n = 240 twigs for each site) (Singer et al. 1994). A twig can be defined as (from Telfer 1969:917), "that part of a branch distal to the point where branch diameter would...equal the largest diameter observed for the stub of a browsed branch of that species." The number of browsed and unbrowsed twigs were counted for each plot (Shafer 1963). The percentage of twigs browsed in each treatment was compared using a one-way ANOVA (Sokal and Rohlf 1995). Differences in the percentage of twigs browsed between 1996 and 1997 within sites were compared using a t-test (Sokal and Rohlf 1995).

Assessing Relative Ungulate Use

Along each browse transect, fecal pellet-group counts were counted to determine which ungulate or herbivore had browsed: elk, deer (*Odocoileus* spp.), moose, and snowshoe hare (*Lepus americanus*). Pellet-groups were counted 1 m on either side of the transect line, in May before the herbaceous vegetation made it difficult to see the pellets (Paquet 1993). Elk-pellet group density (standardised as number of pellet-groups per hectare) was regressed against the percent of twigs browsed to determine the relationship between browse intensity and elk use or density.

Willow Twig Biomass Removal and Production

Twig biomass (g) removal by ungulates, and the production of twig biomass by the willows were measured in the browse plots. To estimate the amount of twig biomass removed by ungulates, 307 unbrowsed twigs of various diameters from several willow species were clipped, dried for 5 days at 70°C and weighed. The twig diameter (mm) was regressed against twig mass (g) to obtain a predictive equation (using Table Curve Software©, Jandel Scientific) to estimate the twig mass removed from bite diameters (diameter of the twig at the point of browse) (Telfer 1969, Potvin 1983). The amount of twig biomass removed by ungulates in each plot was measured in 1997 and calculated as follows: Twig Biomass Removed (g/m^2) = No. of Browsed Twigs x Mean Twig Biomass (g) ÷ Plot Area (m^2). To estimate the amount of twig biomass produced by willows, each plot was revisited in the fall of 1997, and the diameter of the current annual growth (CAG), was measured at the base of 12 twigs. The twig CAG biomass produced in each plot was calculated as follows: Twig (CAG) Biomass Produced = No. CAG Twigs x Mean Twig Biomass (g) ÷ Plot Area (m^2) (Singer et al. 1994). Twig biomass production was measured only in the 1997 season.

Willow Stand Structure

In each browse plot, the height (cm) of 4 willows were measured (point quarter measures) and placed into 5 categories: 0-50 cm. 51-100 cm, 101-150 cm, 151-200 cm, 201-250 cm, 251-300 cm, >300 cm (Kay 1990, Singer et al. 1994). To determine if there were any differences in the distribution of willow height classes between treatments, the frequency of willow height (%) was compared using Chi-square analysis (Sokal and Rohlf 1995). Each willow was identified to species.

Exclosures

To examine the full effects of ungulate browsing on willow growth and productivity, five experimental (20 m x 20 m) exclosures were measured in August and September of 1997. The exclosures were located as follows (year of exclosure establishment in brackets): Cave and Basin Marsh (1996), 1st Vermilion Lake (1995), Johnson Lake (1995), Industrial Compound (1995), and the Trans Canada Highway Fence (1984). A 20 m transect was placed inside of the exclosure, with a replicate outside. Twig CAG biomass production (g/m^2) (same methods as measured for browse production) was measured in five 1 m radius plots along the transect line. CAG leader (twig) length (cm) was measured along 1 x 20 m transect (same transects as for biomass production). The amount of biomass and leader length was compared inside and outside the exclosure using a t-test (Singer et al. 1994, Sokal and Rohlf 1995).

Willow height (cm) with and without elk browsing was analysed for the Trans Canada Highway exclosure using a t-test. Willows at this exclosure had been protected from ungulate browsing for 13 years, therefore major differences in willow height (if any) should be observed.

All statistical calculations were made at the 95% confidence level. All statistical calculations were first tested for equality of variance and normality. If either of these criteria failed, then an equivalent non-parametric test was performed (Sokal and Rohlf 1995, Sigma Stat Software, © Jandel Scientific).

Stem Diameter Versus Willow Age

To estimate the time required for willow to grow tall (>250 cm), a relationship between stem diameter versus age was obtained. The ages (in years) of 13 willow stems of various diameters were measured. Thirteen stems were selected since most stem classes were represented and an equation with adequate predictive capability (an $r^2 \cong 0.80$) was obtained. Willow stems were randomly selected, and cut at the base of the shrub. The annual growth rings were counted in the lab with the aid of a low power microscope.

The age (years) of the willow stems was regressed against the diameter (cm) (Sokal and Rohlf 1995). Mean willow stem diameters that beaver select for (from Chapter 2), were used to calculate the number of years that it will take for willow to reach that size.

RESULTS

Browse Intensity

The highest browse intensity (expressed as percent of twigs browsed) was in Treatment 1 (high elk and beaver), where the average percent of twigs browsed was 71.6 % (± 3.7 % S.E.) in 1996, and 73.8 % (± 7.2 %, S.E.) in 1997 ($P > 0.05$, n.s., d.f. = 19) (Figure 3.1a). In areas with low elk and high beaver (Treatment 2) the mean percent of twigs browsed was 19.8 % (± 1.5 % S.E.) in 1996, and 4.8 % in 1997 (± 2.6 % S.E.) ($P < 0.001$, d.f. = 19) (Figure 3.1 b). The lowest browse intensity was in Treatment 4 (low elk and no beaver), where the mean percent of twigs browsed was 6.7 % (± 2.4 % S.E.) in the 1996 season, and 6.2 % (± 1.6 % S.E.) in 1997 ($P > 0.05$, n.s., d.f. = 19) (Figure 3.1 d).

In areas with high elk and no beaver (Treatment 3), 53.3 % (± 13.9 % S. E.) were browsed in 1996, while 60.3 % ± (12.0 % S. E.) were browsed in 1997 ($P > 0.05$, n.s. d.f. = 19) (Figure 3.1 c).

In 1996, using a post-hoc test on browse, all treatments differed significantly ($P < 0.001$, d.f. = 19), while in 1997 all treatments differed except treatments 2 and 4 ($P > 0.05$; d.f. = 19, bonferroni adjustment).

Ungulate Pellet-Group Densities

A strong correlation was obtained between elk pellet-group density (number of pellet-groups per hectare) and browse intensity, where the percentage of twigs browsed increased significantly with elk pellet-group density ($r^2 = 0.77$, $F = 37.34$, $P < 0.001$). This relationship is linear, defined by the equation, $Y = 0.042325X + 11.83073$ (Figure 3.2). Pellet-group densities ranged from 0 to 1900 per hectare, and the percentage of twigs browsed ranged from 0 to 97 %.

Mean elk pellet-group densities in the high elk density sites were 1150 pellet-groups per ha (Treatment 1) and 1380 pellet-groups per ha (Treatment 3), while elk pellet-group densities for low elk density sites were 0 pellet-groups per ha (Treatment 2) and 187 pellet-groups per ha (Treatment 4). In treatment 2, these sites were flooded with water due to the damming activities of beavers. Other pellet-group surveys done in 1996 and 1997 throughout the Bow Valley revealed mean elk pellet-group densities of approximately 200 per hectare in this area (Hurd 1999). The most dominant ungulate at all sites was elk. Only two deer pellet-groups were found at the Lac Des Arcs site

(Treatment 2) and some scattered snowshoe hare pellets at the Lac Des Arcs, and West of Muleshoe sites.

Willow Twig Biomass Removal and Production

A strong correlation was obtain between twig diameter and twig mass ($r^2 = 0.89$, $F = 2491.75$, $P < 0.001$) (Figure 3.3). The shape of the curve is defined by a power function, $Y = 0.011X^{3.502}$ (Sokal and Rohlf 1995). However, to predict twig mass from twig diameter, these data were log-log transformed (namely to reduce variation in the larger twig diameters), yielding a stronger linear relationship ($r^2 = 0.92$, $F = 3777.16$, $P < 0.001$):

$\log(\text{mass}) = \log(0.550725) + (0.235617)\log(\text{diameter})$. This equation was used to calculate the twig biomass removed by ungulates, and the twig biomass produced by willows.

Where elk use and browse intensity was high (Treatment 1), elk removed more twig biomass than was produced by the willow (Figures 3.4 a). However, in Treatment 3 with high elk densities, two of the three sites elk removed less of the twig biomass than was produced by the willow (Figure 3.4 c). In the low elk use areas (Treatments 2 and 4), the willows produced substantially more twig biomass than was removed by elk (Figures 3.4 b and d).

Willow Stand Structure

In each treatment, similar willow species were present, with *Salix maccalliana* (McCall's willow) and *S. planifolia* (Tea-leafed willow) being most common (>60 % of the willow species). Other willow species included *S. myrtillifolia, S. bebbiana, S. pyrifolia, S. pedicellaris, S. scouleriana, S. prolixa, S. lanatra,* and *S. drummondiana.*

The combination of elk browsing and high beaver use (Treatment 1) had predominantly short willow (< 100 cm height class) (Figure 3.5a). Willows in areas of high beaver use and low elk use (Treatment 2) were generally taller than 150 cm, and fairly evenly distributed in taller height classes (Figure 3.5b). In areas without beavers but with high elk densities (Treatment 3) or low elk use (Treatment 4), the majority of the willow were in tall (>300 cm) height classes (Figures 3.5c and d).

Treatments differed significantly in their distribution ($P > 0.001$), except treatments 3 (high elk and no beaver) and 4 (low elk and no beaver) ($\chi^2 = 3.637$, $P = 0.73$) (Figure 3.5c and d). This confirms that beaver stem cutting with low browsing by elk shifts the willow height class distribution to shorter height classes, while in the absence of beaver with either high or low elk densities, willows reach their maximum height.

Exclosures

To further assess the effect of elk on willow, I compared willow productivity in five ungulate proof exclosures with productivity outside of the exclosure. These exclosures assess the impacts of elk on willow without the effects of beaver harvesting. Willows protected from ungulate browsing (inside the exclosure) produced more biomass (g/m^2) than willows outside the exclosure (Figure 3.6 b). However, at one site (Johnson Lake), though there were statistically significant differences inside and outside of the exclosure in terms of biomass productivity, there was not an order of magnitude difference as observed in the other exclosures (Figure 3.6). Using another measure of willow productivity (CAG leader length), four of the five exclosures had willow that produced significantly greater CAG leader lengths inside of the exclosure ($P < 0.05$-0.001, non-parametric t-test) (Table 3.1). At the Johnson Lake exclosure, there were no significant differences in CAG leader length inside and outside of the exclosure ($P = 0.62$, non-parametric t-test) (Table 3.1).

Large differences in willow height (cm) were found along the Trans Canada Highway fence, the only long-term exclosure in this study. Protected willow had a mean height of 254.8 cm, while willow subjected to ungulate browsing had a mean willow height of 57.4 cm ($P < 0.001$, $T = 153.00$, non-parametric t-test) (Figure 3.7). Moreover, unprotected willow only had two height classes (0-50 cm and 51-100 cm), while protected willow had willow in height classes from 100 cm up to > 300 cm (Figure 3.7). This protected willow had a height distribution pattern different from that of Treatments 2 and 4 (high elk and no beaver, and low elk and no beaver). When this exclosure was established, there was previous beaver activity (as observed from cut stems and a silted beaver pond at this exclosure), resulting in short willow. Since that time, these willows have only grown for 13 years and have not reached their maximum height (may take > 20 years), which may explain the slightly shorter height classes (see below).

Stem Diameter Versus Willow Age

I found that the time required for willow to grow to the diameter that beavers select (2.5 cm to 3.2 cm) was 12 to 15 years of age.

A strong positive correlation between willow age and stem diameter was obtained ($r^2 = 0.82$, $F = 51.047$, $P < 0.001$). The shape of the curve is nonlinear, and is defined by the power function, $Y = mX^b$ where,

diameter (cm) = $0.099969492(\text{age[years]})^{1.2942513}$ (Figure 3.8). This equation can be rearranged to predict age, where age $= \sqrt[1.2942513]{\text{diameter}} / 0.099969492$.

DISCUSSION

I found that the combination of beaver and elk utilising willow can cause a major decline in willow height (most of the willow is <100 cm), and has the potential to eliminate willow. The cutting of large stems by beaver followed by heavy browsing by elk may have eliminated tall willow near beaver lodges and shorelines in the Vermilion Lakes Wetland area in Banff National Park. Willow subjected only to heavy browsing by elk tended to be in the taller height class >300 cm. Similarly, willow subjected to no beaver cutting and minimal browsing by elk were primarily >300 cm tall. However, willows subjected only to beaver cutting with minimal browsing by elk are distributed in slightly lower height classes. Beaver cutting tends to shift willow height classes only slightly to the lower end of the spectrum.

Effects of Beaver on Willow

Beavers are very selective foragers, cutting stems in certain size classes (e.g. Jenkins 1980). In Banff, beavers tend to cut larger than average willow stems, usually in the 2.5 cm range (Chapter 2). These willows were typically >250 cm tall (Chapter 2). By removing these large tall stems, beavers tend to shift willow to the slightly lower height classes. I found that beavers remove approximately 12.5% to 17.4% of the willow biomass each year or 571.0 g/m^2 to 702.2 g/m^2 (mean of 665.8 ± 29.2 g/m^2) of the total stem biomass each year (Chapter 2). This is considerably more biomass than elk remove per year. I found that elk remove a maximum of 200 g/m^2 per year, though usually it is below 50 g/m^2 per year (Figure 3.4 a, b, c, d).

Willow is unique in that it responds to beaver by producing long leaders when cut (Hall 1960, Beier and Barrett 1987, Kindschy 1985, 1989). Kindschy (1989) found that in southeastern Oregon, willow responded to simulated beaver cutting by producing long leaders, growing approximately up to 2 m after the first growing season. In my study, the growing season is substantially shorter and leader lengths of willow after being cut by beavers were approximately 1 m in height after the first year. Hall (1960) studied beaver, aspen and willow ecology on Sagehen Creek, California, and found that large vigorous willows tolerated at least one or two seasons of rather large harvesting by beaver, showing good vigour (producing long leaders). However, willow that had been consistently overbrowsed tolerated less, and subsequently lost vigour (Hall 1960). Similarly, Beier and Barrett (1987) also found that willow showed good vigour despite heavy use by beavers in the Truckee River Basin, California. Kindschy (1985) also found that red willows (*S. lasiandra*) used by beaver were able to maintain high growth rates and increased in basal diameter similar to the rates of unused plants. However, willow may be able to persist in the long-term because beavers abandon their lodge when their food is exhausted, allowing for recovery of the willow (Hall 1960, Beier and Barrett 1987, Kindschy 1985).

Effects of Elk on Willow

Browsing by high densities of elk can have a significant impact on willow. I found that in the area of high elk densities (Treatment 1), not only was the browse intensity high, but they also removed more of the twig biomass than was produced by the plant. In the other high elk density area where there was no beaver use, (Treatment 3), the willow produced more twig biomass than what was removed by the elk (in two of the three sites). I suggest that in Treatment 1 with two large herbivores utilising willow, these willow cannot tolerate such intense herbivory. Normally, the response of willow would be to produce long leaders when browsed or cut (Kindschy 1985, Beier and Barrett 1987). However, prolonged browsing of willow (in this case by elk) at a constant high rate may cause willows to produce shorter leaders (less biomass) and hence lose vigour (Hall 1960). In Treatment 3, these willows had no previous beaver use, and are only subjected to browsing by elk. Also, these were predominately tall willows (mostly > 300 cm) which may be more tolerant to heavy browsing than short willow, where the entire plant is vulnerable. This is evidenced by Treatment 3 (no beaver and high elk), where these willows produced high twig biomass per unit area (highest among the four treatments), despite having high amounts of twig biomass removed (Figure 3.4c). Moreover, in two of the three sites, these willows produced more twig biomass than was removed.

Heavy elk browsing may be particularly detrimental to willows that are ≤ 200 cm in height, where the entire willow is subjected to browsing. For example, Singer et al. (1994) and Singer (1996) found that about one-half of the willows on northern range of YNP were height suppressed (≤ 50 cm) due to heavy browsing by elk. However, I found that on willows that were >250 cm in height, elk usually did not browse the top twigs and browsed only the perimeter stems, leaving the stems in the centre of the plant protected. Thus heavy browsing over time produces tall willow with a "mushroom" shape (Kay 1997).

Given this, if high densities of elk move in to an area where willow has been cut by beavers, willow will not have a chance to grow back, especially if these leaders are < 2 m in length. As the tall willow is cut, the shoots become browsed, and if elk densities remain high, short willow cannot grow taller due to heavy browsing, and are in essence caught in a predator pit (Boutin 1992, Messier 1994). Similarly, Kindschy (1989) found that beaver cutting of willow followed by use by livestock can be particularly detrimental to willow, inhibiting regrowth.

Population Dynamics of Beaver and Elk Relative to Willow

Beavers are obligate predators of woody vegetation, such as aspen and willow, and their abundance is to a large degree dependent on the abundance and availability of woody vegetation (Hall 1960, Slough and Sadlier 1977, Howard and Larson 1985, Beier and Barrett 1987, Broschart et al. 1989, Dieter and McCabe 1989, Robel et al. 1993). Easter-Pilcher (1990) found that food cache size correlated significantly with beaver colony size. Elk, unlike beaver, are generalist herbivores and browse on woody vegetation (twigs and bark), but preferentially graze on grasses and herbaceous vegetation (Houston 1982, Coughenour and Singer 1996). The abundance of elk is not entirely dependent upon the abundance of woody vegetation, because elk are sustained in high densities by the biomass of grasses and herbaceous vegetation in the absence of predators (Coughenour and Singer 1996). During winter months however, crude digestible protein is greater in woody browse than in grasses, and snow depth may limit foraging opportunities on grasses (Houston 1982). Hence, woody browse is a component of an elks winter diet (Hobbs et al. 1981, Houston 1982, Morgantini and Hudson 1985), though in relation to grass, it is a relatively small component (Coughenour and Singer 1996, Hurd 1999). Therefore since the numerical abundance of elk is not dependent upon woody browse and elk do browse on willow, high densities of elk may have a long lasting and disproportionate impact on woody vegetation over a long period of time.

In the VLW, a decline in the number of active beaver lodges coincides with an increase in elk densities (Chapter 4). I found that beaver and elk interacted through a food resource, in this case willow, which may be interpreted as exploitative competition (Holt et al. 1994). The winner in this interaction between elk and beaver appears to be elk, although it cannot be clearly demonstrated that the elk have competitively excluded the beavers since no data are available at a time when both species were high.

Willow Exclosures

I found that willows protected in exclosures from ungulate browsing produced longer leaders and more biomass per m^2 than did browsed willows. In a related study, Singer (1996) found that willows in YNP protected in exclosures were 200-400 % taller, with average crown areas 200-500 % larger than browsed willows, and unbrowsed willow produced 400 % more biomass per square meter than did browsed willows. It must be noted that exclosures represent an extreme or unnatural situation since there is no browsing at all (Cole 1971, Singer et al. 1994). Typically, as in this study and others (e.g. Singer et al. 1994), ungulate proof exclosures are located in areas of high elk densities, where these areas lack major predators. I suggest that a more realistic comparison would be exclosures in areas where predators are present with lower elk densities. This appears to be the case at the Johnson Lake exclosure, where I found that there were no significant differences in the leader lengths inside and outside the exclosure. Though there were statistical significant differences in the CAG biomass per m^2, there was not an order of magnitude of difference as was observed in the other exclosures. This may be explained by changes in the use of this area by wolves, which affected elk densities outside of the exclosure. At Johnson Lake, wolves from the Cascade Valley began to use this area in the winter of 1995 (Hebblewhite pers. comm.), and kill rates of elk were causing a significant decline in the elk population in this area (Hebblewhite pers. comm.). Similarly, McLaren and Peterson (1994), found that wolf predation lowered moose numbers to the point where balsam fir (*Abies balsamea*) was able to regenerate.

Elk Density and Browsing on Willow

I found that there was a strong positive correlation between the percentage of twigs browsed and elk pellet-group density. As elk densities increased, so did browsing rates. Based on elk aerial censuses, in areas where elk were considered to be low (Treatments 2 and 4), elk densities were approximately ≤ 1 elk per km^2 (Hurd 1999). In contrast, in YNP, Singer et al. (1994) and Singer (1996) found no significant difference in percent leader use during a period of elk reductions (1963-69), when compared to the 1980's (1987-1989) when elk densities were higher. Since their low (7 elk per km^2) and high

($16-20$ elk per km^2) elk densities were relatively high, their low density treatment may not have been low enough to see any significant differences in percent browse or range damage. Similarly, Bergerud and Manuel (1969) found that when moose densities in Newfoundland were greater than two moose per km^2, balsam fir and white birch failed to regenerate.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

I found that the combined effects of beaver cutting followed by elk browsing eliminated tall willow communities. Willows that had been cut by beavers and browsed by high densities of elk were in shorter willow height classes (< 100 cm) than willow communities affected by either beaver or elk alone. Browsing by high densities of elk may have a disproportionate effect on willow since elk densities are not determined or sustained by the abundance of willow. Unlike beaver, elk do not abandon a site when woody browse has been depleted. Moreover in the VLW, elk, due to high human use, are protected from the effects of wolf predation. The loss of tall willow may be particularly detrimental to the beaver population since the abundance of beaver is dependent upon the abundance of willow. The loss of tall willow in the VLW may be a case of exploitative competition between elk and beaver.

Willow may regenerate at low elk densities (≈ 1 elk per km^2). The Johnson Lake enclosure provided some evidence that wolf predation may have lowered elk densities to the point where willow regenerated. This has management implications for restoring willow in YNP, where wolves have recently been introduced, and I predict that browsing on willow by elk will be reduced due to wolf predation. It takes approximately 12-15 years for willow to reach the height and diameter that are preferred by beaver. It is critical that studies on elk and wolf population dynamics be integrated with studies on willow and aspen to assess this top-down control of the ecosystem.

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Table 3.1: Differences in the length of current annual growth (CAG) for willow inside and outside of five ungulate-proof exclosures (measured August 1997). Note that there were no significant differences in CAG length for the Johnson Lake exclosure. The areas outside the Johnson Lake exclosure has wolf predation on elk populations.

Exclosure Location	**Year of Establishment**	**CAG Length (cm) ± SE**	
		Inside	Outside
Industrial Compound	1995	18.2 ± 0.8***	7.9 ± 0.4
1st Vermilion Lake	1995	30.8 ± 0.6***	10.2 ± 0.3
Johnson Lake	1995	18.6 ± 0.6*	20.8 ± 0.9
Cave and Basin	1996	40.0 ± 1.2***	7.3 ± 0.5
TCH	1984	24.7 ± 1.5**	21.2 ± 1.3

*n.s., **P < 0.05, ***P < 0.01 (non-parametric t-test)

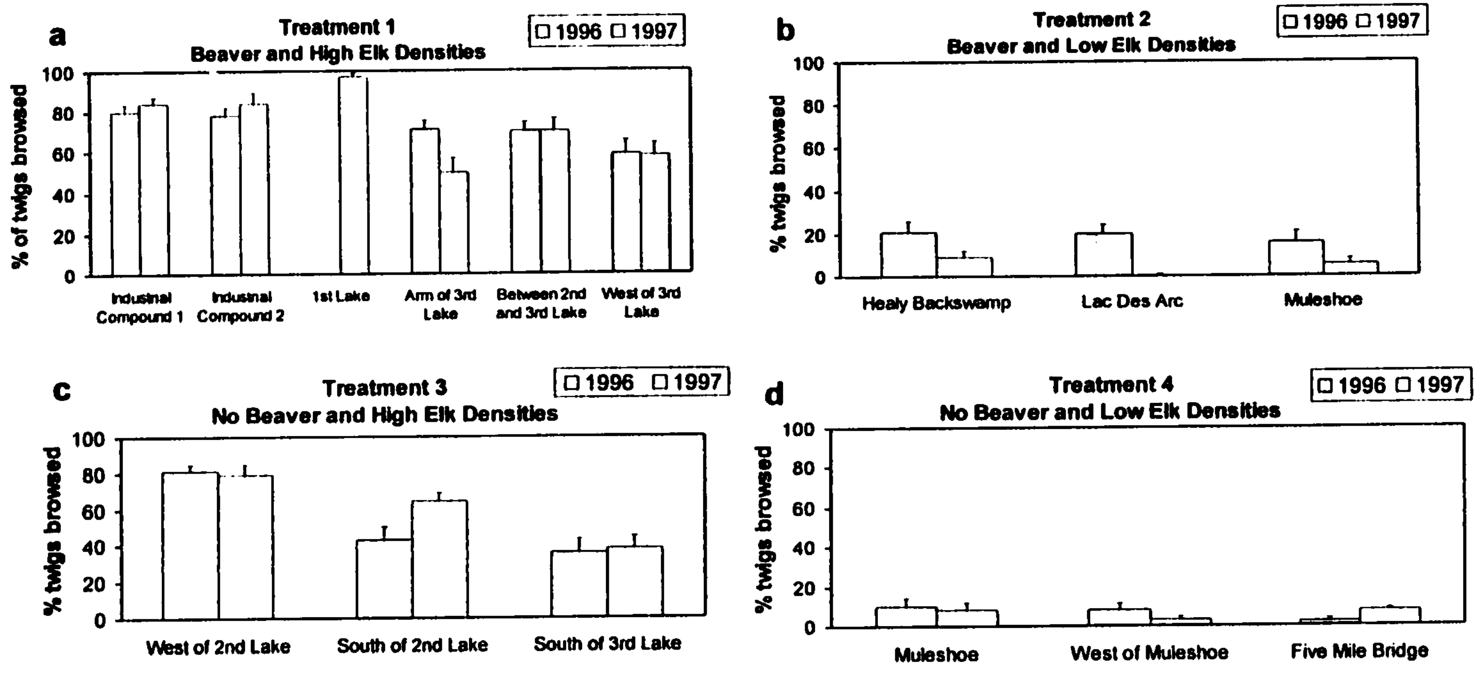

Figure 3.1: The percent of twigs browsed for each treatment. Treatment 1 (beaver and high elk densities) (a), had the highest browse intensity (71.6 % ± 3.7 % S.E. in 1996, and 73.8 % ± 7.2 % S.E. in 1997; P > 0.05, n.s.), while in Treatment 2 (beaver and low elk densities) (b), the mean percent twigs browsed was 19.8 % ± 1.5 % in 1996, and 4.8 % ± 2.6 % in 1997 (P < 0.001). The lowest browse intensity was in Treatment 4 (low elk and no beaver) (d), where the mean percent of twigs browsed was 6.7 % (± 2.4 % S.E.) in the 1996 season, and 6.2 % (± 1.6 % S.E.) in the 1997 (P > 0.05, n.s.).

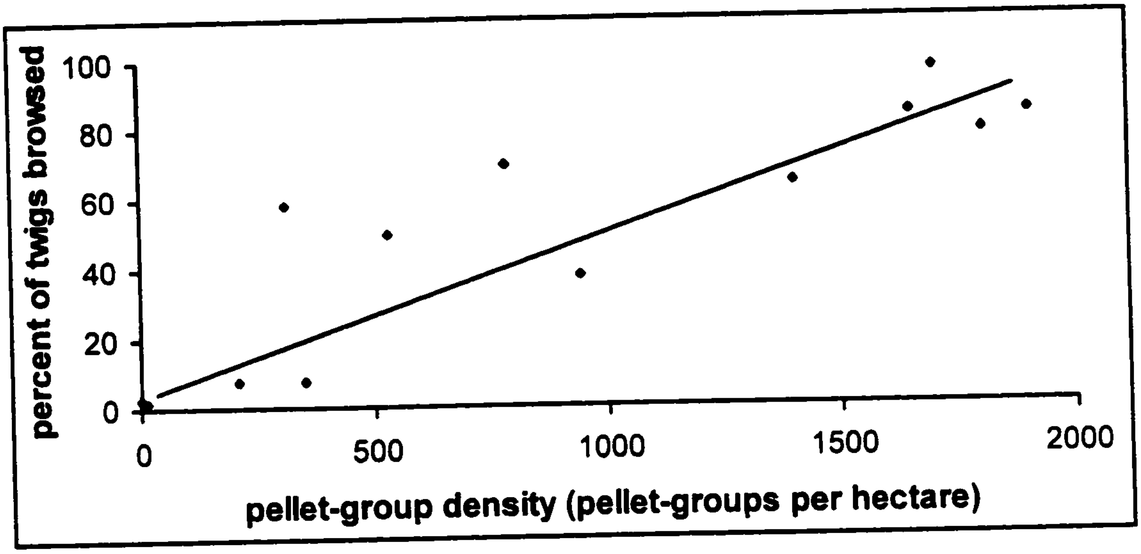

Figure 3.2: The percent of twigs browsed as a function of elk pellet-group density. The percentage of twigs browsing increased significantly with elk pellet-group density ($r^2 = 0.77$, $F = 37.34$, $P < 0.001$).

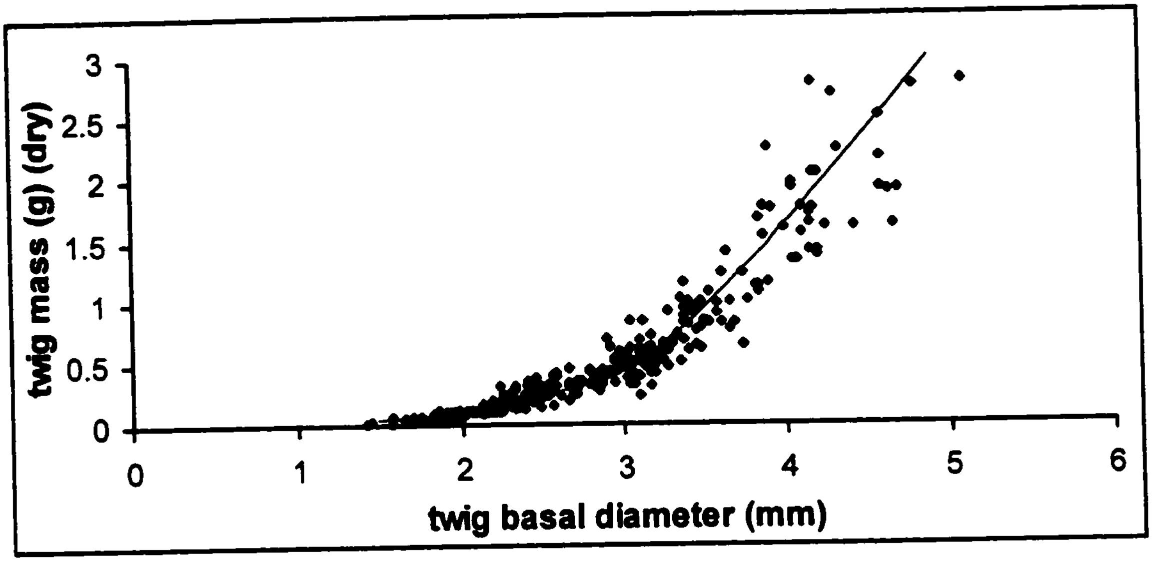

Figure 3.3: Willow twig biomass as a function of twig diameter. A strong correlation was obtained between twig diameter and twig mass ($r^2 = 0.89$, $F = 2491.75$, $P < 0.001$). The shape of the curve is defined by a power function, $Y = 0.011X^{3.502}$.

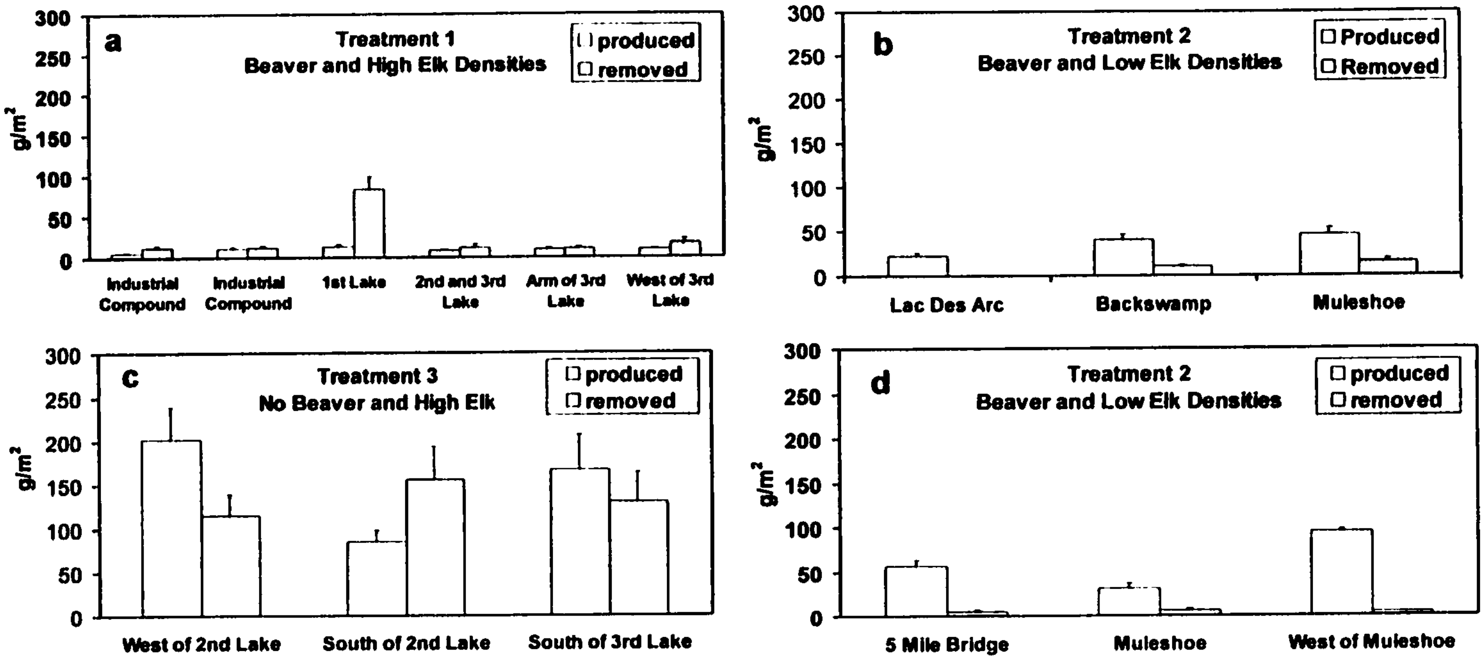

Figure 3.4: Twig biomass (g/m^2) of willows produced annually in the four treatment areas compared to the twig biomass removed annually by elk.

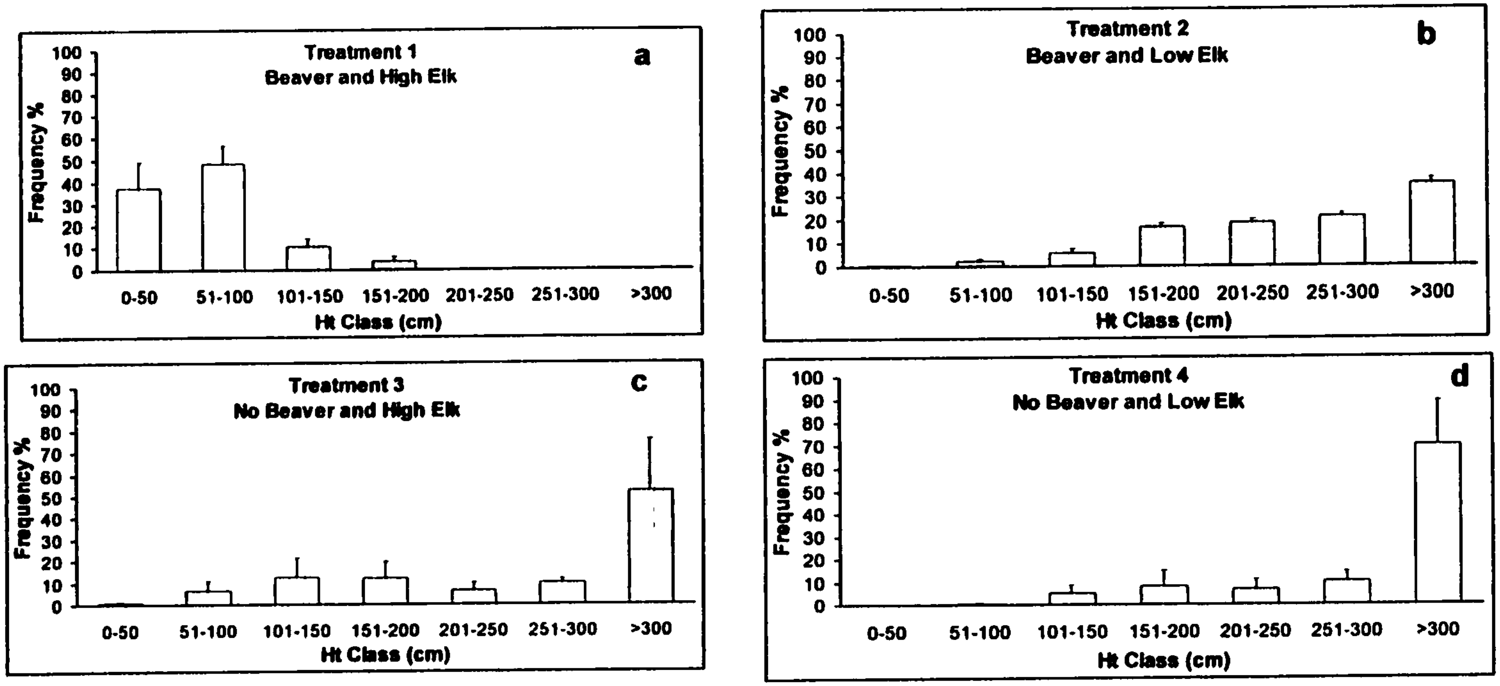

Figure 3.5: Frequency distribution (%) of willow height classes in each treatment. The combination of elk browsing and high beaver use (Treatment 1) had predominantly short willow (<100 cm height class) (a). Willows in high beaver use and low elk use (Treatment 2) were generally taller than 150 cm, and fairly evenly distributed in taller height classes (b). In areas without beavers but with high elk densities (treatment 3) or low elk use (treatment 4), the majority of the willow were in tall (>300 cm) height classes (c and d). Treatments differed significantly in their distribution (P > 0.001), except Treatments 3 (high elk and no beaver) and 4 (low elk and no beaver) ($\chi^2 = 3.637$, P = 0.726) (c and d).

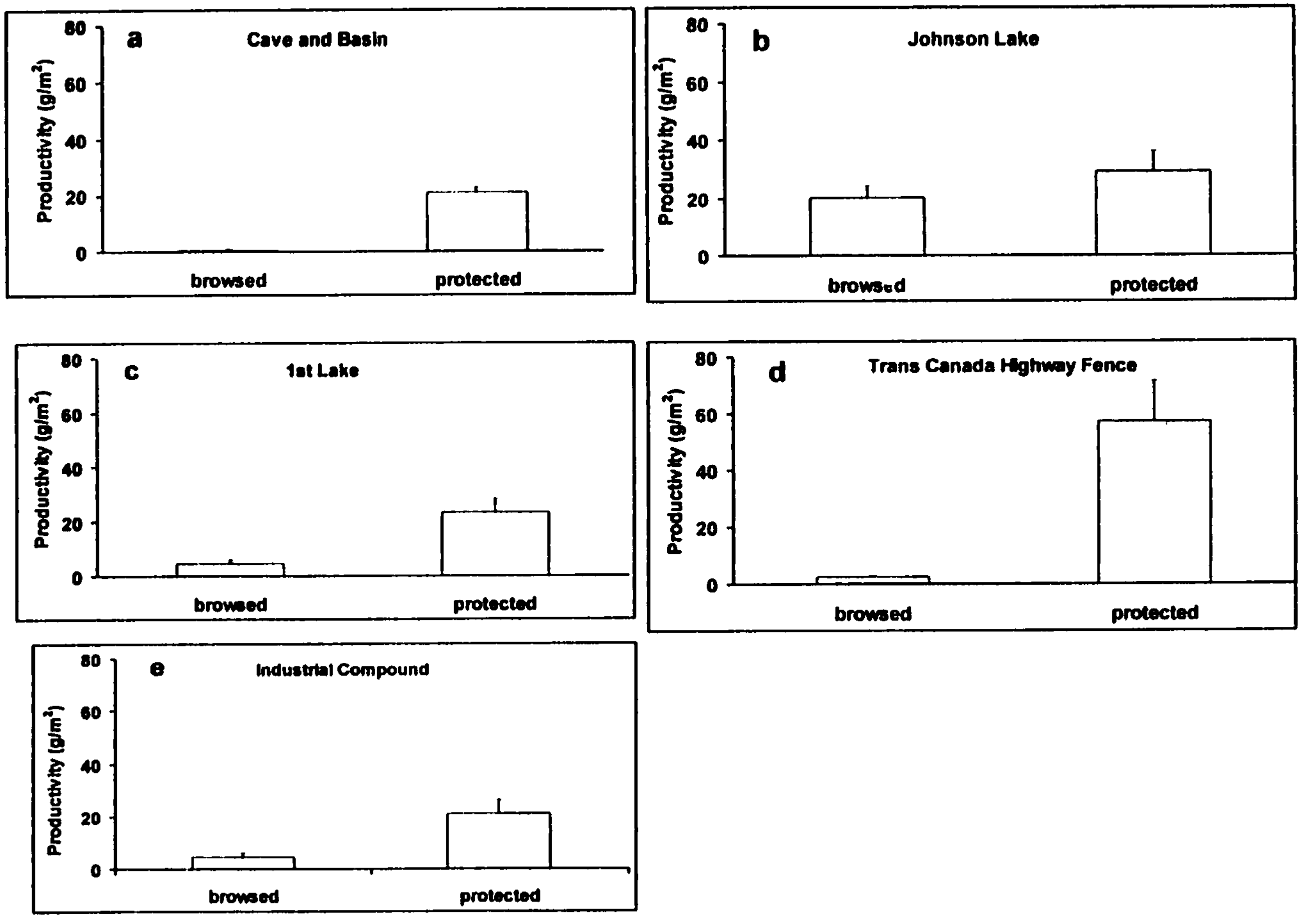

Figure 3.6.—Annual production of twig biomass (g/m^2) inside and outside ungulate proof exclosures. At all five exclosures where willows were protected from ungulate browsing (inside the exclosure), willows produced more biomass (g/m^2) than willows outside the exclosure ($P < 0.05$-0.001).

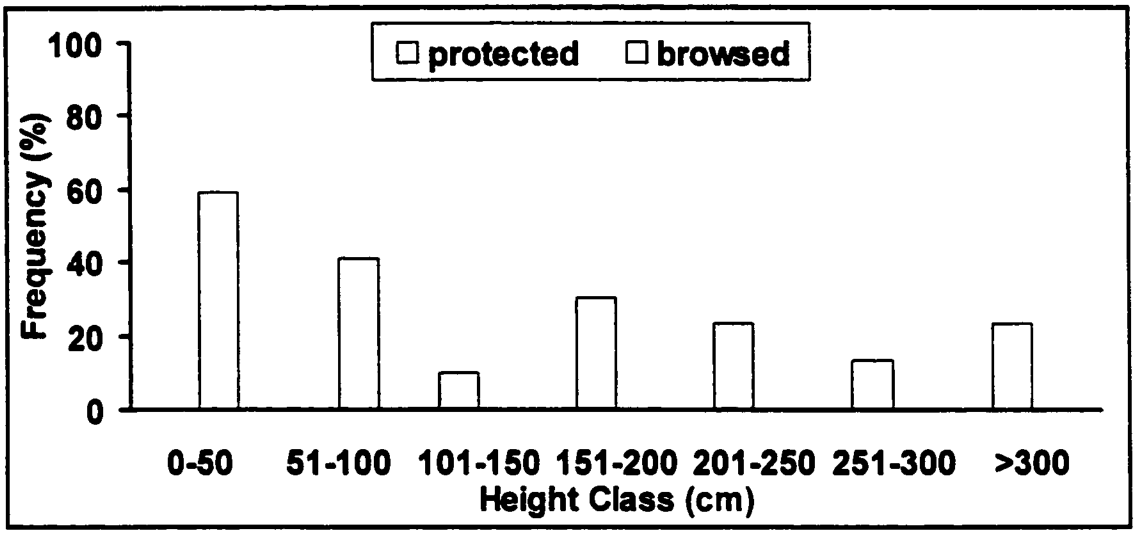

Figure 3.7: Frequency distribution (%) of willow height classes along the Trans Canada Highway fence, where willow has been protected for 13 years from ungulate browsing. Protected willow had a mean height of 254.8 cm, while willow subjected to ungulate browsing had a mean willow height of 57.4 cm ($P < 0.001$, $T = 153.00$, non-parametric t-test). Unprotected willow only had two height classes (0-50 cm and 51-100 cm), while protected willow had willow in height classes from 100 cm up to > 300 cm.

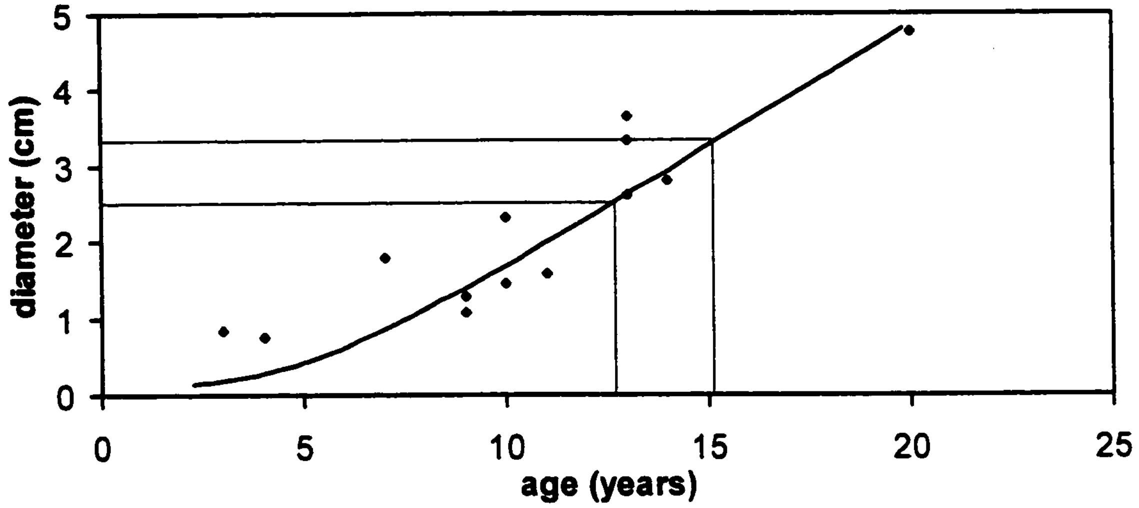

Figure 3.8—The relationship between willow stem diameter (cm) and the age of willow (years). A strong positive correlation between willow age and stem diameter was obtained ($r^2 = 0.82$, $F = 51.047$, $P < 0.001$). The shape of the curve is nonlinear, and is defined by the power function, $Y = mX^b$ where diameter (cm) = $0.099969492\{\text{age(years)}\}^{1.2942513}$. This equation can be arranged to predict age, where age = $\sqrt[1.2942513]{\text{diameter}} / 0.099969492$. The time required for willow to grow to the diameter that beavers select (2.5 to 3.2 cm) was 12 to 15 years of age (indicated by the vertical and horizontal bars).

CHAPTER 4

INTERACTIONS BETWEEN BEAVER, ELK AND WILLOW IN BANFF NATIONAL PARK, ALBERTA: EVIDENCE FOR A TROPHIC CASCADE IN A WETLAND ECOSYSTEM

INTRODUCTION

Few researchers have studied the interactions between predators, herbivores and vegetation in terrestrial ecosystems (Estes 1996). Previous research generally looked at either the interactions between predators and prey, or herbivores and the vegetation (Hunter and Price 1992, Estes 1996). However, predators influence the behaviour and numerical abundance of herbivores, which affect the vegetation (Brander et al. 1990, McLaren and Peterson 1994, Krebs et al. 1995, Henke and Bryant 1999, Peterson 1999). A classic aquatic example is the effect of sea otters (*Enhydra lutris*) and kelp forests on the Pacific coast of North America (Estes and Palmisano 1974, Estes and Duggins 1995). By comparing areas where humans had eliminated sea otters through hunting with areas where otters were present, they found that sea otter predation regulated the herbivorous sea urchin (*Strongylocentrotus* spp.) populations, preventing the sea urchins from destructive grazing of the kelp. Areas without sea otters experienced loss of kelp, which changed ecosystem structure, negatively affecting many species (Estes and Palmisano 1974). This ecosystem is structured from the "top-down" rather than from the "bottom-up" (Hunter and Price 1992). In a top-down ecosystem, predators and top consumers influence lower trophic forms (a trophic cascade), as opposed to a bottom-up ecosystem where herbivores, are regulated by food supply (resource driven) (Hunter and Price 1992, Estes 1996).

A terrestrial example of a trophic cascade is the wolf (*Canis lupus*) and moose (*Alces alces*) interactions on Isle Royale, Michigan (Peterson 1999). McLaren and Peterson (1994) found distinct patterns in balsam fir (*Abies balsamea*) reproduction, wolf and moose populations. When wolf numbers were depressed, moose numbers were high, and herbivory from high densities of moose prevented fir regeneration. Conversely when wolf numbers increased, moose numbers decreased to the point where fir was able to regenerate. Peterson (1999) suggests that the Isle Royale ecosystem Isle Royale ecosystem is driven from the top-down (predator driven).

Predation is often considered a major factor influencing ungulate population dynamics in North America (Seip 1995). Most studies have addressed the direct lethal effects of predation (predators killing prey), and how this controls ungulate (prey) populations (e.g. Boutin 1992). Indirect effects of predation on ungulate population dynamics have received less attention. Potential indirect effects include alteration in life history and behaviour of prey, especially predator avoidance or antipredator strategies (Sih 1987). This may result in such behaviours such as risk sensitive foraging, where the risk of being preyed on may influence the distribution and feeding habits of prey (e.g. Hik 1994, Krebs 1996, Boonstra et al. 1998, Bowyer et al. 1999, Kie 1999).

Here, I present the potential trophic interactions involving beavers (*Castor canadensis*), elk (*Cervus elaphus*), willow (*Salix* spp.), wolves, and human use in the Bow River Valley (BRV) of Banff National Park (BNP), Alberta. The distribution of elk in the BRV has changed dramatically since the mid-1980's (Woods et al. 1996, Hurd 1999). Elk populations have declined west of the town of Banff, and increased near town

(Woods et al. 1996). In areas west of town, wolf predation, highway and railway mortality have caused a decline in elk numbers (Woods et al. 1996). Near the town of Banff (the central zone of the montane ecoregion), since the early 1980's, elk have benefited from reduced road mortality (due to the fencing of the Trans Canada Highway), and these elk receive little predation from wolves (Paquet et al. 1996, Woods et al. 1996).

In the Vermilion Lakes Wetland (VLW), in the central zone, there have been declines in the number of active beaver lodges since the early to mid-1980's, coinciding with the increase in elk densities near the town. Aspen (*Populus tremuloides*) and willow have been heavily browsed in the VLW, (White et al. 1998, Chapter 3), and are the main food sources for beavers in the montane ecoregion of BNP (Holroyd and Van Tighem 1983). In the VLW, willow is the staple food (Bow Valley Naturalists 1978, Chapter 2).

Beavers are an important animal in the VLW ecosystem, where beaver dams retain most of the standing water (Sentar 1992). Beavers, because of their damming activity are regarded as a keystone species (Naiman et al. 1986, Mills et al. 1993). They affect hydrology, nutrient cycling, productivity, and help maintain wetland and riparian habitats (Naiman et al. 1988).

The objective of this paper is to examine the potential trophic interactions between beavers, elk, willow, wolves, humans and biodiversity in the Bow River Valley of Banff National Park, Alberta. I will attempt to quantify ecological processes in two treatment areas of the BRV: the central zone (high elk densities, few predators, heavily browsed willow, and few beaver); and the western zone (low elk densities, presence of predators, lightly browsed willow, and active beaver lodges). I will present data on:

1) The condition of willow in the central and western zone summarised from Chapter 3;

2) Population trends of wolves and elk in the central and western zones, and how the populations trends of wolves and elk relate to anthropogenic influences;
3) Population trends of beavers in the VLW (central zone) and how they relate to the populations trends of elk;
4) Brief documentation of songbird diversity and abundance in tall and short willow communities. Short willow communities with heavy browsing should support low bird species diversity and abundance;
5) Use these data to present conceptual models of these interactions.

STUDY AREA

I compared elk, beaver, and willow interactions in the western and central zones in the Bow River Valley (51° 07' N, 116° 30' W). The central zone encompasses the VLW and the Town of Banff, while the western zone extends from the Continental Divide to just west of the VLW (Woods et al. 1996, Figure 4.1).

Both the central and western zones are located in the lower elevation (1400 m) montane (valley bottom) ecoregion in the Bow River Valley of Banff National Park, Alberta Canada (Holland and Coen 1983). The montane ecoregion, the lowest region of the valley is characterised by a mosaic of willow, white spruce (*Picea glauca*), aspen, balsam poplar (*P. balsamifera*), pine (*Pinus contorta*), and Douglas fir (*Pseudotsuga menziesii*) (Holland and Coen 1983). Plots (from Chapter 3) were located in the relatively rare wetland-willow communities (Holland and Coen 1983, Achuff et al. 1986).

The Vermilion Lakes Wetland, located immediately west of the Banff Townsite, is a relatively small area (4.4 km^2), with three lakes, dominated by willows, sedges

(*Carex* spp.), and some spruce, aspen, balsam poplar, pine, and Douglas fir in the area (Bow Valley Naturalists 1978, Holroyd and Van Tighem 1983, Sentar 1992). While the VLW is a relatively small area (2.6 % of BNP), it is an important habitat used by over 220 wildlife species (Sentar 1992), and is vitally important to maintain the biodiversity in the park (Banff-Bow Valley Study 1996). Approximately 79% and 63% of all bird and mammal species in BNP occur in the VLW and similar wetlands (Sentar 1992).

METHODS

Willow in the Central and Western Zones

Willow condition in the central and western zones was compared using data from Chapter 3. Mean willow heights (cm) and the percent of twigs browsed from Treatment 1 (beaver and high elk densities) and Treatment 2 (beaver and low elk densities) was compared along a distance (km) gradient from the central zone to the western zone using a multiple linear regression (with height being the dependent variable) ($\alpha = 0.05$) (Sokal and Rohlf 1995). Treatments 1 and 2 were selected to compare and contrast the combined effects of beaver and elk on willow with low and high elk densities.

Patterns in elk use [elk pellet-group density (pellet-groups per ha)] and browse intensity (% of twigs browsed) (Chapter 3) were examined along a distance (km) gradient from the central zone to the western zone using a multiple linear regression, with browse intensity being the dependent variable (Sokal and Rohlf 1995).

Beaver Population Trends in the VLW

I analysed beaver population trends in the VLW only, since this area has the longest continual monitoring. I selected the beaver lodge as the population unit for three reasons: 1) all recorded beaver activity [with the exception of Green (1954)], report the number of active lodges rather than an absolute beaver count; 2) attempts to estimate the number of beavers in each lodge using visual counts is said to be unreliable, unless individuals are tagged (Busher et al. 1983); and 3) counts of beaver lodges can be compared to estimates of active lodges acquired from aerial photographs.

Known localities of previous active beaver lodges in the VLW were documented by Green (1944, 1954), Ferris (1956), the Bow Valley Naturalists (1978), Olson (1982), and Kunelius (1983, 1984). Active beaver lodge counts were also conducted in October 1996 and 1997. By October, beavers have constructed a food cache and settled into a lodge for the winter (Jenkins and Busher 1979). The following criteria were used to determine if a lodge was active: 1) evidence of fresh woody stems on the lodge, dam or food cache; 2) presence of scent mounds composed of mud and castoreum (from the beaver's castor gland); and 3) animals observed entering and exiting the lodge (Jenkins and Busher 1979).

To obtain estimates of active beaver lodges when censuses were not done, air photos were examined (1947, 1958, 1965, 1983, 1987, 1991). Several criteria were used to estimate which lodges were assumed to be active: 1) Lodges appeared to be white on a high contrast black and white or colour photo, indicating fresh branches and mud on the lodge; inactive lodges are frequently grown over with grass; 2) A lodge as described above, with a dam that is still intact; 3) an adequate food supply (aspen or willow) in the proximity of the lodge (Howard and Larson 1985). To test the validity of this method, I estimated the number of active lodges using an air photo for a year that lodge census counts was done (in 1983).

To examine trends in the number of active beaver lodges in the VLW, I correlated the number of active beaver lodges as a function of year ($\alpha = 0.05$) (Sokal and Rohlf 1995). Two time periods were analysed separately for trends in the number of active beaver lodges: 1944 to 1983, and 1984 to 1997. From 1944 to 1983, elk populations were lower, while from 1984 to 1997 represents an increase in elk numbers and a decrease in beaver lodges.

Since there were no historical data available in the western zone on the number of active beaver lodges, no population trends could be developed. Beaver lodge population dynamics were limited to food biomass and twig dynamics near active beaver lodges in the western zone (Chapters 2 and 3).

Elk Population Trends

An aerial spring census of elk was made each year by Banff National Park from 1985 until present in both the central and western zones (Parks Canada files). This is the only reliable and continual census of elk populations of the Bow Valley, which includes the VLW. Regression analysis was used to analyse trends in the elk population in the central and western zones (as a function of year) ($\alpha = 0.05$) (Sokal and Rohlf 1995).

Before 1985, park census data were used to estimate the elk population in the central zone 1944 to 1984 (Parks Files). During this 40 year period, data are missing for the following years: 1949, 1954, 1960-67, 1969, and 1977.

Elk population trends for the entire Bow Valley were obtained from Woods (1991), in three discrete time periods: 1944-53, 1959-68, and 1985-90.

Wolf Population Trends

Wolf population trends and activity in the VLW were summarised by Holroyd and Van Tighem (1983) and Paquet et al. (1996). Since there were no absolute counts of wolves in the Bow Valley from 1940 to 1990, Paquet et al. (1996) estimated the wolf population as a percentage of the historical population (that is before 1880). Holroyd and Van Tighem (1983) summarised wolf management from Park Files since the 1920's.

Distribution of Wolves and Elk in the Bow Valley

The distribution of wolves and elk in the Bow Valley from 1985-1993 was mapped by Paquet et al. (1996). Point locations were determined by radio telemetry, which will illustrate the spatial use by elk and wolves in the central and western zones.

Human Use in the Central and Western Zones

Human use data was taken from Pacas (1996). Winter human use was summarised for both the Western and Central zones [Figure 3.20 in Pacas (1996)]. These data were represented in logarithmic categories, with the units persons per months: 1-10, 11-100, 101-1000, 1001-10,000, 10,001-100,000, and 100,001-1,000,000. I only used data from trails, and secondary roads.

Songbird Surveys

A preliminary assessment of the effect of heavy elk browsing (> 50 % of the twigs browsed) on songbirds in willow communities was conducted.

Five treatments were used: 1) Short willow (≤150 cm), heavy browsing; 2)

Medium willow (150-250 cm), heavy browsing; 3) Tall willow (>250 cm), heavy browsing; 4) Medium willow (150-250 cm), low browsing; 5) Tall willow (>250 cm) (beaver pond), low browsing. A short willow site with low browsing could not be located. For each treatment, two sites were sampled, except for medium willow and low browsing, where only one was sampled (due to time and budget constraints).

A point count method was used to survey the birds (Finch 1989). At each point, counts were conducted for 10 minutes, where species were identified by sight or sound. All bird species were recorded within a 50 m and 100 m radius, and plotted onto a map. Each point was visited only once in late June. Bird counts were made between 0500 and 0900 hours, when breeding birds are most vocal (Finch 1989).

A Spearman's rank correlation was calculated ($\alpha = 0.05$) to detect relationships between avian diversity and abundance at different willow heights and levels of browsing (Sokal and Rohlf 1995). A two-way ANOVA was used to test differences in species diversity and abundance in relation to willow height and browse intensity (Sokal and Rohlf 1995).

Conceptual Models for the Central and Western Zones

I constructed a conceptual model for both the central and western zones and quantified the main parameters with empirical data presented below.

RESULTS

Willow in the Central and Western Zones

Willow heights were substantially shorter in the central zone (82.0 cm ± 2.4 cm) versus the western zone (295.7 cm ± 6.4 cm) (Figure 4.2). There was a strong correlation with distance from town and browse intensity and willow height ($r^2 = 0.91$, $F = 25.3$, $P < 0.01$, multiple linear regression). The area close to Town (the central zone) had evidence of high beaver use and high elk densities (see below).

There was a highly significant correlation between browse intensity, elk pellet-group density, and distance from town ($r^2 = 0.87$, $F = 32.49$, $P < 0.001$, multiple linear regression). Both browse intensity and pellet-group density decreased as distance from town increased (Figure 4.3).

Beaver Population Trends

The number of active beaver lodges in the VLW varied from a high of 11 active lodges in 1977, to 6 active lodges in 1982 and 1984 (Figure 4.4) ($r = 0.071$, $P = 0.86$; n.s.). From 1984 to 1997, the number of active beaver lodges declined significantly from 6 lodges to a low of one active lodge in 1996 ($r = -0.95$, $P < 0.01$) (Figure 4.4).

Elk Population Trends

Elk populations in the central zone have increased significantly from 1985 to 1997, increasing from 283 elk to 463 elk ($r = 0.84$, $P < 0.001$) (Figure 4.5). Data on elk in the central zone before 1985 indicates that the elk population was near 200 (Figure 4.5). Although there is some variation in these data, none of the counts indicate that the elk population was in excess of 200 (± 20 animals). Elk in the western zone have decreased significantly between 1985 and 1997 ($r = -0.95$, $P < 0.001$) (Figure 4.6).

Elk populations in the entire BRV summarised by Woods (1991) show an increasing trend: 1944-53: 648 ± 66 (± S.E.); 1959-68: 725 ± 92; 1985-1990: 978 ± 54.

Elk management in the Bow Valley is well documented. Elk slaughters were initiated in 1941 and were terminated in 1969 due to public criticism (Holroyd and Van Tighem 1983). After 1969, elk were lived trapped and shipped to other areas for elk restoration programs (Holroyd and Van Tighem 1983). By the late 1970's there was a concern that elk were declining (Holroyd and Van Tighem 1983), especially due to high highway mortality (Flygare 1978, Holroyd 1979). Since the twinning of the Trans Canada Highway in 1981, mitigation measures such as fencing along the highway substantially reduced elk mortality (Woods 1991, Woods et al. 1996).

Wolf Population Trends

Wolves were present in the BRV in the 1940's, including the VLW (Holroyd and Van Tighem 1983, Parks Files). Wolf control by various means caused a dramatic decline in wolf numbers during the 1950's throughout BNP (Figure 4.7). After an absence of over two decades, denning of wolves was confirmed in 1981 to 1984 in the Front Ranges of BNP (Paquet et al. 1996). In 1987, two or more packs became established in the Bow Valley (Paquet 1993).

Distribution of Wolves and Elk in the Bow Valley

Plotted telemetry data (from Paquet et al. 1996) shows that wolves clearly avoid the VLW (Figure 4.8). The majority of wolves were located from in the western zone and on the western periphery of 3rd Vermilion Lake (Figure 4.8). Conversely, the majority of the elk locations were located within the VLW and Banff Townsite area (Figure 4.8).

Patterns in Human Use

There was higher human use in the central zone versus the western zone (Figure 4.9). In the central zone, excluding the main roads, most of the trail use in the 1,001-10,000 persons per month category, and on secondary roads it is 10,000-100,000 persons per month (Figure 4.9). Vehicle traffic on a small road in the VLW is in the 1001-10,000 persons per month category (Figure 4.9). In the western zone, most trails receive much less human use (1-10 persons per month), while the 1A secondary highway receives approximately 1,001-10,000 persons per month. Vehicle traffic on the Trans Canada Highway is as high as 100,001-1,000,000 persons per month (in both the central and western zones) (Figure 4.9).

Songbird Diversity and Abundance

Songbird species diversity and abundance was greater in tall versus short willow, and in low versus heavy browsing sites ($P < 0.05$) (Figure 4.10). However, no interactive effect could be tested due to a lack of a short willow / low browsing treatment (short willow did not occur except under the conditions of beavers use and high elk browsing). There were over twice as many (2.5 times more) bird species in the beaver pond / tall willow / low browsing sites than in the short willow / high browsing sites.

There was a strong correlation between willow height (cm) and the number of songbird species when high browsing sites were analysed ($r_s = 0.84$, $P < 0.05$) (Figure 4.10). However, a weaker though significant relationship between willow height and songbird species diversity was obtained when low browsing sites were added ($r_s = 0.62$, $P < 0.05$). Bird abundance increased significantly with willow height (using high browsing sites) ($r_s = 0.89$ $P < 0.05$). Bird species abundance (number of individual birds) increased significantly with the number of species (high browse sites) ($r_s = 0.94$, $P < 0.05$).

Conceptual Models for the Central and Western Zones

Using these data, conceptual models for both the central and western zones were made (Figure 4.11a and b). In the central zone, there is high human use [10,001-100,000 (trails) and 100,001-1,000,000 (roads) persons per month], little wolf activity, and elk densities are high (10-20 elk per km^2), which resulted in herbivory interactions between elk and beaver. Beaver food biomass is low (11-300 g/m^2). Beaver removal of tall ($\geq$ 250 cm) willow stems followed by heavy browsing by elk (> 50 % of twigs browsed) resulted in short (82.0 cm ± 2.4 cm) willows, which supported low songbird diversity and abundance (Figure 4.11a). In the western zone, human use is lower [101-1000 (trails) and 1001-10,000 (roads) persons per month], wolves are present, and predation on elk was observed. Elk densities are lower ($\approx$ 1 elk per km^2). Willow is lightly browsed (< 20 % of twigs browsed), and it is tall (295.7 cm ± 6.4 cm). Active beaver lodges are present with adequate willow food biomass ($\geq$ 2000 g/m^2). Songbird diversity and abundance is high (Figure 4.11b).

DISCUSSION

Data on the interactions of beavers, elk, willow, wolves and humans in the central and western zones of BNP is consistent with a top-down trophic cascade ecosystem

(Hunter and Price 1992). In the central zone where wolves have been displaced due to high human use, elk numbers have increased, while the number of active beaver lodges have decreased. Willow is short and heavily browsed, which has negatively affected both beaver populations and songbird communities. In the western zone, elk numbers have decreased due to wolf presence, and willow is tall and lightly browsed. Active beaver lodges are present with adequate food biomass, and songbird diversity and abundance is higher.

Beaver and Elk Population Trends and Herbivory Interactions

The decline in the number of active beaver lodges in the VLW coincides with an increase in the elk population in the central zone. From the 1944 to 1984, the number of active beaver lodges did not drop below six. During this time period, the elk population was artificially controlled through culling, and the elk population was low (< 200 elk).

I attribute the decline of beavers in the VLW in the central zone to the increase in elk densities in the VLW (Chapter 3). I found that the combination of beaver and elk utilising willow can cause a major decline in willow height (most of the willow is <100 cm), and the potential to eliminate beaver (Chapter 3). The cutting of large stems by beaver followed by heavy winter browsing by elk may have eliminated tall willow near beaver lodges and shorelines in the VLW. I suggested that this may be a case of exploitative competition between beaver and elk (Chapter 3). Sih (1987) predicted that if two species are forced to share a common refuge, competition between the two species would increase. Moreover, willow food biomass along shorelines in the VLW was substantially less than what was present near active beaver lodges in other areas of the valley (Chapter 2).

In contrast, in the western zone I found that willows subjected only to beaver cutting with minimal browsing by elk were predominantly in taller height classes (> 250 cm) (Chapter 3). Both elk densities and browsing rates decreased significantly along a gradient from the central to the western zone.

Large declines in the number of active beavers have been noted in Yellowstone National Park, Wyoming (Jonas 1955, Kay 1990, Singer et al. 1994, Yellowstone National Park 1997), and this decline has been attributed to heavy browsing on aspen and willow by high densities of elk (Jonas 1955, Kay 1990, Yellowstone National Park 1997).

There are important distinctions in the ecological consequences of beaver versus elk herbivory. Beavers require a high abundance of woody vegetation to sustain their population, while the abundance of elk is not entirely dependent on the abundance of woody vegetation (Chapter 3). Elk can be sustained in high densities by grasses and herbaceous vegetation in the absence of predators (Coughenour and Singer 1996, Chapter 3). However, since elk do browse on woody vegetation during the winter months when the crude digestible protein is greater in woody browse than in grasses (Hobbs et al. 1981, Houston 1982, Morgantini and Hudson 1985), browsing may have a disproportionate impact on woody vegetation when elk densities are high (Chapter 3). Since beavers require > 2000 g/m^2 of accessible willow biomass (Chapter 2), I suggest that the effects of elk herbivory has caused a substantial decline in the beaver populations in the central zone of the Bow River Valley. Herbivory from both beaver and elk is required to reduce willow height and biomass to levels below that required for beaver (Chapter 3).

While there may be other proximate causes for the decline of beavers in the VLW such as predation (Page 1989, Smith et al. 1994), and disease (Strenlund 1953, Lawrence 1956), I suggest that these factors may not be as important to beaver populations as the lack of adequate woody vegetation (Chapter 2).

Spatial Distribution of Elk and Wolves in the Central and Western Zones

Observed patterns of elk herbivory in the central and western zones are supported by the telemetry distributions plotted by Paquet et al. (1996). It has been suggested that the Town of Banff and adjacent areas are acting as a refuge for elk from wolf predation (Paquet et al. 1996, Woods et al. 1996). The spatial distribution of elk and wolves resulted in these two different vegetation conditions in the central and western zones. Risk sensitive foraging may explain some of the spatial distribution patterns between elk and wolves. Elk may not venture west of the VLW due to the risk of being preyed on by wolves (Woods et al. 1996). Risk sensitive foraging is an important indirect top-down effect of predation on snowshoe hares (*Lepus americanus*) (Gilbert and Boutin 1991, Hik 1994, Krebs 1996, Rohner and Krebs 1996, Boonstra et al. 1998), and may prove to be an important indirect effect on ungulates as well (Edwards 1983, Messier and Barrette 1985, Fryxell et al. 1988, Messier et al. 1988, Bowyer et al. 1999, Kie 1999).

Similar patterns in herbivory and elk densities have been observed with aspen in Kootenay National Park, British Columbia. Kay (1997) found that aspen regenerated outside of the park boundary where elk densities were lower due to hunting, while aspen failed to regenerate inside the park where elk numbers were higher.

Influence of Human Use

Human use has had a significant influence on ecosystem dynamics in the Bow Valley of BNP (Banff-Bow Valley Study 1996). Paquet et al. (1996) found that human disturbances in the Bow Valley (roads, infrastructure) had a significant influence on wolf movement and habitat use. They found that much of the prime wolf habitat in the Bow Valley was impacted by humans. In contrast, elk are very tolerant of humans, and can occupy areas that are too "stressful" for wolves, such as the Town of Banff (Paquet et al. 1996). Hence, as mentioned, the spatial distribution of elk and wolves in the Bow Valley of BNP is largely determined by patterns of human activity (Paquet et al. 1996).

Effects on Songbirds

Beaver-elk interactions could negatively affect species such as songbirds. I found a significant correlation between willow height and songbird diversity, where sites characterised by short willow / high browsing and abandoned beaver lodges had 60 % fewer species and 64 % lower abundance than the beaver pond / tall willow / low browsing sites. This suggests that the elimination of tall willow is detrimental to songbird diversity and abundance. Other studies have also found that heavy browsing and grazing by ungulates can be detrimental to songbirds. Casey and Hein (1983) found that over-browsing by high densities of ungulates [elk, white-tailed deer (*Odocoileus viginianus*), and Mouflon sheep (*Ovis musimon*)] caused changes in the breeding bird community, in the Rachelwood Wildlife Research County, Pennsylvania. Similarly, deCalesta (1994) observed that over-browsing by high densities (as high as 24.9 deer / km^2) of white-tailed deer negatively affected songbirds and their habitats, causing a decrease of species richness in canopy-nesting songbirds by 27 %, and an abundance decline of 37 %. In Oregon, Taylor (1986) found that excessive grazing by cattle caused a decline in bird species diversity by reducing shrub height and volume. He found that bird species and abundance increased significantly with shrub height and volume.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

I found that the interactions between beavers, elk, willow, wolves, and human use were consistent with a top-down trophic cascade ecosystem. Comparison of two treatments areas, the central zone (high elk densities, few beaver, few wolves, short heavily browsed willow, and heavy human presence), and the western zone (low elk densities, beaver with adequate habitat, wolves, tall lightly browsed willow) supports this view. This is one of the few examples of a top-down trophic cascade in a wetland ecosystem with large herbivores and carnivores.

These trophic interactions have been influenced to a large degree by human use in the Bow Valley. Unlike an ecosystem such as Isle Royale where human use is relatively low and has little infrastructure, the Bow Valley in Banff National Park is a human dominated landscape (Banff-Bow Valley Study 1996). Careful management of human use is needed to help restore more natural predator-prey relations in the Bow Valley of Banff National Park

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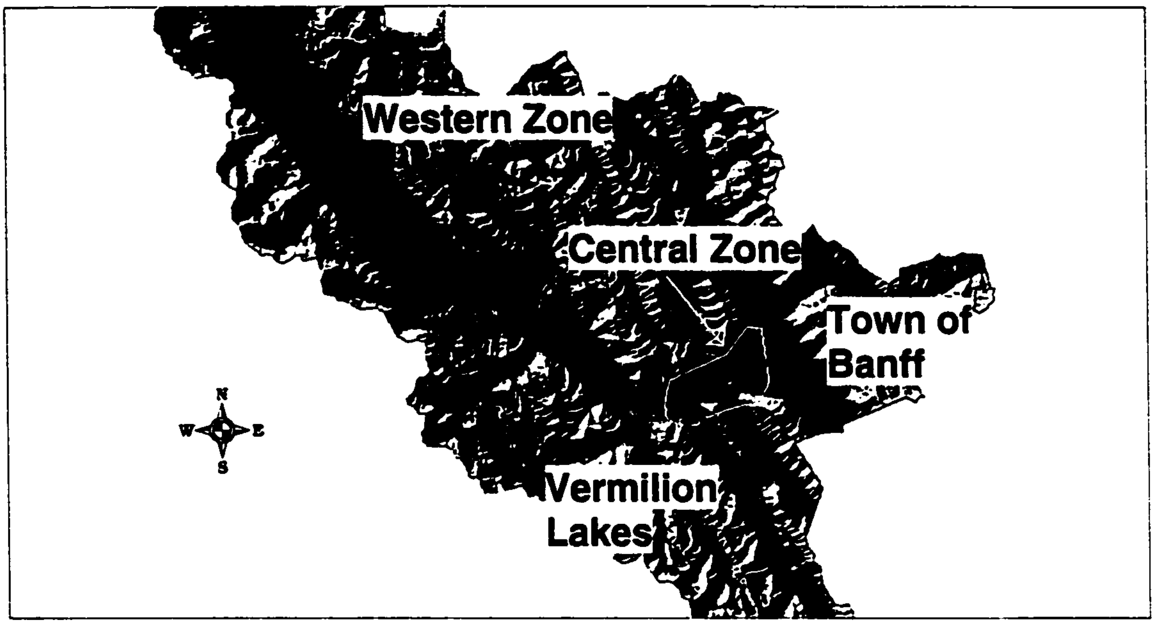

Figure 4.1: The western (red) and central (yellow) zone in the Bow River Valley of Banff National Park, Alberta.

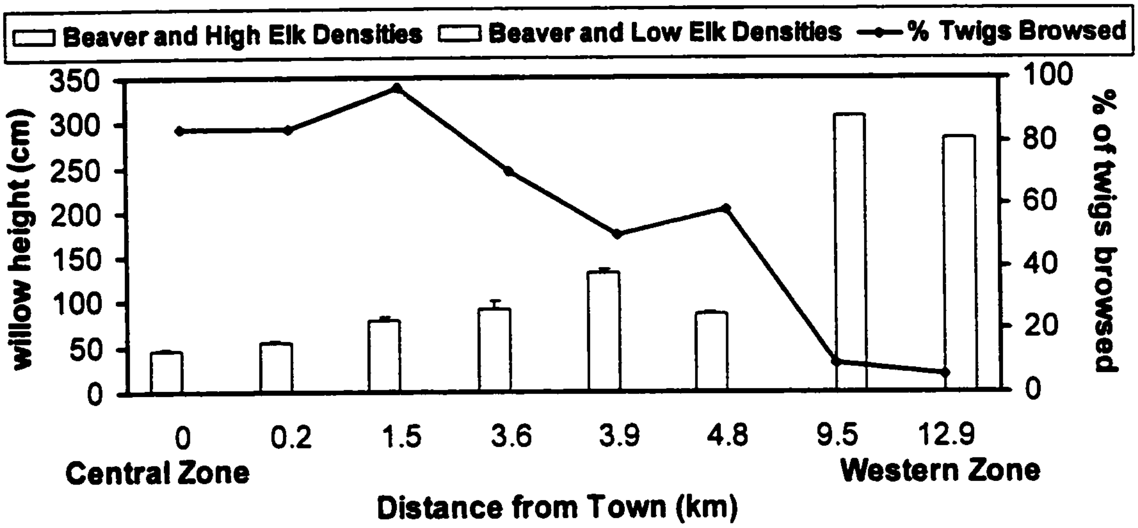

Figure 4.2: Willow height (cm) and browse intensity in the central and western zones near beaver lodges. Willows in the central zone were short (81.96 cm ± 2.35 cm) and heavily browsed (> 50 % of twigs browsed), while in the western zone, willows were tall (295.66 cm ± 6.38 cm) and lightly browsed (< 20 % of twigs browsed). There was a strong correlation with distance from town and browse intensity and willow height (r^2 = 0.910, F = 25.27, P < 0.01, multiple linear regression).

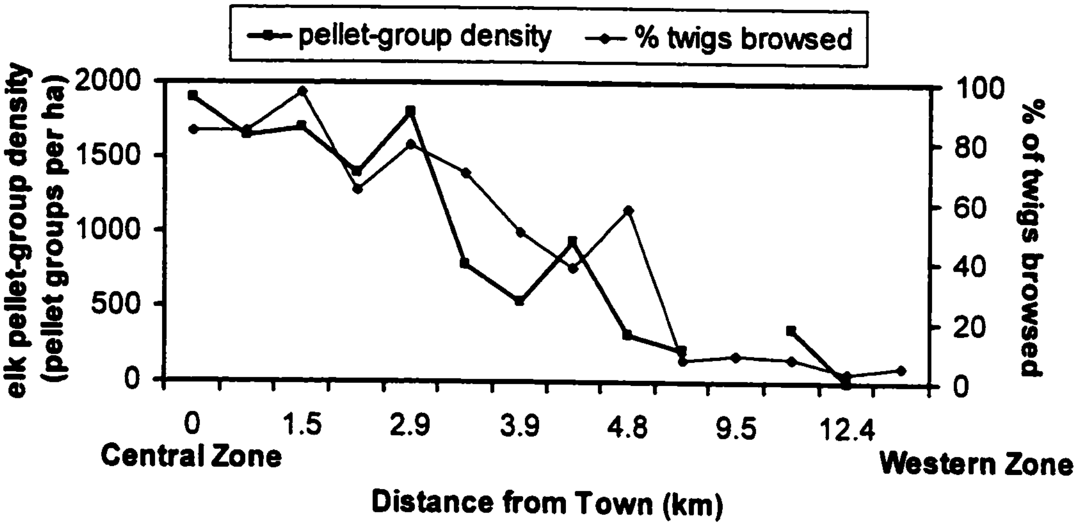

Figure 4.3: Browse intensity as a function of elk pellet-group densities and distance from town in the central and western zones of the Bow River Valley in Banff National Park. There was a highly significant correlation between browse intensity, elk pellet-group density, and distance from town ($r^2 = 0.87$, $F = 32.49$, $P < 0.001$, multiple linear regression).

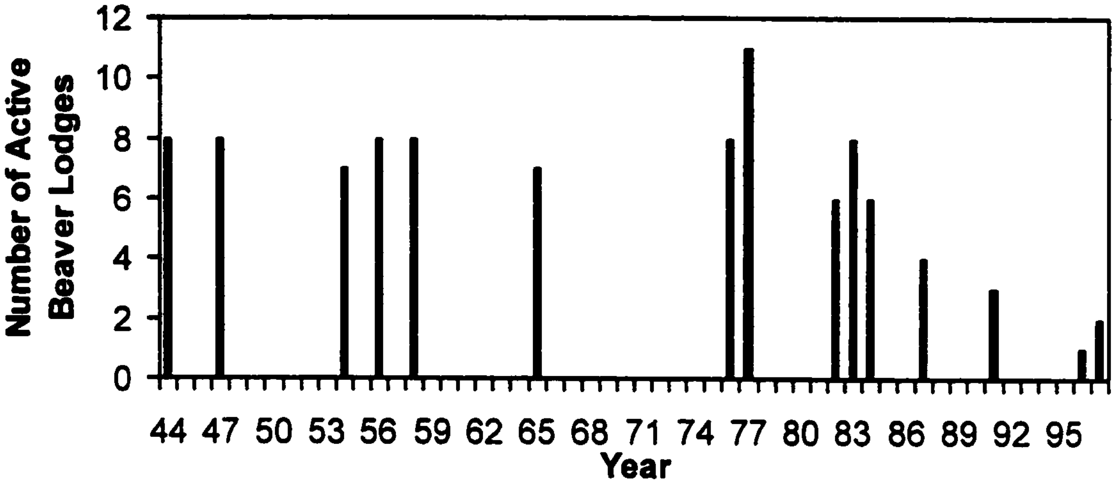

Figure 4.4: The number of active beaver lodges in the Vermilion Lakes Wetland, Banff National Park from 1944 to 1997. The number of active beaver lodges in the VLW varied from a high of 11 active lodges in 1977, to 6 active lodges in 1982 and 1984 ($r = 0.071$, $P = 0.86$; n.s.). However, from 1984 to 1997, the number of active beaver lodges declined significantly from 6 lodges to a low of one active lodge in 1996 ($r = -0.95$, $P < 0.01$).

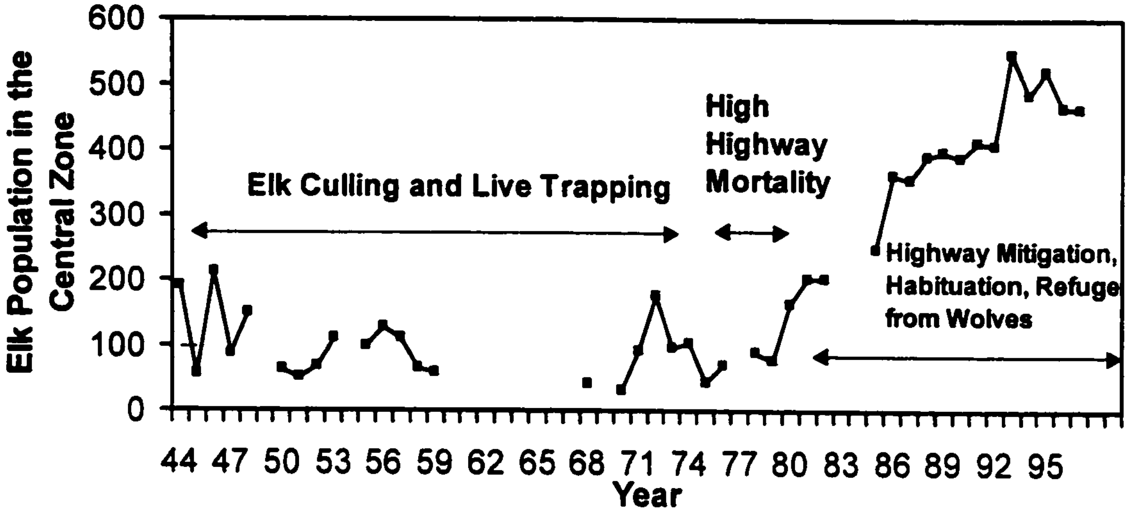

Figure 4.5: The elk population the central zone from 1944 to 1997. Elk populations have increased significantly from 1985 until 1997, increasing from 247 elk to 463 elk ($r = 0.84$, $P < 0.001$). Before 1985, the elk population in the central zone was ≤ 200.

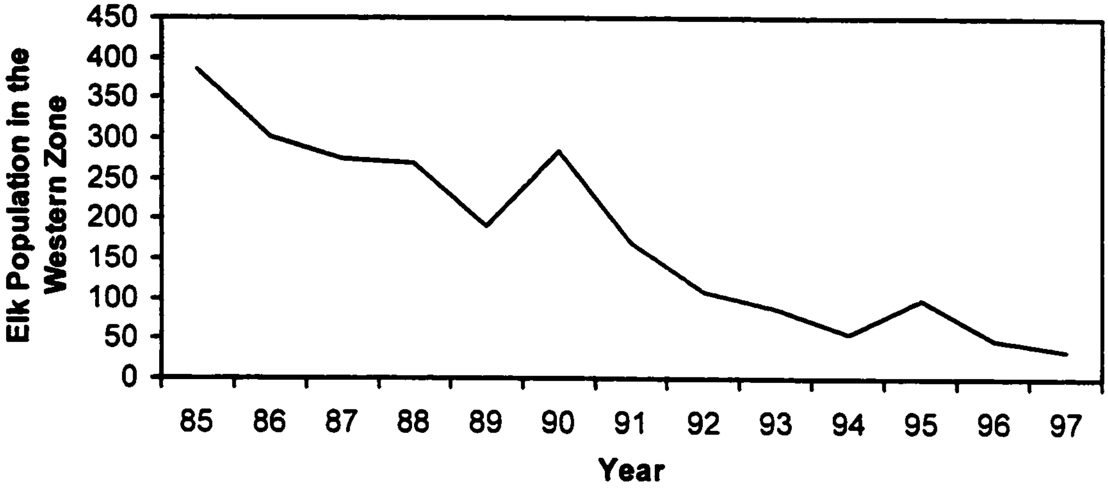

Figure 4.6: The elk population in the western zone from 1985 to 1997. Elk in the western zone have decreased significantly from 1985 to 1997 ($r = -0.95$, $P < 0.001$).

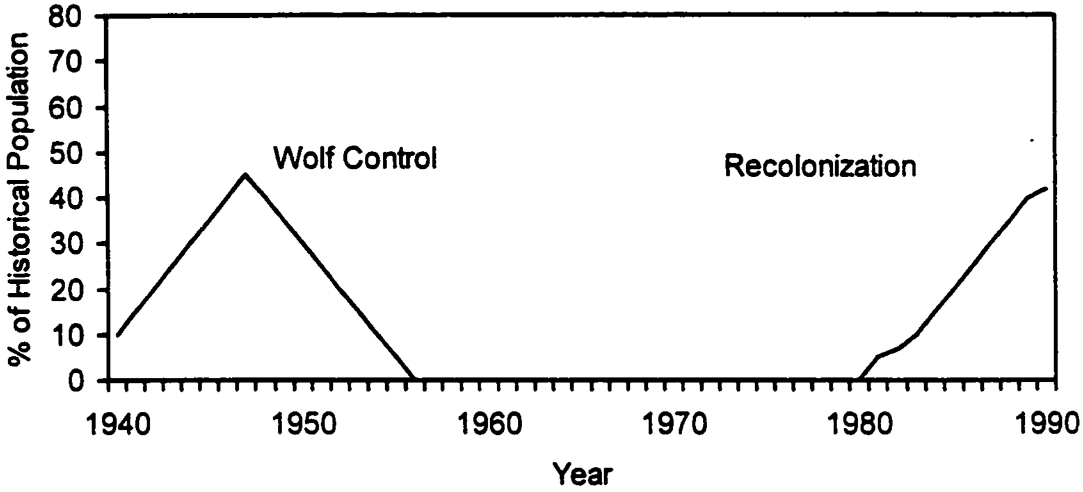

Figure 4.7: Wolf population trends from 1940 to 1990 (After Paquet et al. 1996). Wolf control in the 1950's caused wolves to decline, while in 1987, 2 or more packs became established in the Bow Valley.

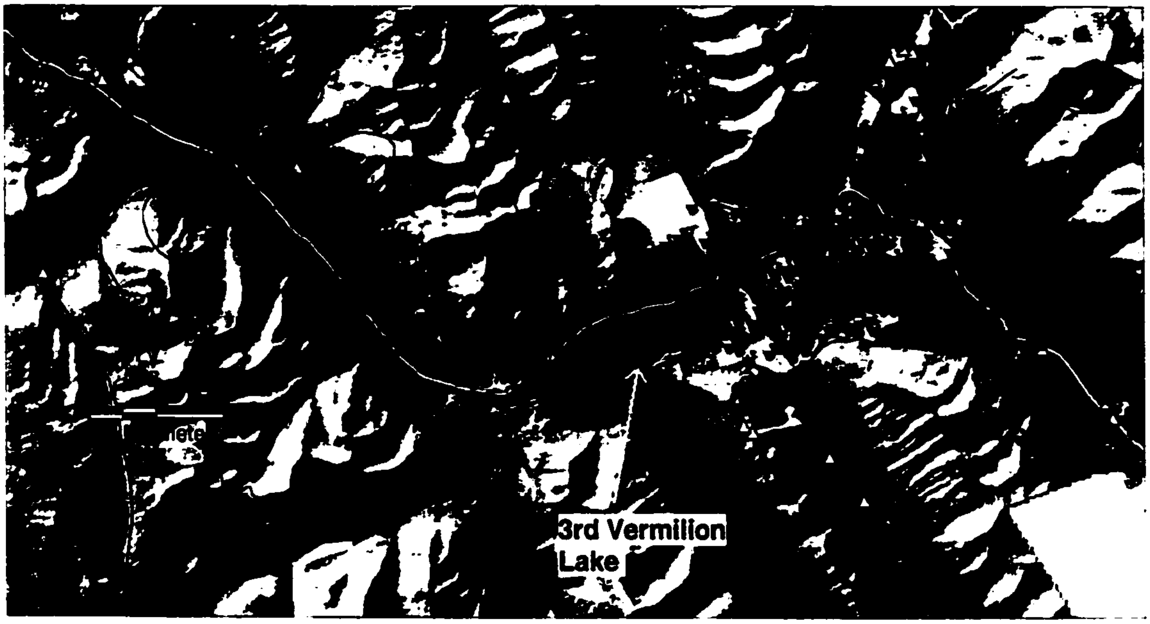

Figure 4.8: Telemetry locations of wolves (red) and elk (blue), from 1985-1993 in the Bow Valley of Banff National Park, Alberta (from Paquet et al. 1996). The majority of the wolf locations are west of the Vermilion Lakes Wetland, while elk use was concentrated in the central zone, especially near town.

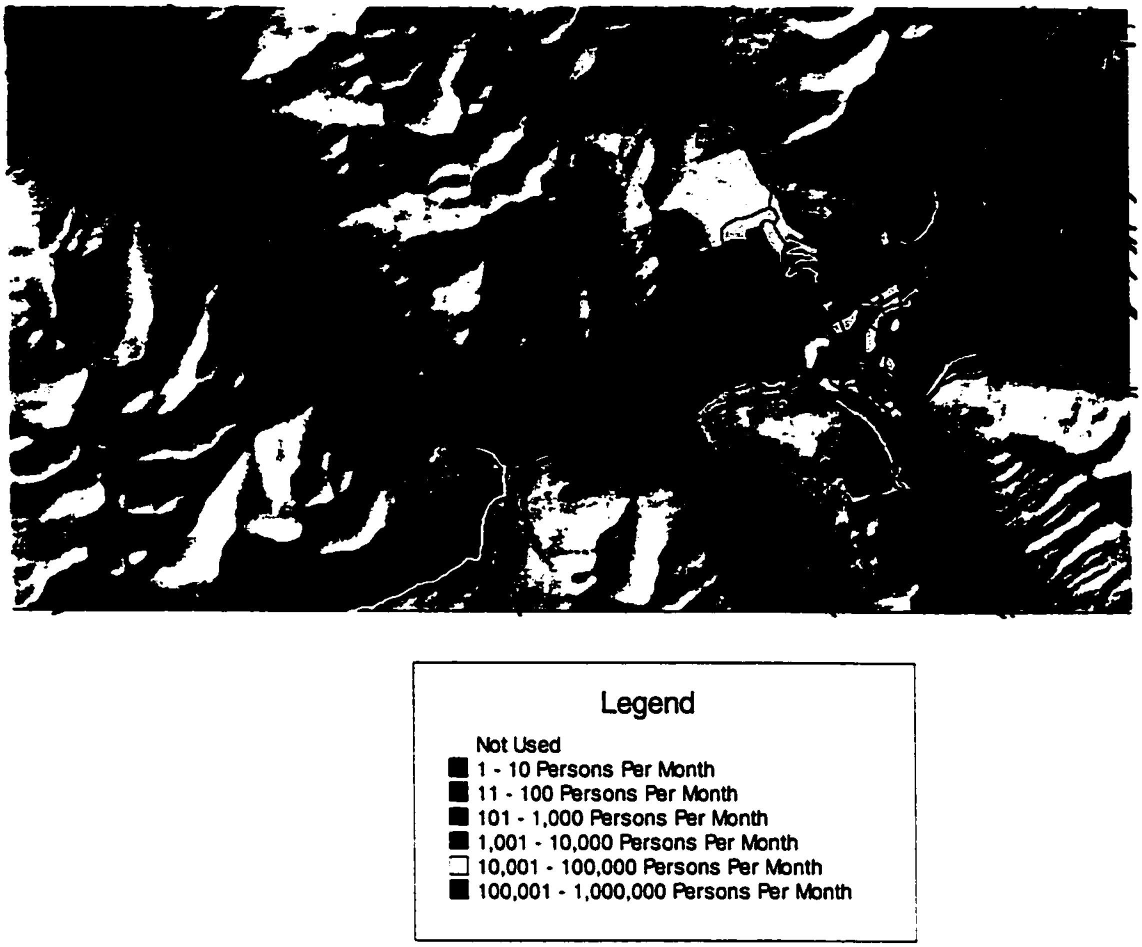

Figure 4.9: Winter Human use in the central and western zones in the Bow Valley, Banff National Park (from Pacas 1996). Most of the human use in the central zone is 10,001-100,000 persons per month on trails, and 100,001-1,000,000 persons per month on secondary roads.

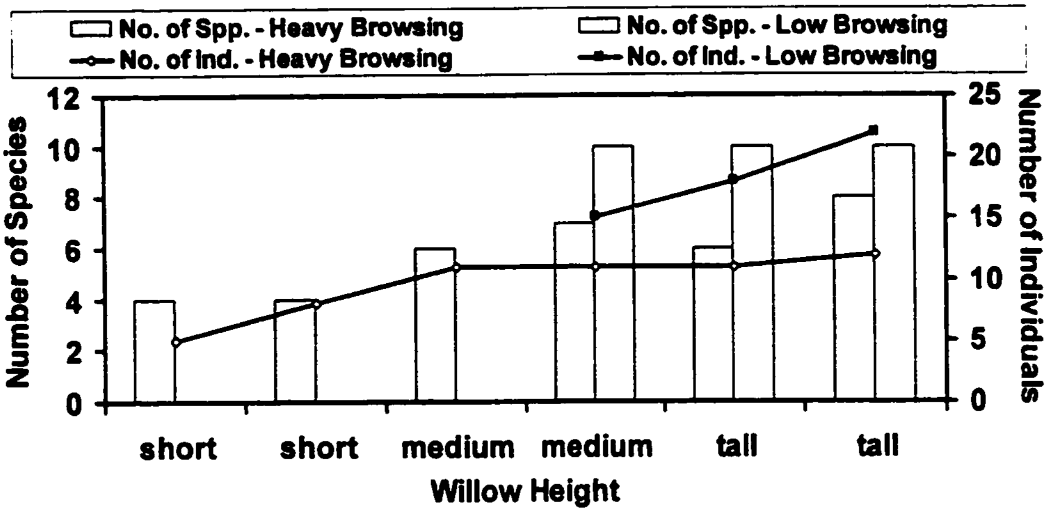

Figure 4.10: The relationship between songbird diversity and abundance, willow height and browse intensity. Songbird species diversity and abundance was greater in tall versus short willow, and in low versus heavy browsing sites ($P < 0.05$). Bird species diversity and abundance increased with willow height.

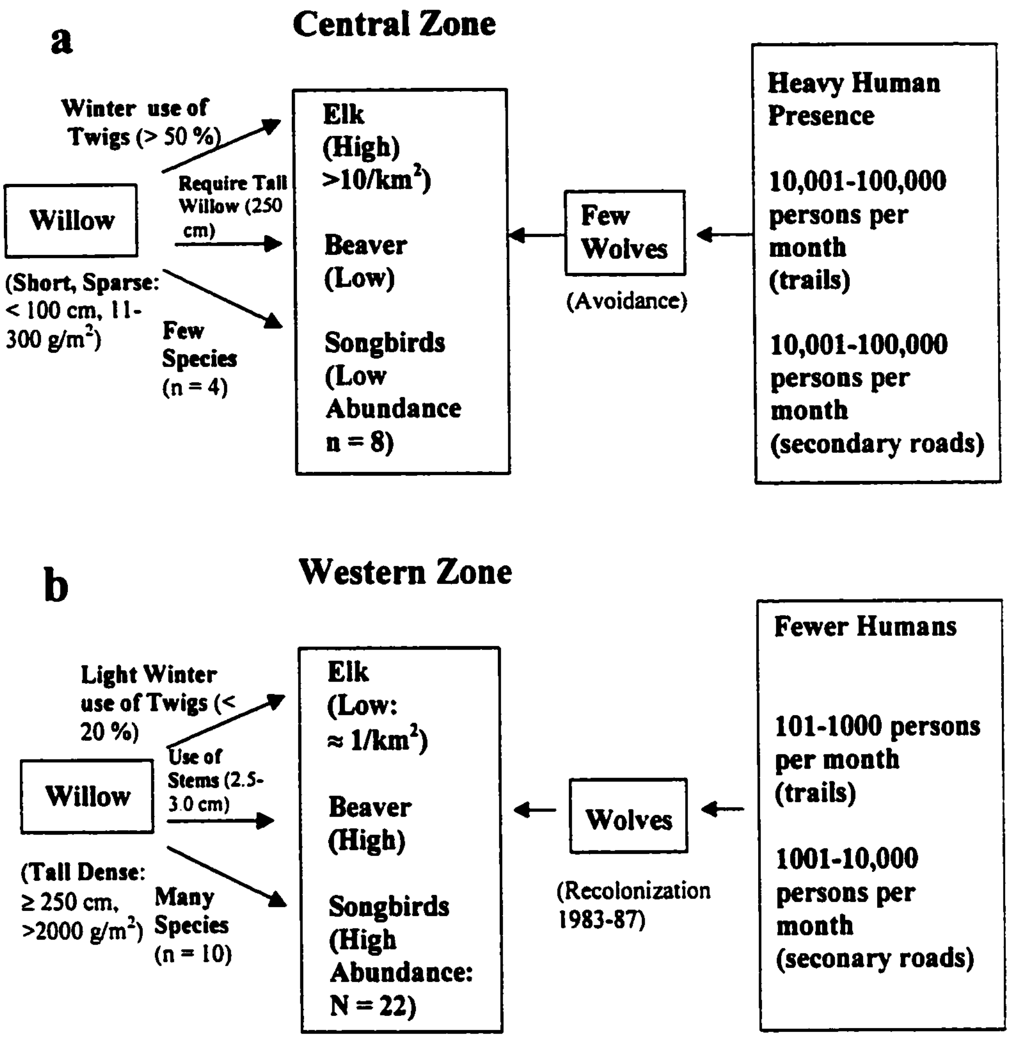

Figure 4.11: Conceptual models of trophic levels for the central (a) and western (b) zones in the Bow Valley of Banff National Park in 1995-1997.

Appendix: Raw data for songbird species diversity and abundance in relation to willow height and ungulate browsing.

Site and Treatment	**Songbird Species**	**Species Code**	**Number of Individuals**
Industrial Compound Short Willow High Browsing	Lincoln's Sparrow	LISP	1
	Common Yellowthroat	COYE	1
	Savannah Sparrow	SASP	2
	Song Sparrow	SOSP	1
		Total = 4	**Total = 5**
1st Vermilion Lake Short Willow High Browsing	Lincoln's Sparrow	LISP	3
	Common Yellowthroat	COYE	2
	Wilson's Warbler	WIWA	1
	American Robin	AMRO	1
		Total = 4	**Total = 8**
2nd Vermilion Lake Medium Willow High Browsing	Lincoln's Sparrow	LISP	2
	Common Yellowthroat	COYE	4
	Yellow Warbler	YEWA	1
	Red-winged Blackbird	RWBB	2
	Clay-coloured Sparrow	CCSP	1
	Alder Flycatcher	ALFL	1
		Total = 6	**Total = 11**
Vermilion Lake Drive Medium Willow High Browsing	Lincoln's Sparrow	LISP	1
	Common Yellowthroat	COYE	2
	Red-winged Blackbird	RWBB	3
	Savannah Sparrow	SASP	1
	Le Conte's Sparrow	LESP	1
	Chipping Sparrow	CHSP	2
	Alder Flycatcher	ALFL	1
		Total = 7	**Total = 11**
Across 2nd Vermilion Lake Tall Willow High Browsing	Common Yellowthroat	COYE	1
	Yellow Warbler	YEWA	3
	Red-winged Blackbird	RWBB	2
	Alder Flycatcher	ALFL	2
	American Robin	AMRO	1
	Brown-headed Cowbird	BHCO	1
	Magnolia Warbler	MGNW	1
	Swaison's Thrush	SWTH	1
		Total = 8	**Total = 12**
2nd Vermilion Lake Tall Willow High Browsing	Common Yellowthroat	COYE	1
	Yellow Warbler	YEWA	3
	Red-winged Blackbird	RWBB	4
	Alder Flycatcher	ALFL	1
	Brown-headed Cowbird	BHCO	1

	Savannah Sparrow	SASP	1
		Total = 6	**Total = 11**
3rd Vermilion Lake Tall Willow Moderate Browsing	Common Yellowthroat	COYE	2
	Yellow Warbler	YEWA	3
	Red-winged Blackbird	RWBB	2
	Alder Flycatcher	ALFL	1
	American Robin	AMRO	1
	Brown-headed Cowbird	BHCO	1
	Lincoln's Sparrow	LISP	1
	American Redstart	AMRE	1
	Warbling Vireo	WAVI	1
	Swaison's Thrush	SWTH	1
		Total = 10	**Total = 14**
Moose Meadows West Medium Willow Low Browsing	Common Yellowthroat	COYE	3
	Yellow Warbler	YEWA	1
	Red-winged Blackbird	RWBB	1
	Alder Flycatcher	ALFL	3
	American Robin	AMRO	1
	Wilson's Warbler	WIWA	2
	Clay-coloured Sparrow	CCSP	1
	Chipping Sparrow	CHSP	1
	White-crowned Sparrow	WCSP	1
	Orange-crowned Warbler	OCWA	1
		Total = 10	**Total = 15**
Beaver Pond – Muleshoe Tall Willow Low Browsing	Common Yellowthroat	COYE	2
	Yellow Warbler	YEWA	3
	Red-winged Blackbird	RWBB	4
	Alder Flycatcher	ALFL	4
	Brown-headed Cowbird	BHCO	1
	Least Flycatcher	LEFL	3
	Lincoln's Sparrow	LISP	1
	Song Sparrow	SOSP	2
	Tennessee Warbler	TEWA	1
	Wilson's Warbler	WIWA	1
		Total = 10	**Total = 22**
Beaver Pond - Lac Des Arc Tall Willow Low Browsing	Common Yellowthroat	COYE	2
	Yellow Warbler	YEWA	3
	Red-winged Blackbird	RWBB	4
	Alder Flycatcher	ALFL	2
	American Robin	AMRO	1
	Chipping Sparrow	CHSP	1
	Song Sparrow	SOSP	2
	American Redstart	AMRE	1

	Tennessee Warbler	TEWA	1
	Least Flycatcher	LEFL	1
		Total = 10	**Total = 18**