## ASPEN, ELK, AND FIRE IN THE CANADIAN ROCKY MOUNTAINS

by

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#### Abstract

Trembling aspen (*Populus tremuloides*) is failing to survive through the sapling stage (2 to 4 m) to tree size in many national parks in western North America. Hypotheses for aspen decline include reduced burning, climate change, high herbivory by native ungulates (mainly elk (Cervus elaphus)), or interactions between these factors. Historic and current aspen condition was investigated in several watersheds, inside and outside of national parks, in the Rocky Mountains of Alberta, Canada to determine the causes of aspen decline. Methods included repeats of historical photographs, fire history by dendrochronology, time-series analysis (of climate, burned area, elk density, and aspen regeneration), wildlife exclosure measurements, analysis of elk functional herbivory response to aspen density, and effects of predation risk on elk-aspen foraging patterns. Aspen regeneration was abundant in historic photographs, is currently abundant in areas with low elk density (<2 elk/ km<sup>2</sup>), but has declined precipitously in national park areas with high elk density. Historic anthropogenic burning appeared to be important along valley-bottom corridors occupied by aspen, but declined c. 1900 due to changes in cultural land uses. Yearly fluctuations in climatic conditions or burned area did not appear to be factors in aspen decline. Aspen is regenerating in wildlife exclosures on a range of site moisture conditions. Thus, climate or disturbance, either individually, or interactively with herbivory, do not appear to be major factors in aspen decline. However, elk herbivory was a highly significant factor. Elk-aspen herbivory followed a Type 2 functional response (decreased rates of browsing at higher densities of aspen regeneration) that may have occurred because predation sensitive elk avoided dense aspen stands. Historically, valley-bottom aspen habitats were heavily used by predators (humans and wolves) which reduced elk herbivory, and were frequently human-burned which stimulated regeneration of dense stems. Current land uses in national parks (with control of hunting and fire, and high human use that displaces wary predators but habituates elk) are the opposite of these long-term processes. Successful aspen regeneration will likely require a period of very low densities of elk that are wary of predators and humans, followed by restoration of anthropogenic burning.

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### CHAPTER 1. GENERAL INTRODUCTION

Trembling aspen (*Populus tremuloides*) forests are an important community type in the Rocky Mountain national parks of Canada and United States. In Banff and Jasper (Alberta, Canada), Yoho and Kootenay (British Columbia, Canada) national parks, aspen covers <5% of the low elevation montane ecosystem, where large stands occur on alluvial fans, or small stands are dotted through lodgepole pine (Pinus contorta) and Douglas-fir (Pseudotsuga menziesii) forests (Achuff and Corns 1982). In Yellowstone National Park (Wyoming, U.S.), aspen is limited to <1% of the park, and occurs mostly on seeps and swales in grasslands at low elevations (Houston 1982, Kay 1990). In Rocky Mountain National Park (Colorado, U.S.), aspen stands are found throughout the montane ecoregion (Olmsted 1979, Suzuki et al. 1999). Because current conditions for regeneration from seed are not favorable, the clones constituting these stands may be several thousand years old (DeByle and Winokur 1985, Mitton and Grant 1996). Frequent (<40 years return interval), low-intensity fires in low elevation areas (Houston 1973, Tande 1979, Arno 1980, White 1985a) regenerated large clones by removing competing conifers, top-killing the aspen, and stimulating growth of suckers from surviving roots (Bartos and Mueggler 1979, 1981; Bartos et al. 1994; Romme et al. 1995; Kay et al. 1999). Small aspen stands in conifer forests may survive through long fire-free intervals (>100 years) by periodic release of suckers in forest gaps (Kay 1997b).

Because aspen stands often occupy moist, nutrient rich sites at low elevations, they have very high biodiversity, exceeded only by riparian zones and wetlands in the Rocky Mountains (Finch and Ruggiero 1993). Holroyd and Van Tighem (1983) rated montane aspen vegetation types in Canada as high-quality habitat for large mammals such as elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*) and a diverse range of small mammal species. Bird diversity is also high in aspen stands (Flack 1976, Turchi et al. 1995).

Aspen can be tied to ecosystem condition through a 4-level trophic model (Figure 1) that links humans, wolves (*Canis lupus*), elk and aspen through the processes of predation, herbivory, burning and differential wildlife behavioral responses to humans (White et al. 1994, Kay and White 1995). These processes have been altered substantially during the last



Figure 1.1. Trophic model linking humans, wolves, elk and aspen.

150 years of human land-use change in and around Rocky Mountain national parks by activities such as removal of Native peoples, predator control, fire suppression, elk culling, and construction of roads and visitor service facilities (White et al. 1998a). However, the effects of these changing land uses on aspen and other montane ecological communities remains highly controversial (Chase 1987, Hess 1993, Wagner et al. 1995, Singer et al. 1998, Huff and Varley 1999).

### Hypotheses for Aspen Decline

Since the 1940's, researchers have reported that aspen stands in Rocky Mountain national parks were declining in vigor (Packard 1942, Cowan 1947, Flook 1964). These aspen stands have declining numbers of large diameter stems with extensive black bark due to elk bark-stripping, and few younger aspen stems in the understory (Kay 1990, 1997a; Romme et al. 1995). In some areas, conifers are also encroaching into aspen stands, and shading out the less shade-tolerant aspen (Achuff et al. 1996, Kay 1997b). As older aspen stems die, they are not replaced due to few younger aspen, and aspen stands may change to grass, shrub, or conifer communities (Kay 1990, Kay 1997a).

Explanations for aspen decline are based upon whether, over the long-term, elk population levels were generally high and regulated by "bottom-up" factors such as food availability and vegetation disturbance (1 principal hypothesis with 2 variants), or generally low and regulated by "top-down" predators and humans (Kay 1990, Keigley 1997, White et al. 1998a, Singer et al. 1998).

## High-herbivory hypothesis

This theory predicts that a long-term stable state of montane areas occurs when aspen and other species are utilized extensively by abundant, food-regulated elk (Cole 1971, Houston 1982, Coughenour and Singer 1996, Huff and Varley 1999). Heavily browsed aspen persist in the ecosystem due to regeneration by fire (Gruell 1979, Houston 1982, Boyce 1989), variable chemical defence levels that protect aspen suckers against herbivory (Despain 1991), or a complex interaction of factors such as fire, elk starvation, winter severity and climate change (Houston 1982, Boyce 1991, Romme et al. 1995). The current degeneration of aspen is due to an increase in the number of elk back to a normal foodregulated equilibrium following intense human hunting during the late 1800s. Wolf and other predation on elk is considered a "non-necessary adjunct" (Cole 1971), which removes animals that will die anyway due to starvation, and thus cannot substantially lower elk populations below food-regulated levels (Boyce 1996). Existing data does not tend to support this viewpoint in any of the Rocky Mountain parks. Photographs of mature aspen taken at the time of Yellowstone's establishment show no bark stripping, indicating longterm low elk density (Kay and Wagner 1994). Furthermore, archaeological site data and early explorer journals for both the Rocky Mountains in the United States (Kay 1990, 1994, 1997a) and Canada (Kay and White 1995, White et al. 1998b, Kay et al. 1999) repeatedly show a pattern of low elk abundance.

## **Disturbance** hypothesis

A variant of the high herbivory hypothesis is based upon fire effects. Loope and Gruell (1973), Gruell (1979, 1980) and Houston (1982) proposed that widespread fire suppression was the primary cause of aspen decline. According to this view, fires caused extensive aspen suckering that could theoretically offset herbivory effects in areas with moderate or higher elk density. This would allow at least some aspen suckers to grow into sapling or tree form (Bartos and Mueggler 1979, Romme et al. 1995). However, monitoring of numerous burn areas in and near Rocky Mountain national parks shows that this has not happened (Bartos et al. 1994, Romme et al. 1995, Kay et al. 1999). Instead, the combination of fire and browsing by high densities of elk appears to have actually accelerated the demise of aspen (Kay and Wagner 1996). Given the long-term historical regime of frequent fires (<40 year fire cycle) in the montane ecoregion (Houston 1973, Tande 1979, Arno 1980, White 1985a), the change of the role of fire in these ecosystems— from acting as a stimulant to becoming a deterrent of aspen growth—has many ecological implications. However, the failure to observe disturbance effects has only been evaluated under conditions of high elk (>5/km<sup>2</sup>) densities in and near Yellowstone (Bartos et al. 1994, Kay and Wagner 1996), and Banff (Kay et al. 1999) national parks.

#### Climate change hypothesis

A further elaboration of the high-herbivory hypothesis proposes that periods of cool and moist climate are essential for prolific aspen regeneration, and that a warmer and drier climate since the 1930s has been a significant factor in the recent aspen decline (Houston 1982, Romme et al. 1995). Initial observations provide no evidence for this effect because of the consistent regeneration and growth of aspen in numerous wildlife exclosures in parks throughout the Rocky Mountains (White et al. 1998a). If climate were a significant factor, aspen condition in exclosures should be the same as outside (Kay 1990, 1997a; Baker et al. 1997). Also, if climate was a major factor, aspen outside of park boundaries should also be declining, but this is often not the case (Kay 1990, Kay et al. 1999). However, similar to evaluations of disturbance, the failure to observe climate effects has been limited to a narrow range of contrasts, and site conditions (e.g., soil moisture and habitat type) have not been controlled.

## Low-herbivory hypothesis

Some researchers have concluded that heavily browsed aspen is not a long-term state. It is a recent phenomenon due to unusually high elk populations (Packard 1942, Cowan 1947, Olmsted 1979, Kay 1990, Baker et al. 1997, White et al. 1998a, Ripple and Larsen 2000). These researchers posit that the current die-back of aspen stands inside parks is due to recent human-caused changes to the long-term ecological conditions that once favoured aspen survival. These changes include: (1) release of elk from intense additive predation from humans, wolves and other carnivores, (2) habituation of unhunted elk to human presence, and (3) decrease in fire occurrence by elimination of cultural burning by native peoples, and suppression of current human and lightning caused fires. Numerous lines of evidence support the low-herbivory hypothesis (Kay 1990, Kay and White 1995; Kay 1997a, b; White et al. 1998a, b; Kay et al. 1999) including archaeological data, early explorer's journals, repeat photography, fire-scar dendrochronology, fire effects, aspen stand analyses, wildlife exclosure data, and current elk and wolf population studies. Kay (1990, 1994) and White et al. (1998a) predicted that aspen was historically abundant because elk density was generally low (<1 elk/km<sup>2</sup>) due to intense predation from humans, wolves and other carnivores. However, some areas may have had slightly lower predation and higher

elk density, such as zones between warring tribes (Kay 1994, Martin and Szuter 1999), or wolf packs (Mech 1977), but these areas were not fixed, and could shift with time. Frequent burning, often caused by humans (Barrett 1980; Lewis 1980,1982; Pyne 1995, Boyd 1999), and low ungulate browsing structured aspen and other species into vigorously regenerating plant communities. A few older stands occurred, which by chance alone, escaped frequent burning (Johnson et al. 1995). However, beyond positing low elk densities and frequent fire, and some general predictions for montane ecosystem pattern (White et al. 1998a), the lowherbivory hypothesis currently provides few specific quantitative predictions for mechanisms that would lead to aspen persistence.

#### General Research Approach

Predator-prey models (e.g., Solomon 1949, Holling 1965, Taylor 1984, Sinclair and Peche 1996), as applied to herbivory (Noy-Meir 1975, Caughley 1976, Schmitz and Sinclair 1997), can provide a theoretical basis to clarify elk and aspen interactions. The key assumption in applying predation theory to aspen is that the condition and size of individual aboveground plant stems (ramets) of a plant are an important indicator of belowground root condition, and clonal viability at the clonal (genet) level (Harper 1977, 1980). For ungulateaspen herbivory analysis, the most important size class of stems is aspen saplings (>2 meters and <4 m in height and <5 cm diameter at breast height) that provide both browsing forage for herbivores, and a measure of aspen stand productivity. In lightly browsed aspen stands, disturbances such as fire stimulate dense sucker (stems <2 m in height) production (> 5000 stems/100 m<sup>2</sup>) from surviving roots which rapidly self-thin to approximately 200 sapling stems/100 m<sup>2</sup> at 6 years after disturbance (Peterson and Peterson 1992). However, disturbance is not required for suckering, and suckers frequently occur at the edge of aspen clones, or even under conifer stands (DeByle and Winokur 1985, Kay 1997b). Periodic survival of aspen stems through the sapling stage is likely important to develop root-shoot biomass that sustains clones through periods of high herbivory (Kay and Wagner 1994), or relatively frequent disturbance (Shepperd and Smith 1993).

For any predator/prey interaction, the stability properties of prey are determined by the rates of prey productivity under varied conditions, and the rates of mortality imposed by

predators or herbivores at varied densities (Noy-Meir 1975, Taylor 1984). For a declining species where predation or herbivory is a suspected causal factor, an evaluation of stability properties is critical to define predation rate response to varying prey densities, and the ranges for predator and prey abundance where prey populations can persist (Pech et al. 1995). This information is essential to define what, if any, conservation strategies are required (Sinclair et al. 1998).

In this thesis, I evaluated the multiple hypotheses for aspen decline by analysing prey productivity (aspen sapling density) versus predator caused mortality (herbivore browsing intensity) over a range of aspen and elk densities, and varied time and spatial scales. The underlying approach was to use natural experiments, where elk densities or aspen productivity have been influenced at a landscape level by human land-use patterns. For this purpose, Alberta's Rocky Mountains provide an excellent study area due to replicate watersheds along the eastslopes that have different histories of landscape disturbances due to fire and logging, and elk density due to establishment of parks, and predator and hunting controls (White et al. 1995). Study areas were inside and outside national parks, and have a variety of aspen stand conditions, elk densities, and disturbance histories. I sought answers to two main questions: 1) What is the long-term history (100 to 150 years) of aspen communities in the montane ecoregion of the eastslopes? And 2) Where aspen has declined, what factors, or combination of factors have important effects? Specifically, I tested predictions from the four hypotheses for aspen decline. Where appropriate, I evaluated results in terms of the underlying predatorprey theory and experimental protocols to conserve declining species (Pech et al. 1995, Sinclair et al. 1998).

## Thesis Outline

In Chapter 2, I used repeat photographs to test specific predictions of the lowherbivory hypothesis that aspen stands developed under conditions of intense human and carnivore predation on elk, low ungulate herbivory, and frequent human-caused fires. I obtained 165 historic views (1874 to 1949) showing detailed aspen stand conditions in 7 areas. Historic and current aspen stand conditions (e.g., stem spacing by height class and species, barking, and browse class) were quantified for 195 stands visible in photographs.

Changes evident in the historic and current photographs were used to evaluate whether long-term conditions changed with reduced burning by First Nation cultures by 1875, and were accelerated in Waterton Lakes, Banff and Jasper national parks where, in addition to fire, hunting and predators were also controlled.

Chapter 3 is an analysis of disturbance history relevant to aspen stands. Two alternative hypotheses for recent decreases in fire frequency are described: 1) climate change reducing the number of lightning fires, or 2) reduced cultural burning due to changes from long-term First Nation and early settler land use patterns. I used dendrochronology on fire-origin or fire-scarred lodgepole pine trees surrounding valley-bottom meadows to test the cultural burning hypothesis that spring meadow burning was common.

Chapter 4 deals with the "complex interaction" hypothesis that posits that aspen decline is caused by a combination of factors including reduced disturbance, climate change, and increased herbivory by elk. I evaluated the hypothesis with long-term (70 to 190 years) time-series information from the Bow Valley in Banff National Park, Alberta on aspen stand regeneration by year, area disturbed by fire, drought indices, and elk population levels. Further, I measured the response of aspen saplings to 3 site moisture levels (moist, mesic, dry) and 3 levels of browsing and disturbance (inside cleared wildlife exclosures, next to exclosures, away from exclosures).

In Chapter 5, I evaluate hypotheses for aspen decline with specific predator-prey models as applied to herbivory. The functional response of elk-aspen herbivory is used to test the hypothesis that aspen regeneration could result from interaction of elk herbivory and factors that affect aspen productivity (e.g., fire or forest competition). For this analysis, I used elk census data from 9 study areas (30 to  $100 \text{ km}^2$ ) with 3 areas at each of 3 elk density levels (<2, 2 to 4, >4 elk/km<sup>2</sup>). In each study area, I sampled aspen stand conditions in 10 plots in each of 4 tree cover levels (recently disturbed (<25 years ago), open, moderate, and closed canopy) that effect aspen regeneration.

In Chapter 6, the proposition is tested that fine scale, risk-sensitive foraging patterns by elk on aspen may be influenced by distance from roads or trails, the type of user on road or trail (park visitor, hunter, or predator), and condition of aspen stand (open grown or thicket). I hypothesized that these elk behaviour patterns may create 2 general states for aspen stand conditions: 1) mature, open stands with no stems in the sapling

height class in unhunted areas with few predators, or 2) dense stands of aspen saplings in hunted areas with abundant predators, and low densities of risk-sensitive elk.

Chapter 7 concludes with a summary of main findings, an integration supporting a new hypothesis for long-term ecosystem states and processes, management recommendations, and needs for future research.

#### CHAPTER 2. REPEAT PHOTOGRAPHY

#### Introduction

Historic photographs and current retakes from the same camera station, often called repeat photographs, can be used to evaluate long-term (>50 years) landscape change over large regions. The technique was applied as early as 1888 by Finsterwalder to map glacier movement in the eastern Alps (Hattersley-Smith 1966). It has also been used to evaluate long-term wildlife, fire, and climate effects on landscapes and vegetation in various situations— from rangelands of the western United States (Gruell 1980, Rogers et al. 1984, Hart and Laycock 1996, Meagher and Houston 1998), to the African Serengeti (Sinclair 1995).

Repeat photography studies of trembling aspen (Populus tremuloides) forests in the Rocky Mountains of North America can provide useful information on changing ecological conditions over time (Houston 1982, Kay 1990, Kay et al. 1999). Aspen twigs and bark are valuable forage for cervids such as elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (Odocoileus virginianus), and mule deer (O. hemionus) (Nelson and Leege 1982, DeByle and Winokur 1985). Twig-browsing and bark-stripping, visible in historic and current photographs, can provide a long-term record of herbivore abundance (Kay 1990). Further, aspen stands are generally found on the valley-bottoms, within the montane ecoregion (Achuff and Corns 1982, Houston 1982, Suzuki et al. 1999), where historically fires were frequent (Houston 1973, Tande 1979, Arno 1980, White 1985a). Evidence of fire such as recently burned trees and logs, and young forest regeneration is often visible in historic photographs (Gruell 1980). Because aspen has low flammability during the summer (Fechner and Barrows 1976, DeByle et al. 1987), it is likely that many of these fires were spring or fall season fires with a more heterogenous pattern than mid-summer fires (Kay et al. 1999). In the absence of fire, aspen stands mature with larger and fewer trees (DeByle and Winokur 1985, Peterson and Peterson 1992). Conifers such as white spruce (Picea glauca), or lodgepole pine (Pinus contorta) often gradually increase in abundance and size (Achuff and Corns 1982). These fire-related characteristics are easily visible in historic photographs (Gruell 1980). In contrast, using dendrochronology techniques to date fires can be difficult in forests dominated by multi-aged tree regeneration (Johnson and Gutsell 1994) and heterogenous fire regimes (Lertzman et al. 1998).

Aspen is tied to ecosystem condition through a 4-level trophic model (Figure 1.1) that links humans, wolves, elk, and aspen through the processes of predation, herbivory, burning, and differential wildlife responses to humans (White et al. 1994, 1998a; Kay et al. 1999). These processes have been altered substantially during the last 150 years of human land-use change in the Rocky Mountains by activities such as removal of native peoples, fire suppression, elk hunting, predator control, and national park establishment. However, the effects of changing land uses on montane ecology are controversial (Wagner et al. 1995, Singer et al. 1998, Huff and Varley 1999). Explanations for an observed decline in the cover and vigor of aspen and willow (Salix spp.) in both Canadian and US national parks fall into three general categories (Keigley 1997, Singer et al. 1998): fire suppression (Loope and Gruell 1973, Gruell 1980, Houston 1982), climate change (Singer et al. 1994, Romme et al. 1995), or recent human land use changes that have caused high densities of elk in national parks (Cahalane 1941, Cowan 1947, White et al. 1998a). These alternative explanations are based upon a fundamental ecological question (Kay 1998). Was the long-term Rocky Mountain montane ecosystem generally structured from the "bottom up" (e.g., abundant resource-limited ungulates that utilized vegetation influenced primarily by climate and midsummer lightning fires), or from the "top-down" (e.g., few predator-regulated ungulates in a human-burned landscape)?

This study used repeat photography of aspen inside and outside of national parks in seven areas along Alberta's eastslope of the Rocky Mountains to test predictions made by the "top-down" hypothesis for aspen decline. I used historic photographs with current retakes to test 5 specific predictions from the hypothesis (Table 2.1).

Table 2.1. Statistical tests and sample sizes for predictions evaluated with attribute data through repeat photography analysis. Saplings are aspen stems 2 to 4 m high, and suckers are 1 to 2 m high. Sample sizes for montane fire frequency predictions are broken down by north (N) and south (S) regions.

Prediction	Statistical Hypothesis and Null Hypothesis	Statistical Test	Sample Size
Long-term low elk herbivory therefore low bark scarring on aspen trees that originated prior to 1870 where visible in historic pictures	H: mean bark scarring is <35% H <sub>0</sub> : mean bark scarring is ≥35%	Single sample t -test	n = 14 from all historical photographs and all areas showing aspen stems that are large enough to have originated prior to 1870
High montane fire frequency reduced by cessation of native burning therefore increasing stand age in historic photographs after 1870	H: estimated aspen stand age increases by 20 year periods (1870 to 89, 1890 to 1909, 1910 to 29) $H_o$ : estimated stand age equal for initial 20-year periods, increases after 1910	Two factor ANOVA of estimated aspen stand age in photographs for 2 areas (north and south), and the 3 time periods	$\begin{array}{rrr} \text{Period} & n = & \\ & N & S \\ 1874-94 & 14 & 16 \\ 1895-1914 & 25 & 21 \\ 1915-34 & 47 & 14 \end{array}$
Low herbivory and high fire frequency created a single age class of closely spaced young aspen visible in photographs taken prior to 1885	H: mean spacing of saplings is <4 m and suckers is <2 m $H_0$ : mean spacing of saplings is $\ge 4$ m, suckers is $\ge 2$ m	Single sample t -tests	Sectors showing saplings: n = 25 Sectors showing suckers: n = 16 from all photographs taken <1885
High vigor aspen due to low herbivory (1874 to 1940), therefore historic photos in all areas should show numerous aspen suckers and saplings with low barking and low browsing	H: for all areas, mean spacing of saplings and suckers <10 m, stem barking <20%, and stem browsing class < 2 $H_0$ : mean spacing in at least one area $\geq$ 10 m, barking $\geq$ 20%, or browse class $\geq$ 2	Single sample t- tests for historic sapling and sucker spacing (log-transformed) and barking for 7 areas, with Bonferroni multiple test adjustment.	n = 15 for each of 7 areas for all attributes except barking where n = 10 per area
Declining aspen vigor in areas of high elk density (1940 to1999), therefore substantial increase in spacing of aspen stems in 1 to 2 m and 2 to 4 m height classes in Banff and Jasper national parks compared to other areas	H: significant difference in differences between historic and current spacing of aspen stems between Banff and Jasper parks, and other areas H <sub>o</sub> : no significant difference in differences between current and historic spacing between areas	One-way ANOVA of difference between current and historic aspen stem spacing for 7 study areas	n = 15 for each of 7 areas

<u>Prediction 1.</u> Long-term elk densities were low and regulated top-down predation. Therefore large diameter aspen trees visible in historic photographs should not have the extensive bark-scarring caused by elk herbivory. The alternative bottom-up hypothesis predicts that long-term elk densities were generally high, less effected by predation, and likely regulated by bottom-up processes related to production of forage such as moisture conditions (Coughenour and Singer 1996). Elk at moderate to high density on winter ranges will strip the bark from aspen with their lower incisors (DeByle 1985a). Aspen trees surviving a period of high elk herbivory will have a minimum of approximately 35% of their lower stem blackened with bark scars, and in some cases, almost the whole stem, as high as elk reach, will be scarred (Packard 1942). Thus, the bottom-up hypothesis would predict extensive bark-scarring on aspen trees originating prior to c. 1860.

<u>Prediction 2.</u> High montane fire frequency was reduced when First Nation's burning was curtailed prior to organized fire suppression. Thus early historic photographs should show evidence of young-aged forests with few, older stands, due to frequent fires started by native peoples (Kay et al. 1999). The time-since-fire (years), as estimated from vegetation conditions visible in photographs, should increase due to reduced presence of native peoples. In contrast, the bottom-up model holds that there were minimal effects of cultural burning on fire regimes. It therefore predicts no changes in fire frequency until government-organized fire suppression programs in the Rocky Mountains and foothills became effective in about 1900 (White 1985a, Murphy 1985).

<u>Prediction 3.</u> Prior to 1880, most aspen stands were young with high vigor due to low herbivory and frequent fires. The "top-down" hypothesis predicts low herbivory and frequent fires are the essential conditions that created a young age-class of aspen originating prior to 1880. If tests for these conditions are supported (see above predictions), aspen stands prior to 1880 (when fire frequency began to decrease) should almost all have a single young age class with prolific, unbrowsed stems. An alternative hypothesis (Romme et al. 1995) predict that the age class of aspen stems originating prior to 1880 resulted from a complex set of interactions between climate, herbivory and fire. Therefore, some stands visible in the oldest historic photographs might have no young stems due to variable climatic, herbivory, or fire effects.

<u>Prediction 4.</u> Consistent high vigor, multi-aged aspen should have occurred in all areas due to low herbivory for the period 1880 to 1940. High hunting pressure maintained very low herbivore densities throughout most areas of Alberta's eastern slopes for over 50 years after 1880 (Millar 1915), and nearly extirpated elk (Stelfox 1964). Forests may have aged due to increasingly effective fire suppression (Murphy 1985, White 1985a). However, the top-down hypothesis predicts that low herbivory is the essential condition that permits aspen regeneration, even in the absence of fire (Kay et al. 1999). Therefore, historic photographs should consistently show vigorous aspen (dense multi-aged stands with no bark scarring) in all eastern slope areas. Alternative "bottom-up" hypotheses would predict aspen vigor to be low in at least some areas due to variable effects of decreasing fire or climate change (Loope and Gruell 1973, Romme et al. 1995).

<u>Prediction 5</u>. Aspen vigor should have declined in current photographs of highdensity elk areas, and maintained high vigor in other areas. High elk densities occurred in the montane ecoregion of Banff and Jasper national parks after 1940 (Cowan 1947, White et al. 1998b). The top-down hypothesis predicts that aspen vigour should decline in those areas, but remain high in other areas of low elk density. Alternative variants of the "bottomup" hypothesis (climate change and fire suppression) would predict a general decline of aspen throughout the eastslopes due to ongoing fire suppression or climate change.

The use of historic photographs is important to test these predictions because recent human impacts such as fire suppression, predator control, forestry, ranching, farming, urbanization, and road building have seriously impacted Alberta's montane ecoregion (White et al. 1995). Thus, at present, there may be few aspen stands, either in or out of protected areas and parks, in environments characteristic of long-term ecosystem states and processes (Banff Bow Valley Study 1996, White et al. 1998a, Kay et al. 1999).

#### Methods

Historic and current aspen conditions were evaluated in 7 areas along the eastslope of the Rocky Mountains in Alberta, Canada (Figure 2.2, Table 2.2). All aspen stands were located in the montane ecoregion with relatively low elevations ranging from <1800 m near Jasper townsite to >2200 m in Waterton Lakes National Park. Vegetation cover is predominantly wetlands, grasslands, trembling aspen, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine and white spruce (Achuff and Corns 1982, Archibald et al. 1996, Beckingham et al. 1996).

The montane ecoregion is important winter range for elk, moose and deer (Cowan 1947, Flook 1964, Holroyd and Van Tighem 1983). Based on recent Parks Canada and Alberta Environmental Protection winter elk counts (White et al. 1995, Dekker et al. 1995, Van Tighem pers. comm.), 2 national park study areas have relatively high winter elk density (Athabasca-Jasper Townsite vicinity (AJ) and Bow-Banff Townsite vicinity (BB), >4 elk/km<sup>2</sup>). Three areas have moderate elk density (Eastslopes North (EN), Bow-Kananaskis (BK), and Waterton Lakes (WL), 2 to 4 elk/km<sup>2</sup>), and 2 areas have low elk density (East-slopes South (ES) and Oldman (OM), <2 elk/km<sup>2</sup>). Originally, it was planned to include the Ya Ha Tinda Ranch area in the Red Deer valley, but that high elk density area had to be deleted because few historic photographs of aspen could be located.

I searched the following collections for historical photographs taken before 1940: Whyte Museum of the Canadian Rockies (Banff, AB), Glenbow Museum (Calgary, AB), the Yellowhead Museum (Jasper, AB), the Alberta Provincial Museum (Edmonton, AB), the National Archives of Canada (Ottawa, ON), the Canadian Geological Survey (Ottawa, ON), and the Dominion Forestry Collection at the Alberta Forest Technology School (Hinton, AB). I obtained 20.3 x 25.4 cm (8 x 10 inch) black and white prints of all photographs showing trembling aspen stands with the exception of those photographs that duplicated other views. Photographs selected generally had aspen in the foreground or midground, and were detailed enough to see individual stems and branches. Wherever possible, the photographs had features that provided details for relocation (landscape or land-use features) or scale (people, horses, wagons, cars, or structures).



Figure 2.1. Locations of the 7 study areas for repeat photography analysis. Codes are: Athabasca-Jasper (AJ), Bow-Banff (BB), Eastslopes-North (EN), Bow-Kananaskis (BK), Eastslopes-South (ES), Oldman River watershed (OM), and Waterton Lakes (WL).

Study Area	Code	Description	Elk Density
Athabasca-Jasper	AJ	Jasper townsite area in Jasper National Park. Valley bottom from Old Fort Point east to Palisades Training Centre. Highly human habituated elk, probably non-migratory (W. Bradford, Parks Canada, pers. Comm.)	> 5 elk/km <sup>2</sup> (Dekker et al. 1995)
Bow-Banff	BB	Bow Valley in Banff National Park from Castle Junction east to park boundary. Highly human habituated elk, mostly non-migratory (Parks Canada 1999)	2 to 4 elk/km <sup>2</sup> west of Banff, >5 elk/km <sup>2</sup> near Banff townsite (White et al. 1995, Paquet et al. 1996)
Eastslopes-North	EN	North Saskatchewan (from Kootenay Plains east to Nordegg), Red Deer, Panther and Ghost valleys (excluding the Ya Ha Tinda Ranch)	Generally < 1 elk km <sup>2</sup> except on Kootenay Plains (2 to 4 elk/km <sup>2</sup> ) (White et al. 1995, Parks Canada 1999, J. Allen, Alberta Natural Resources, pers. comm.)
Bow-Kananaskis	ВК	Bow Valley from Canmore to Exshaw, and Kananaskis Valley from Barrier Lake south to Evans Thomas Creek	1 to 2 elk/km <sup>2</sup> (White et al. 1995)
Eastslopes-South	ES	Lower Kananaskis River, Morley First Nation, Jumping Pound, Elbow, Sheep, and Highwood valleys	<2 elk/km <sup>2</sup> (White et al. 1995)
Oldman	ОМ	Oldman River near the Gap, Happy Valley, Crowsnest Pass, and Castle River valley	<2 elk/km <sup>2</sup> (R. Quinlan, Alberta Natural Resources pers. comm.)
Waterton Lakes	WL	Waterton Lakes National Park: Blakiston Brook, Belly River	< 1 elk/ km <sup>2</sup> in most areas, >5 elk/km <sup>2</sup> on lower winter range grassland (K. Van Tighem, Parks Canada, pers. comm.)

Table 2.2. Description of study areas for repeat photography study.

From 1996 to 2000, I took repeat images of photographs from the same location at a similar time of year as the original with a 35 mm camera and variable zoom lens. For some photographs, it was necessary to move the photopoint to avoid current obstructions, and to evaluate aspen condition at the edge of stands where saplings should be more abundant, and susceptible to herbivory. To facilitate analysis, each historical photograph was divided into 9 sectors  $(3 \times 3)$ . While in the field, I estimated historic and current aspen and conifer stand attributes along an ocularly-located transect of approximately 30 meters across the historic photograph sectors where aspen was most visible (maximum 3 per photograph). Attributes estimated were: time-since-fire (years); conifers (>2 m height) spacing and crown width (m); spacing (m), height (m), diameter at breast height (DBH, cm), and relative area of black bark (%) for aspen trees (>4 m in height) and saplings (2 to 4 m height); and spacing and browse class (1 to 4) for aspen suckers (1 to 2 m height). The spacing of suckers <1 m height was not estimated because these were often obscured by shrubs and herbaceous plants. Where no individual trees, saplings or suckers were observed in a transect, the spacing was recorded as 100 m. In the field, a magnifying glass was used to view historic prints, and binoculars to view the current scene. Where an attribute could not be estimated due to poor visibility in the current or historic scene, it was recorded as missing.

Ocular attribute estimates were calibrated with other, more quantitative data. Timesince-fire estimates, for instance, were available from fire history maps for the Jasper area (Tande 1979), Banff National Park (Rogeau and Gilbride 1994), North Saskatchewan valley (Rogeau 1999), Kananaskis valley (Johnson and Larsen 1991), Waterton Lakes National Park (Barrett 1996), the whole province of Alberta (Delisle and Hall 1987), and fire history from a concurrent study (Chapter 3). Accuracy in estimating aspen stand conditions was improved by reviewing photographs from other quantitative aspen stand research (Kay 1990, Kay et al. 1999), and photographs and field experience from over 400 plots in a concurrent study (see Chapters 4, 5 and 6).

Other data collected included general site location, UTM coordinates (from Global Positioning System or 1:50,000 maps), elevation, aspect, and general plant species cover estimates for the selected sectors. I made all current photographs with 35mm colour slide

film (Kodak Ektographic 200 ASA). Slide format provided maximum capability for subsequent viewing of images. Historic prints and current slides were digitally scanned for report preparation and stored on compact disks for archiving. All materials will be archived at the Whyte Museum of the Canadian Rockies in Banff, Alberta.

For statistical analysis (Table 2.1), historic and current attributes observed for each sampled photograph sector were entered in a database. As recommended by Underwood (1997), I obtained balanced sample sizes for most comparisons between areas (Predictions 4 and 5) through an unbiased selection of photo-sectors from each area that had complete historic and current observations for the attribute being tested. This selection was done by first ordering data by study area, archives, photograph archival number, and sector (Appendix A). Then, observations were systematically selected by database order until the appropriate sample size was obtained. For example, when 20 complete paired observations were available for a study area, and a sample size of 10 was required, every other observation was selected. This procedure minimized the number of sectors selected per photograph. Since time-since-fire, and historic and current aspen sapling spacing distributions were not normally distributed, they were log<sub>10</sub> transformed, with the geometric mean and standard error used as the measure of central tendency and variance. All statistical analyses were performed with SYSTAT (Release 7.0).

Long-term herbivory conditions were evaluated by searching photographs for large diameter aspen stems whose origins pre-dated 1870. To analyse fire frequency predictions, I combined five study areas to create a "south region" (Waterton and Oldman) and a "north region" (Eastslopes-South, Bow-Banff and Bow-Kananaskis). This combination of areas provided a minimum of 14 historic photographs per region for each of 3 periods (1874 to 1894, 1895 to 1914, and 1915 to 1934). Because of limited data, unequal sample sizes (Table 1) were used to evaluate the effects of two factors (2 regions  $\times$  3 periods of historic photographs) on the variable time-since-fire (years). I used a subset of data, from the earliest photographs (taken from 1874 to 1885) to evaluate tests from Prediction 3 (Table 2.1) on the combined effects of low herbivory and fire on aspen.

#### Results

In all, several thousand historic photographs were reviewed in the various archival collections. I obtained 270 images that clearly depicted aspen stand structure and for which it was thought the original camera station could be relocated. In the field, though, only 156 photographs could be re-photographed, with "then and now" aspen stand data collected on 195 sectors (Table 2.3, Appendix A). The majority of the photographs and sectors dated to the period 1910 to 1929. George Mercer Dawson took the earliest clear photographs of aspen stands in the collection during the 1874 International Boundary Survey near Waterton Lakes. Dawson's photographs from the Canadian Geological Survey expeditions of 1883 and 1884 (Dawson 1886, Byrne 1968) are also the earliest in the collection for the Oldman, Bow, and Red Deer watersheds. The Canadian Pacific Railroad commissioned several professional photographers to visit the Bow Valley during the 1880s after completion of the Canadian Pacific Railroad in 1885 (Hart 1983). Horetsky's 1874 photographs of Jasper National Park's Athabasca Valley do not clearly show aspen stands. Jasper was not photographed extensively until the 1904 Moore-Hussey expedition and construction of the Grand Trunk Railroad in 1911 (Hart 1979). After 1910, photographs of aspen stands become more available for Jasper and other eastslope areas through the work of the Dominion Surveys Branch (Bridgland 1924, Rhemtulla 1999) and Forestry Branch (Murphy 1985), and other individual sources.

Historically, aspen trees (>4 m) showed no evidence of bark-scarring due to elk herbivory. The estimated area of black bark on stems in historic photographs averaged <15% for all areas (Table 2.4; Figures 2.2*a*, 2.3*a*, 2.4*a*, 2.5*a*). Position and shapes of the few scars visible in photographs (eg., Figure 2.2*a*) indicated that they originated from pruned branches or fires, not elk browsing. Only 14 images contained trees that likely predated 1860 based upon stem diameter at the time of the photograph (Figure 2.2*a*). Mean barking on these stems was only 12% (SEM 11). The single sample *t* test rejected the null hypothesis that these observations could have come from a population where the mean stem barking was at least 35% (P < 0.05). Current black bark cover remained low (mean <15%) on trees in all areas except in Banff and Jasper where it averaged >50% in current views (Table 2.4, Figure 2.2*b*).

Decade			Area Code					Total
	AJ	BB	EN	BK	ES	OM	WL	
1870-79							11 (11)	11 (11)
1880-89		5 (5)		5 (9)		2 (3)	1 (2)	13 (19)
1890-99		1 (2)						1 (2)
1900-09	1 (1)	11 (12)	4 (4)	2 (3)		6 (8)	1 (2)	25 (30)
1910-19	14	5 (5)	13 (14)	4 (4)	3 (4)	8 (11)	2 (2)	49 (55)
	(15)							
1920-29	4 (4)	8 (12)	4 (5)	11 (14)	9 (12)	4 (5)	5 (7)	45 (59)
1930-39		3 (3)		1 (3)	6 (11)			10 (17)
1940-49					1 (1)		1 (1)	2 (2)
Total	19 (20)	33 (39)	21 (23)	23 (33)	19 (28)	20 (27)	21 (25)	156 (195)

Table 2.3. Total number of historic images and sectors (in brackets) that clearly show aspen stands on the Eastern Slopes repeat-photographed from 1996 to 1999. Photographs are classed by sample area code (see Table 2.2) and decade of original photograph.

Table 2.4. Sample sizes per area, means and SEM (in brackets) for attributes estimated in aspen stands classed by study area and historic (H) and current (C) view

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						Study A	rea									
Attribute	u	A	U	ш	3B		N	BK		ES		NO		M		
		Н	с С	Н	U	Η	ပ	Η	ပ	Н	J	Н	َ د	H	C	
Stand age	15	26	109	31	120	27	81	32	62	28	85	27	84	24	117	
(years)		(C)	(2)	(4)	(5)	(3)	(8)	(J)	(8)	. (9)	6	(5)	(9)	(5)	· (1)	
Conifer (>2 m)	15	39	13	31	9	66	20	59	30	77	45	72	25	124	69	
Spacing (m)		(6)	(9)	(9)	(1)	(24)	(26)	(10)	(8)	(11)	(11)	(18)	(8)	(43)	(33)	
Conifer	15	3.6	3.6	2.6	3.5	1.0	3.0	1.8	2.8	1.5	3.0	4.8	4.2	2.2	4.8	
Width (m)		(.8)	(.3)	(.4)	(.3)	(.3)	(.5)	(.4)	(.3)	(.4)	(.4)	(.7)	(.5)	(.3)	(.3)	
Aspen (>4 m)	15	36	9	22	25	30	£	38	6	50	6	61	10	54	9	
Spacing (m)		(12)	(I)	(8)	(6)	(12)	(1)	(12)	(9)	(13)	(-)	(20)	(5)	(11)	(2)	
Aspen (>4 m)	15	7	12	5	11	7	6	9	6	5	8	5	8	S	7	
Height		(2)	(I)	(]	(1)	(1)	(1)	(1)	(1)	(1)	(1)	· (1)	(1)	(1)	(1)	
Aspen (>4 m)	15	10	18	6	18	11	16	11	17	11	14	6	14	6	12	
DBH (cm)		(2)	(2)	(])	(2)	(1)	(2)	(1)	(2)	(2)	(2)	(1)	(1)	(1)	(1)	
Stem (>4m)	10	15	50	5	68	12	12	4	12	2	4	7	9	, m	m	
Barking (%)		6	(8)	(4)	(9)	(8)	(4).	(2)	(4)	(2)	(2)	(1)	(3)	(2)	(1)	
Aspen (2 to 4 m)	15	18	78	÷	72	2	8	11	7	9	4	8	9	ę	ε	
Spacing (m)		(6)	(10)	(])	(6)	( <u>-</u> )	6	6	(1)	(4)	(2)	(1)	(3)	(1)	(1)	
Stem (2 to 4 m)	10	1	74	4	11	1	4	0	9	0	0	-	6	7	1	
Barking (%)		( <u>-</u> )	(8)	(4)	(11)	(1)	(3)	(0)	(4)	(0)	(0)	(1)	(5)	(2)	(1)	
Aspen (1 to 2 m)	15	3.9	61.7	9.	77.3	1.2	1.6	2.3	1.8	1.2	1.6	7.5	11.8	<u>.</u> 80	1.7	
Spacing (m)		(3.3)	(10.3)	([.])	(9.1)	(:2)	(9)	(1.6)	(9)	(9)	(9)	. (9.9)	(7.1)	(.1)	(4)	
Stem $(1 \text{ to } 2 \text{ m})$	15	1	4	1	4	1	7		2	1	1	-	-	-	1	
Browse Class		•	•	•		۱	•	1	·	•	•			,	,	

Figure 2.2. Jasper townsite (foreground) looking east towards Signal Mountain in c. 1915 and 1999. UTM Coordinates: 0426325-5858625. (*a*) Shows an open overstory of large diameter aspen trees with an understory of dense sapling and tall sucker regeneration. The large trees likely originated prior to 1860, and show partial, uneven bark-scarring indicative of understory burning or other non-elk herbivory causes. Dense regeneration likely resulted from fires across this area in 1889 and 1905 (Tande 1979). Foreground clearing was done during construction activities of two railroads being built through the valley at this time. Photograph by D. F. Webb, courtesy of Glenbow Museum (NA915-41). (*b*) The same general area ( $\pm$  200 m) approximately 85 years later is now an urban park inside Jasper townsite. Aspen trees are all relatively even-aged, with a consistent height of bark-scarring ( $\cong$  2 m height) indicative of past stripping by elk. All suckers in the foreground of the photograph were recently browsed down to a height of less than 0.5 m, and several elk pellets groups were found in the stand. Photograph by Cliff White (99-07c-34)


Figure 2.3. From aspen stands near NW shore of Middle Waterton Lake looking northward towards Mt. Crandell (left background) and Bellevue Hill (right background) in 1874 and 1998. UTM Coordinates: 0288874-5438586. (a) Shows dense aspen sucker and sapling regeneration (< 4 m high) with a few larger trees interspersed through the stand. There is no evidence of large herbivore twig browsing, stem breakage, or bark-stripping. Fires appear to have recently swept across almost all low elevation areas, maintaining low conifer cover (background), and young aspen age classes (foreground). Photograph by George Mercer Dawson, courtesy of the National Archives of Canada (C-7377). (b) The repeat photopoint, 125 years later, was moved approximately 100 m eastwards due to mature, tall aspen blocking landscape view at original location. Dense young aspen regeneration continues to occur along the edge of the stand with spacing of 2 m for saplings, and 1 m for suckers. No stem browsing or bark stripping was visible although over 300 elk utilize a large grassland area immediately east of the area. However, few elk pellets groups were found in or near the aspen stands. Due to decreasing fire occurrence, spacing of conifer forest cover has increased remarkably on background mountain slopes. Photograph by Cliff White (99-08c-27).



Figure 2.4. Hillsdale Meadows in Banff National Park looking north towards Mt. Ishbel in 1902 and 1999. UTM Coordinates: 0584825-5675683. (a) Dense, multi-aged aspen surround the meadow with aspen saplings and willows along intermittent stream in the centre of the photograph. There is no evidence of large herbivore twig browsing, stem breakage, or bark-stripping. Prior to 1902, the most recent fires in the meadow area and mid-ground slopes had occurred in at least the years 1885, 1877, and c. 1853 (see Chapter 3), and appear to have maintained open conifer spacing interspersed by grasslands and dense aspen stands. Photograph by Y.G. Shoup, courtesy of the Glenbow Museum (NA-4654-11). (b) The repeat photopoint, taken 97 years later, was moved approximately 10 m westward due to large white spruce blocking the view at the original location. No aspen stems 1 to 10 m high occur in the area, and all suckers were browsed by elk to height <.5 m. Mature aspen (left and centre midground) all have extensive bark-scarring to 2 m high which resulted from extensive elk bark stripping that began in approximately 1940 (Cowan 1947). Portions of the view were burned by wildfires in 1905, 1931, 1945 (see Chapter 3), and most recently by prescribed burns in 1993 and 1998. However, these fires appear to have been patchy, and large white spruce and mature aspen and balsam poplar (Populus balsamifera) continued to occupy the centre-view stream course. Much denser conifer cover occurred in mid-ground and background areas. Photograph by Cliff White (99-09c-26).



Figure 2.5. Site of old Red Deer Ranger Station looking southeast towards upper Panther and Red Deer river valleys in c. 1915 and 1999. UTM Coordinates: 0623279-5724372. (*a*) Shows closely-spaced, young aspen saplings in draws in right midground with a few trees >4 m high. Periodic fires appear to have maintained these young aspen stands, and removed conifers and tall willow along the Red Deer River (left midground and background). Photograph by Dominion Forest Service courtesy of Glenbow Museum (NA-1943-30). (*b*) From about 20 m east of the original location (due to aspen regeneration obscuring view) approximately 85 years later. The ranger station had been moved 2 km upvalley, and road construction had altered much of the terrain and valley-bottom vegetation. Aspen stands continued to be unbrowsed, multi-aged and dense, although some cattle herbivory impact occurred near the road on willows. No elk pellet groups were observed in this area. Conifers (mostly white spruce on valley bottom, and lodgepole pine on background slopes) appeared much more dense in the recent photograph. No large fires had occurred in the previous 70 years in the Red Deer valley (Delisle and Hall 1987). Photograph by Cliff White (99-09a-9)



Aspen stands in historic photographs had, in almost all cases, been recently burned, as evidenced with young forest regeneration combined with burned but still standing, saplings and trees (Figure 2.3*a*, 2.4*a*, 2.5*a*). The historic estimated mean time-since-fire ranged from 24 years in Waterton Lakes to 32 years in Bow-Kananaskis (Table 2.4). By 1996, all stands had long fire-free periods, with the means ranging from 79 to 120 years. The mean time-since-fire for the northern (Bow-Banff and Bow-Kananaskis) and southern (Oldman and Waterton) areas was about 15 years in photographs taken during the period 1874 to 1894 (Figure 2.6). This lengthened to about 25 years in the 1895 to 1914 views, and to about 35 to 40 years in the 1915 to 1934 photographs. Two-way factorial analysis showed a significant main effect of photograph period on time-since-fire when  $log_{10}$  transformed ( $F_{2,131} = 13.1$ , P < 0.001), but no significant difference between areas ( $F_{1,131} = 0.041$ ), or interaction between area and period of photograph ( $F_{2,131} = 0.676$ ).

The frequent fires likely limited the abundance of conifers >2 m in height. Conifers were widely spaced in historic views for most watersheds, but were taller and more closely spaced in current views (Table 2.4). The Banff and Jasper areas, historically and currently, had closer conifer spacing in and near aspen stands. In some areas, the estimated mean crown width of conifers declined over time. Widely-spaced, open conifers with broad crowns were replaced by dense stands of younger trees with narrow crown widths.

The earliest historical images (Figure 2.3*a*) indicate that most aspen stands in the 1874 to 1885 period were dominated by a young age class of very densely spaced stems (Table 2.5). Single sample *t* tests on the  $\log_{10}$  of stem spacing confirm predictions (Table 2.1) of spacing means <2 m for tall suckers, and <4 m for saplings (*P* < 0.005). Stems also had no evidence of ungulate barking or browsing. Larger-sized aspen were widely spaced, and where they occurred, were of low height and narrow DBH, indicative of young ages.



Figure 2.6. Means  $\pm$  SEM for time-since-fire (years) as estimated from vegetation conditions visible in historic pictures taken during 3 periods for 2 regions. North region is the combined BB, BK, and ES study areas. South region is the combined OM and WL study areas. See Table 2.1 for sample sizes.

Attribute	Sample Size	Mean ± SEM
Aspen (> 4 m) spacing (m)	25	77±27
Aspen (>4 m) height (m)	18	5±1
Aspen (> 4 m) DBH (cm)	13	9±1
Aspen (2 to 4 m) spacing (m)	25	2±1
Aspen (2 to 4 m) barking (%)	10	3±2
Aspen (1 to 2 m) spacing (m)	16	$0.7 \pm 0.1$
Aspen (1 to 2 m) browse class (4 levels)	17	1

Table 2.5 Sample sizes and means  $\pm$  SEM for selected attributes of aspen stands for historic pictures taken from 1874 to 1885. Sample sizes are uneven because some attributes were not visible in historical photographs.

Aspen saplings and tall suckers were also relatively closely spaced in the complete set of historic images (e.g., Figures 2.2a, 2.4a and 2.5a) with arithmetic mean spacing <18m(Table 2.3), and the geometric mean spacing of less than 3 m (Figure 2.7) for all study areas. Single sample t tests for all areas rejected the null hypothesis that the  $\log_{10}$  transformed mean sapling or tall sucker spacing in any area was historically >10 m (P < 0.05). In the current views, saplings or tall suckers were rarely seen in the Banff or Jasper national park study areas (e.g., Figures 2.2b, 2.4b) and had mean spacing of >50 m (Table 2.4, Figure 2.7). Saplings remained abundant in other study areas (e.g., Figure 2.3b, 2.5b). There was a significant difference between historic and current sapling and tall sucker spacing in Banff and Jasper (Table 2.6), but no significant difference between current and historic stem spacing in the other 5 study areas (P < 0.005). Historically, aspen saplings showed little evidence of stem barking in all study areas. Currently stems in the Banff and Jasper areas have high black bark cover, but stems in other areas have low black bark cover (Table 2.4). Suckers were lightly browsed (browsing class 1) historically in all study areas. Currently, suckers are currently heavily browsed (browsing class 4) only in the Banff and Jasper study areas (Table 2.4).

# Discussion

## Reliability of observations

Several sources of bias must be recognized in the analysis of information from repeat photography studies (Rogers et al. 1984).

Photograph location bias. Historic photographs selected for repetition may have been taken in locations that are not representative of historic or current landscape conditions (Rogers et al. 1984, Noss 1985). In general, though, this seems unlikely because no photographs that showed details of aspen stands were omitted, and because numerous photographs exist. Further, montane ecoregion aspen occurs most commonly where historical photographs were taken– near valley bottom grasslands (Achuff and Corns 1982) which were favoured sites for trails, roads, camping, hunting, or horse-grazing (Byrne 1968).



Figure 2.7. Geometric means ± SEM for (*a*) spacing (m) of sapling (2 to 4 m), and (*b*) tall suckers (1 to 2 m) height classes in historic and current photographs of study areas. The Athabasca-Jasper (AJ) and Bow-Banff (BB) areas currently have high elk densities, and the remainder of the areas currently have low or moderate elk densities (see Table 2.2 for study area codes and elk density estimations).

Table 2.6. Mean differences ± SEM between current and historic spacing (m) of aspen saplings (2 to 4 m height) and suckers (1 to 2 m height) by study areas. Sample size is 15 for each study area.

Study Area	Saplings	Suckers
Athabasca-Jasper (AJ)	$70^{a} \pm 11$	$57.8^{a} \pm 11.0$
Bow-Banff (BB)	$69^{a} \pm 10$	$76.7^{a} \pm 9.1$
Eastslopes North (EN)	$6^{b} \pm 6$	$7.8^{b} \pm 6.4$
Bow-Kananaskis (BK)	$-9^{b} \pm 7$	$-0.5^{b} \pm 1.8$
Eastslope South (ES)	$-2^{b} \pm 4$	$0.4^{b} \pm 0.9$
Oldman (OM)	$-3^{b} \pm 7$	$4.4^{b} \pm 10.2$
Waterton Lakes (WL)	$0^{b} \pm 1$	$0.9^{b} \pm 0.4$
Oldman (OM) Waterton Lakes (WL)	$-3^{b} \pm 7$ $0^{b} \pm 1$	$4.4^{b} \pm 10.2$ $0.9^{b} \pm 0.4$

<sup>ab</sup> Different supercripts in a column denote significant differences between areas (P < 0.05).

It could be argued that observations from many early photographs are biased because they occur in locations disturbed by early European burning and hunting. However, it appears that the amount of burning may have actually decreased from the period of earliest pictures (1874 to 1894), which predate most early settler use, to later historic periods with more human use (Figure 2.6). Further, the low amount of bark-scarring on the oldest aspen indicates that these areas had low elk densities prior to any significant European use.

However, early land uses, in contrast to modern land uses, could accentuate results through an interesting mechanism. First, I recognize that areas occupied by aspen were often historically heavily used by humans (native peoples and early settlers), and were likely frequently burned, hunted, and possibly even logged. All these activities could favour regeneration of dense, lightly-browsed aspen. Second, as is apparent in more recent photographs, many of these areas have subsequently become the locations for modern roads, ranches, campgrounds, and towns. Third, aspen condition appears to be highly altered by herbivory, as determined by general elk density and use patterns (Figure 2.7). Finally, elk use patterns are, in turn, likely influenced by human use level and type, as well as predator travel routes. For example, elk avoid roads used by hunters (Lyon 1979). This may have occurred historically next to some trails and roads, and currently occurs in areas outside parks. In contrast, inside modern parks where hunting is prohibited, elk are now attracted to heavy human use areas avoided by more wary predators such as wolves (Dekker et al. 1995, Paquet et al. 1996, White et al. 1998a). This combination of factors that may have created differences in current and historic predator and elk behavior patterns will increase aspen herbivory contrasts reported in this study between historic and current conditions within park areas, and for current conditions between parks and hunted areas.

Quantified estimates of attributes. Quantification of landscape changes from oblique photographs is complex due to varying scales throughout the photographs (Chandler and Cooper 1989). Few studies have attempted to quantify attributes of vegetation in historical photographs. For example, Sinclair (1995) compared numbers of trees in current and historic views to generate instantaneous rates of tree decline on the Serengeti. Rhemtulla

(1999) recently quantified general vegetation cover changes in the Athabasca valley of Jasper National Park by rephotographing the collection of 1914 mountain top images taken by Bridgland (1924). However, it was impossible for Rhemtulla (1999) to compare historic and current aspen stand conditions due to the small scale of the photographs.

In this study, I obtained numerous close-up photographs where aspen stand conditions were visible, and where the original photopoint could be relocated. In the historical photographs, it was possible to recognize three general size classes of stems (trees, saplings, suckers) using plant form, or other features for scale such as people or horses. Similarly, spacing between stems could be quantified, though some bias still exists. Most importantly, in close-up, oblique views of aspen over time, such as those used here, recent tree growth on the edge of stands can obscure areas deeper within stands, which today may have fewer mature aspen stems or more conifers than in original photographs. There is trade-off, though, against more distant, or vertical views where conifer cover increases can be quantified, but where aspen condition cannot be discerned (Rhemtulla 1999). Therefore, many of the observations quantified here should be regarded as relative numbers best used in evaluating general changes over space and time. Effects of conifer encroachment at a landscape level are especially not well-quantified. However, for sapling and sucker spacing at the edge of stands, area of black bark, and browse condition, the differences between areas and time periods are dramatic (Table 2.4, Figure 2.7), and can be compared in relative magnitude to other studies.

### Elk populations before 1870

Although few historic photographs show aspen of large enough diameter to have regenerated before the 1870s (Figure 2.2*a*), they all show aspen with no obvious elk-induced bark-scarring, which strongly indicates that elk density was relatively low (e.g., <2 elk/km<sup>2</sup>) during this period (Prediction 1). The low level of historic bark-scarring corroborates other sources of evidence which support the low elk density hypothesis for this period (Kay and White 1995). Of over 60,000 ungulate bones unearthed at >400 archaeological sites in the Canadian and United States Rocky Mountains, most were identified as bison (*Bison bison*), bighorn sheep (*Ovis canadensis*) or deer, and <3% were

elk (Kay 1994, Kay et al. 1999). Detailed analysis of first-person European explorer accounts for the period 1792 and 1872 (Kay et al. 1999) found that 26 expeditions spent 369 days travelling through the Canadian Rockies, yet reported seeing elk on only 12 occasions, or once every 31 party-days. From 1835 to 1876, 20 different expeditions traversed the Yellowstone National Park area in Montana, Idaho, and Wyoming, but reported seeing elk only once every 18 party days (Kay 1990).

In contrast to these findings, Houston (1982), and Schullery and Whittlesey (1995) provided information that elk may have been abundant in Yellowstone National Park prior to the 1870s. Keigley and Wagner (1998) have recently reanalysed those data and concluded that elk were not as abundant as proposed. Thus, the question remains unresolved. For Banff National Park's Bow River valley, Woods et al. (1996) theorized that long-term high human numbers and low elk numbers could be auto-correlated. Some independent factor caused higher elk numbers during periods when human numbers were lower, and therefore evidence of elk is underrepresented in archaeological sites or explorer journals. Possible auto-correlation mechanisms, however, have not been identified, and there is no data to support Wood et al.'s (1996) hypothesis.

## Decreasing fire frequency

Evidence of frequent, recent fires in historical photographs (Figures 2.2*a*, 2.3*a*, 2.4*a*, 2.5*a*) corroborates dendrochronological findings of short fire return intervals (< 40 years) in the Rocky Mountain montane ecoregion prior c.1930 (Houston 1973; Tande 1979; Arno 1980; White 1985a,b; see Chapter 3). Current photographs clearly illustrate the success of recent government fire exclusion policies (Murphy 1985, White 1985a), which have lengthened the estimated time-since-fire in all Alberta eastslope areas by at least 50 years since the historical photographs were taken (Table 2.4).

Government-organized fire fighting (Murphy 1985), or climate change (Masters 1990) are two possible hypotheses for reduced fire activity prior to c. 1930. However, these effects are not proposed to have occurred until after 1900 contrary to the data provided here. Alternatively, the cultural burning hypothesis (Prediction 2) is that fire activity would have declined prior to 1900 due to changing human-use patterns (Kay et al. 1999). Numerous

sources (e.g., Lewis 1980, 1982; Barrett and Arno 1982, White 1985a, Kay 1990, Kay et al. 1999) conclude that native peoples burned Rocky Mountain valley and foothill areas. First Nations commonly burned meadows and prairies when grasses were dormant (late fall, winter, and spring) for various reasons, including enhancing plants used by people, horses and wildlife; herding wildlife during hunts; and maintaining travel routes (Lewis 1980, Barrett 1980, Kay et al. 1999). Leafed-out aspen stands are relatively fire-proof in mid-summer (Fechner and Barrows 1976, DeByle et al. 1987, Quintilio et al. 1991) when lightning fires most commonly occur in the Canadian Rockies (Nash and Johnson 1996, Kay et al. 1999). However, in Alberta, aspen stands burn readily before spring "green-up", or in autumn after leaf-fall (Anderson and Bailey 1980, Quintilio et al. 1991), when fires would have usually been of cultural origin. Thus, if native burning was historically important, then the age and condition of aspen in early historical photographs should be sensitive to federal government efforts to prevent human-caused fires that began as early as the 1880s (Murphy 1985). The increase in time-since-fire (years) estimated for photographs over consecutive 20-year periods after 1874 (Figure 2.6) support this assertion.

Some researchers have proposed that cultural burning was unimportant in the Canadian Rockies (Johnson and Larsen 1991). They posit that forest cover conditions have not changed over time (Johnson and Fryer 1987) because government agencies lack the capability to suppress high intensity fires started during mid-summer by lightning (Masters 1990, Johnson et al. 1995). This premise is debatable for conifer forests (Kay et al. 1999), but is unlikely for montane ecoregion aspen. Here, federal government programs to resettle native people on reserve lands, and to prevent human-caused fires through legislation and enforcement by the Northwest Mounted Police (Murphy 1985) likely had an early (e.g., before 1890), and significant effect in reducing the area burned. Reduced cultural burning during dormant seasons is therefore a more robust explanation for the observed decline in fire occurrence over time in these forests than is climate change or other factors.

#### Aspen condition in historic photographs (1874 to 1940)

The available evidence supports the hypothesis that herbivory levels were low, and fire frequency high prior to 1880. Under these conditions, the "top-down" hypothesis

predicts a consistent response from aspen (Prediction 3). Due to low browsing and frequent fire, almost all stands should be composed of closely spaced young stems, with few older stems. Few stands should have low vigor (e.g., older trees with little regeneration) due to other factors. Data from photographs taken before 1885 (Table 2.5) support this idea, most showing very dense, young aspen stands which regenerated after recent fires. Moreover, there is no evidence in the early pictures of bark-stripping or twig-browsing by ungulates.

Although early elk numbers are still being debated for the Canadian Rockies (e.g., Woods et al. 1996), there is no question that elk populations were very low throughout Alberta's east-slopes for nearly 40 years after 1880. Elk numbers did not increase in Banff and Jasper national parks until after the 1917 and 1920 relocations from Yellowstone (Holroyd and Van Tighem 1983), and not outside parks until much later (Millar 1915, Stelfox 1964, Morgantini and Hudson 1988, Woods et al. 1996). As predicted by the "top-down" hypothesis (Prediction 4), aspen responded consistently to light browsing in historic views, with moderately, closely-spaced saplings and suckers with few larger stems in all areas (Table 2.4, Figure 2.7). There was little evidence to support the alternative "bottom-up" predictions where decreasing fire occurrence (see above) or potential climate change (Loope and Gruell 1973, Houston 1982, Romme et al. 1995) should result in low aspen vigor in some areas, regardless of herbivory levels. These consistent responses of aspen to low ungulate densities are corroborated by exclosure studies throughout Rocky Mountain national parks (White et al. 1998a), and to aspen conditions outside of parks where elk densities are lower (Kay 1990).

I also compared historical Canadian photographs of Rocky Mountain aspen to those from the Bridger Teton National Forest (Gruell 1980) and Yellowstone National Park (Houston 1982, Kay 1990, Meagher and Houston 1998), and the northern Rockies in Montana (Gruell 1983). Similar to Canadian aspen stands, early US photos show abundant aspen saplings and suckers, but the spacing appears wider in some US views, especially those after about 1910 when elk populations were increasing in Yellowstone and Jackson Hole, Wyoming. However, the older (before 1890) US views show dense thickets of aspen suckers and saplings similar to those in Canadian photographs through the 1920s. This suggests that ungulate, and perhaps cattle populations outside of parks, began influencing Rocky Mountain aspen conditions earlier in the US than in Canada.

# Decline of aspen in high-density elk areas

Elk became abundant in the montane ecoregions of Banff and Jasper national parks by 1940 (Cowan 1947, White et al. 1998b). The "top-down" hypothesis predicts that aspen vigor should decline in these areas, but remain high in other areas of lower elk abundance (Prediction 5). Alternative variants of the "bottom-up" hypothesis (climate change and fire suppression) predict a general decline of aspen throughout the eastslopes. Comparisons of recent photographs (Figures 2.2b, 2.4b), however, provide convincing evidence that high levels of herbivory alone dramatically changed aspen stand conditions in Banff and Jasper areas (Figure 2.7) which have the highest ungulate densities of the 7 study areas (Table 2.1). Aspen stems in Banff and Jasper were heavily barked and browsed by ungulates in comparison to other areas (Table 2.4)

In the remaining study areas, aspen regeneration visible in recent photographs is similar to historical pictures (Figures 2.3*b*, 2.5*b*, 2.7). Researchers confirm this through reports of continual aspen, willow, and shrub birch (*Betula glandulosa*) encroachment on meadows throughout Alberta's foothills and parklands (Johnson and Smoliak 1968, Bailey and Wroe 1974). In contrast to experiments in Wyoming to stimulate aspen regeneration with single fire events (Bartos and Mueggler 1981, Bartos et al. 1994), researchers in Alberta recommend frequent burning to reduce aspen cover (Anderson and Bailey 1980; Bork et al. 1997).

### Integrating herbivory and fire effects

The study supported predictions from the "top-down" hypothesis that recent changes in long-term elk herbivory patterns created a major difference in aspen stand-age distributions between high and low elk-density areas. Data from a concurrent study (Chapter 4) was used to contrast Banff National Park's stand-age distributions (Bow-Banff) to the Eastslopes-South study area (Figure 2.8). In Banff, few stems have reached tree size (>4 m) in the last 40 to 50 years, creating a bell-shaped stand age distribution. In the Eastslopes-South area, however, recruitment into the tree layer has been continual, creating a reverse "J-shaped" stand-age distribution characteristic of multi-aged forests. In both areas, stem ages >120 years are uncommon due to the historically frequent fires that maintained almost all aspen stands in young age classes (see above).

This stand-age pattern allows a reinterpretation of Romme et al.'s (1995) conclusions on aspen age-class structure in Yellowstone National Park. They proposed that the bell-shaped age-class distribution, centred on the period 1870 to 1890, occurred as a result of complex, interacting climatic, disturbance, and herbivory conditions. In contrast, I propose a more parsimonious explanation based upon the "top-down" hypothesis. The single pulse of aspen age classes that originated during this period was the result of three sequential factors that acted independently on aspen. First, frequent fires (Houston 1973) prevented stems from reaching tree size before 1870. Secondly, ongoing low herbivory and decreasing occurrence of fire permitted densely spaced aspen regeneration during the period 1870 to 1890 to reach tree height. And finally, rapid increases in elk density about 1890 (Houston 1982) resulted in intense browsing, and very few stems that reached tree height in Yellowstone after this time.

A similar pattern was found in the Bow-Banff area, but the bell-shaped distribution is broader, and centres on the period 1890 to 1930 (Figure 2.8). The approximately 20 to 30 year shift in years between the Banff and Yellowstone distributions can be attributed to a more gradual implementation of fire suppression policies in Banff (White 1985a), and later (c. 1940) high elk densities (Holroyd and Van Tighem 1983). Thus, I agree with other researchers (e.g., Baker et al. 1997, Kay et al. 1999, Ripple and Larsen 2000) who concluded that complex explanations of interacting climatic, ungulate density, and fire frequency conditions are unnecessary to explain the general pattern of aspen stand age distributions in Rocky Mountain national parks over time.



Figure 2.8. Age distributions (counts and proportion of total sample) for aspen trees (>4 m height) in the Bow-Banff (BB) and Eastslope-South (ES) study areas based on a diameterat-breast-height and tree age relationship (from data in Chapter 5). Although trees aged <20 years were highly abundant in the ES study area, they had not reached tree height, and were not included.

However, it is possible that interaction between herbivory and forest disturbance factors could partially explain aspen stand conditions at low and moderate elk density (e.g., annual mean densities of about 2 to 4 elk/km<sup>2</sup>). In the Waterton Lakes National Park (WL), for example, elk have not heavily browsed aspen saplings and suckers (Figure 2.3*b*, 2.7, Table 2.4). Here, a herd of >300 elk use approximately 30 km<sup>2</sup> of relatively snow-free grasslands for 3 to 6 months each winter (Van Tighem pers. comm) These elk are relatively wary of humans due to periodic hunting seasons on nearby lands. The most common predator in the area is the cougar (Van Tighem pers. comm.), which kills by ambushing prey, often near areas of dense cover (Kunkel 1997).

## Conclusion

The conditions in Waterton Lakes National Park suggest a hypothesis for long-term elk and aspen coexistence in the Rocky Mountains. Historically, frequent fires maintained large areas of open habitat surrounding thickets of recently burned, dense-stemmed aspen. Predation-sensitive elk, held at low densities by humans and other carnivores, preferentially foraged in these open habitats. Forage was abundant here, snow-depths were lowest, and predators most visible. Elk did not frequently forage in or near areas of thick cover, such as dense, young aspen stands. Tests of this hypothesis require further research on elk foraging and vigilance pattern under various elk density, cover, and predation conditions. I evaluate these patterns in Chapters 5 and 6.

### CHAPTER 3. FIRE HISTORY OF MONTANE MEADOWS

### Introduction

Dendrochronology, or the study of tree-rings, provides information for evaluating the frequency and timing of wildland fire (Stokes and Smiley 1968, Arno and Sneck 1977, Johnson and Gutsell 1994, Swetman et al. 1999). In the Canadian Rocky Mountains, numerous dendrochronology studies report that short fire cycles (<50 years) historically occurred in the montane ecoregion (Houston 1973, Tande 1979, Arno 1980, White 1985a). These fires appear to be an important long-term factor in the development and persistence of montane vegetation communities dominated by grasses, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and trembling aspen (*Populus tremuloides*) (e.g., Stringer 1972; Gruell 1979, 1980; Achuff and Corns 1982, Romme et al. 1995). However, most studies (e.g., Tande 1979, White 1985a, Kay et al. 1999) describe a major reduction in fire frequency by the year 1930. Fire occurrence may have also decreased in approximately 1700 AD (Johnson and Larsen 1991).

The causes of historic fires and recent reduction of burned area are controversial for the montane ecoregion on the eastern slopes of the Rockies (Walker 1995). One theory (lightning fire and climate change hypothesis) holds that mid-summer, lightning fires dominated the historical fire regime (Johnson and Larsen 1991, Johnson and Wowchuk 1993, Weir et al. 1995). This theory proposes that fires were usually large, with similar frequencies in the montane and the adjacent cooler and moister subalpine ecoregions. It concludes that high intensity fires cannot be controlled by fire control agencies, and that recent reductions in burned area are due to climate change (Johnson et al. 1995). An alternative model (cultural burning hypothesis) posits that human-caused fires were relatively frequent in low elevation areas, and periodically these fires spread into the lower subalpine (Lewis 1982, White 1985a, Kay et al. 1999, Heathcott 1999). Recent reductions in burned area are due to changes in human land use patterns.

Evidence for either of the above hypotheses remains inconclusive. The lightning fire and climate change hypothesis is difficult to support. The density of lightning strikes is relatively low on the eastslopes of the Rockies (Nash and Johnson 1996, Heathcott 1999), and the frequency of lightning started fires is much lower (< 20%) on the eastern slopes than

on the western slopes (Finklin 1986, Heathcott 1999). However, historical fire frequency was similar in both areas (Masters 1990, Weir et al. 1995, Kay et al. 1999). Climate is variable with no long-term cooling or increased precipitation trend (Luckman 1998). Fire control programs are effective due to fire prevention and rapid initial attack of small fires before they become unmanageably large (White 1985a, Murphy 1985, Kay et al. 1999). Conversely, although many western North American ecosystems have a well-documented history of human-ignited fire (e.g., Stewart 1956, Blackburn and Anderson 1993, Pyne 1995, Boyd 1999), the cultural burning hypothesis is supported by only a few anecdotal comments specific to the Canadian Rockies (Lewis 1982, Kay et al. 1999). After reviewing the evidence, Johnson and Larsen (1991) concluded for their study area in the Kananaskis valley that "Indian fires cannot be substantiated. It is hard to find well-documented evidence about why Indians would have caused fires as part of their lifestyles."

# Cultural burning of montane meadows and grasslands

Isolated grasslands and shrublands (see Figure 2.4, Chapter 2), often ringed with aspen and Douglas-fir stands, lie in a matrix of lodgepole pine, white spruce (*Picea glauca*), and Engelmann spruce (*Picea engelmannii*) in many valley bottoms in the Canadian Rockies (Achuff and Corns 1982). Previous evidence that humans fired these meadows comes from several anecdotal sources (Kay et al. 1999). An aboriginal informant explained why his people once burned bighorn sheep (*Ovis canadensis*) habitat in the Canadian Rockies (Lewis 1982:44).

See, mountain [bighorn] sheep aren't like domestic sheep. Mountain sheep prefer only the tips of green grass; they don't like to graze an area more than once. When the burning stopped there were fewer grassy areas than before, so the sheep came back again and again...Maybe one sick animal, like one with lungworm would pass its sickness on to all the others. When we used to burn there was always plenty of fresh grass and they didn't have to do that (graze the same areas twice). Apparently, spring may have been the favoured season for burning. For instance, in 1906, J.E. Stauffer, a forest ranger in southern Alberta noted that

I always understood that Indians would never set out fires in the forests, but this year I was convinced that they do; for hunting purposes, in season or out, in the Banff Park and out of it. They set out fires in the spring on their fishing or hunting trips in order to draw deer later for grazing (Department of the Interior 1907:29).

Lewis (1982:27) interviewed a Cree-Metis elder living near Grand Cache, Alberta on spring burning techniques. The elder reported that

We'd always wait until the late afternoon and the fire was set at the upper end (of the meadow). It would burn down to the low, damp places where the really wet grasses grow. That's the way we burned mountain meadows. See, you have to know the wind; you have to know how to use it.

Rylatt (1991:163-164) spent the winter of 1873 near Jasper House. Based on after the fact observations, he provided his viewpoint on how native people once hunted bison (*Bison bison*) in Jasper's Athabasca Valley.

The cunning savage year after year crept past the herds as they fed, and attained the upper end (of the valley), then fired the long grass during the heated term, driving a thundering living mass in terror to the only Outlet at the end of the Valley, where the main body of their enemy waited to destroy as many as opportunity offered.

The practice of burning meadows may have even extended into the early 20<sup>th</sup> century by the Dominion Forestry Branch rangers experienced with burning on forest reserves east of the mountains (Murphy 1985). Abraham Knechtel, a government inspector for the forest reserves, described this technique (Department of the Interior 1910):

Last year we began a practice which we know saved the reserves several fires. It is a well-known fact that, early in the spring, the fields become bare and the grass dry before the snow all gone from the woods. While such conditions existed the forest rangers burned the meadows along the reserve boundaries. Fires, coming in from the praires, met this wide fire line and died out for want of fuel.

# Predictions for tests with tree-ring data

The anecdotal information provided the background to postulate that valley bottom meadows in the Canadian Rocky Mountains were routinely fired in spring by native peoples and early settlers to improve wildlife habitat, hunting conditions and stock grazing. In this study, I tested the hypothesis with dendrochronological evidence gathered from lodgepole pine around meadows. Variable fire intensities caused by meadows and adjacent aspen stands (Fechner and Barrows 1976) result in lodgepole pine which is even-aged after intense fires, or multi-aged, with fire-scarred boles on older trees, after lower intensity fires (Tande 1979, White 1985b). With this dendrochronological evidence, I evaluated four specific predictions from the hypothesis.

<u>Prediction 1</u>. Historic fires should have occurred frequently in meadows and less frequently in surrounding forests. If native peoples and early settlers routinely fired meadows during periods when adjacent forests were too moist to burn (as per sources in Lewis 1982), meadow edges should have high fire frequencies (<10 year intervals) and nearby forests much lower fire frequencies (>50 year intervals). Alternatively, under the mid-summer lightning fire hypothesis, forested areas would burn only infrequently (e.g., >50 years, Johnson and Larsen 1991, Weir et al. 1995). Further, with mid-summer fires, fire frequency should be approximately the same in forests as the meadow edges.

<u>Prediction 2</u>. Historic fires should have occurred more frequently on downwind areas of meadows compared to upwind areas. Prevailing westerly and south-westerly winds during periods of weather conducive to burning meadows (White 1985a, Fryer and Johnson 1988) should carry fires started in meadows downwind in an eastward direction. This should result in higher fire frequencies on the downwind (east) edges of meadows compared to the upwind (west) edges.

<u>Prediction 3.</u> Fires should have burned more frequently on warm aspects around meadows than on cool aspects. Valley-bottom meadows are usually bordered on their north and east sides by south-facing slopes that become snow-free early in spring. If humans burned meadows in spring, south facing slopes near meadows should have higher fire frequencies than cool and moist aspects on the opposite sides of meadows. If mid-summer lightning fires predominate in the fire regime, there should be no difference in fire frequency between aspects (Johnson and Larsen 1991, Johnson and Wowchuk 1993).

<u>Prediction 4.</u> If humans burned meadows in spring, fire-scars from trees on the edges of meadows should be located mostly in the dormant (fall or early spring), or early wood (spring and early summer) sections of annual growth rings in trees near meadows. Under the lightning fire hypothesis, most fire scars should occur later in annual growth ring (latewood) when lightning-caused fires are most common (Nash and Johnson 1996), and weather conditions are most favourable for large fires (Johnson and Wowchuk 1993).

#### Methods

I followed Lertzman et al.'s (1998) guidance for fire history research. Data were collected from spatially independent replicate locations to test predictions from an *a priori* hypothesis generated independently of the data.

### Fire history evidence

The study followed a replicated block design. I selected 8 sample meadows in main valley bottoms along the Rocky Mountain eastslopes in Alberta (Table 3.1) based on several criteria. First, I dispersed the meadows along a broad area (Figure 3.1). Secondly, I selected meadows that had evidence of historical human use such as trails or campsites. This was not limiting because valley-bottom meadows in the Rocky Mountains appeared to have been favoured occupation sites for native peoples (Parks Canada 1989). Early European visitors or settlers also used many meadows (see Figure 2.4). Further, I selected meadows of >50 ha whenever possible. This was difficult because there are few large meadows in most valleys (Achuff and Corns 1982). Finally, during an initial survey, I looked for some tree-ring fire history evidence around meadows. This eliminated from study several meadows in the Bow Valley near Banff and Canmore, Alberta where historic logging and recent development appeared to have removed almost all fire-scarred trees.

At each meadow, disks were collected from 1 to 4 trees from each of 24-10 ha sample plots, 2 in each of 12 sectors (Figure 3.2). A meadow edge plot (<100m from perimeter of the meadow), and a forest plot (200 to 400 m into the adjacent forest) were sampled in each sector. Similar to other fire history studies in the Canadian Rockies (Tande 1979, Hawkes 1980, White 1985b, Johnson and Larsen 1991), fire-scars and pith dates for lodgepole pine were the primary sources of tree-ring evidence. Crews ring-counted collected disks in the field as sampling proceeded to obtain an approximate record of burn years. For each field-determined burn year, crews attempted to collect evidence of at least 2 fire-scars or pith years within the plot, or in an adjacent plot.

Meadow	Code	Description, UTM and elevation at centre of meadow
Clearwater River	CW	Confluence of Malloch Creek and Clearwater River in Banff National Park, lower subalpine ecoregion, 80 ha area, UTM: 565200-5742500, Elevation: 1810 m
Hillsdale	HD	18 km NW of Banff in Bow River valley, Banff National Park, montane ecoregion, 40 ha area, UTM: 584900-5675200, Elevation: 1240 m
Panther River	PR	Valley bottom of Panther River, 6 to 9 km west of Banff National Park boundary, montane transitional to lower subalpine ecoregion, 170 ha area, UTM: 592500-5715300, Elevation: 1840 m
Prairie de la Vache	PV	9 km SE of Jasper, Alberta in Athabasca River valley, Jasper National Park, montane ecoregion, 30 ha area, UTM: 432300-5849600, Elevation: 1100 m
Ribbon Creek	RC	1 to 3 km north of confluence of Ribbon Creek and Kananaskis River, montane transitional to lower subalpine ecoregion, 200 ha area ,UTM: 631500- 5642500, Elevation: 1450 m
Sibbald Flats	SF	Confluence of Sibbald Creek and Jumpingpound Creek, 40 km east of Calgary, montane ecoregion, 150 ha area, UTM: 650000-5656000, Elevation: 1460 m
Willow Creek	WC	1 to 3 km north of confluence of Willow Creek and Snake Indian River, Jasper National Park, montane transitional to lower subalpine ecoregion, 100 ha, UTM: 409000-581700, Elevation: 1380 m
Ya Ha Tinda	YH	Valley bottom of Red Deer River, 4 to 20 km east of Banff National Park boundary, subalpine and montane ecoregion, 2000 ha, UTM: 599000- 5734000, Elevation: 1680 m

Table 3.1. Description of meadows for fire history study.



Figure 3.1. Fire history study area meadows in the Alberta Rocky Mountains. Area codes are: Clearwater River (CW), Hillsdale (HD), Panther River (PR), Prairie de la Vache (PV), Ribbon Creek (RV), Sibbald Flats (SF), Willow Creek (WC), and Ya Ha Tinda (YT).



Figure 3.2. Standard plot layout around meadows of 24 plots at the edge of meadows and 200 to 400 m into the surrounding forests. Tree disks were obtained within a 200 m radius of the plot centre.

In the laboratory, disks were dried and sanded with progressively finer sandpaper (to 600 grit). For cross-dating, a master tree-ring chronology (Stokes and Smiley 1968) was made for each meadow with approximately 10 trees that did not contain scars. Ring counts and widths were measured on computer-scanned images of tree disks (WIN-DENDRO II, Guay et al. 1992). The program COFECHA (Grissino-Mayer et al. 1997) was used to cross-date the master chronology samples, identify any possible dating or measurement problems, and maintain accuracy in the assignment of calendar years. Distinct and consistent marker years identified in the master chronologies provided a basis for cross-dating the remaining disk samples. All cross-dated pith and scar information for each meadow were compiled on the same graph-sheet for cross-checking between plots (Arno and Sneck 1977).

Season of burn was estimated by using a binocular microscope to determine the position of the fire-scar within annual tree-growth rings (Ahlstrand 1980), classed as follows: D, dormant season; E, earlywood; or LW, latewood. When possible, earlywood scars were further broken down in EE, early earlywood, ME, mid-earlywood; and LE, late earlywood (Brown and Hull Seig 1996). These estimates were calibrated with fire-scars collected from a series of disks collected from Banff National Park where the fire date is known from either wildfire reports (White 1985a), or prescribed fire reports (Achuff et al. 1996). All disks were stored in the tree disk storage room in the basement of the Banff Warden Office.

### Statistical analysis

Analyses of fire frequency (Johnson and Van Wagner 1985, Johnson and Gutsell 1994, Fall 1999) usually focus on either time-since-fire maps or sample data (e.g., Van Wagner 1978, Johnson and Larsen 1991), or intervals between fire scars (e.g., Houston 1973, Tande 1979). In this study, variable fire intensities around meadows created heterogenous fire history evidence that was difficult to interpret with either of these fire frequency approaches alone (Lertzman et al. 1998, Arno et al. 2000). For forested plots on cool aspects, time-since-fire evidence was common, whereas on meadow edge and warm aspect plots, fire interval evidence predominated. Thus, I used the fire year data obtained from sample plots to analyse both measures of fire frequency. First, for almost all plots, the data existed to compile the discrete time-since-fire distribution (a(t)) as of 1950, the approximate year that fire suppression for Banff National Park (White 1985a) and Alberta's eastslopes (Murphy 1985) became highly effective. Secondly, for plots where trees had fire-scars, I calculated fire interval observations as the time between fires, or between piths and scars, and compiled the plot means as a fire interval distribution, f(t). Because of uneven-aged tree regeneration near meadows, observations of intervals calculated from the time between fire-scars and piths were likely underestimated for many cases.

The a(t) distribution scaled to 1 at time = 0, and the f(t) distributions are equivalent, respectively, to the survivorship  $(l_x)$  and age at death  $(d_x)$  distributions used in population life table analysis (Krebs 1994, Huggard and Arsenault 1999). For distributions sampled from the same area and a constant hazard of burning over time for the period of recorded fire years (e.g., no long term climate, ignition or fire suppression changes to fire frequency), the fire interval distribution is related to the time-since-fire distribution by:

$$A(t) = 1 - F(t)$$

where A(t) and F(t) are the cumulative forms of a(t) and f(t) (Johnson and Gutsell 1994). Under even more constraining conditions of constant hazard of burning over time and for all stand ages (e.g., uniform sample-point flammability with time-since-fire), f(t) equals the unscaled a(t) distribution (or  $n_x$  in life table terminology). Under this unique condition, both observation sets would have the same negative exponential distribution (Van Wagner 1978, Johnson and Gutsell 1994) and could be combined for analysis. However, in this study, preliminary analysis of the a(t) and f(t) observations indicated variations in hazard of burning over time and with stand age, so the a(t) and f(t) distributions were evaluated individually.

Time-since-fire and fire interval observations were grouped by sectors and distance from meadow (edge or forest) to test predictions of edge, wind, and aspect effect. For meadow edge effect, observations were classed as meadow edge or forest. For wind effect, sectors 3 to 9 were classed as upwind, and sectors 10 to 2 as downwind (Figure 3.2). For the aspect effect, plots on aspects from 136° to 315° were classed as warm, and aspects from 316° to 135° as cool. The log<sub>10</sub> transformation of time-since-fire and interval observations provided reasonable fits to a normal probability distribution, and were used in factorial analyses with the linear model:

$$X_{ijk} = u + W_i + E_j + A_k + WE_{ij} + EA_{ik} + WA_{ik} + WEA_{ijk} + e_{ijk}$$

where X is the overall variance in time-since-fire or interval data, W is the 2 levels of wind effect, E denotes the 2 levels of edge effect, and A is the 2 levels of aspect effect. A model including meadows as a fully orthogonal factor could not be tested because fire intervals were not observed for all sectors in some meadows.

Further, I graphically evaluated a(t) and f(t) distributions with histograms of observation counts with sectors grouped into 4 quadrants: 1) upwind-warm aspect, 2) downwind-warm aspect, 3) downwind cool aspect and 4) upwind cool aspect. The distribution of fire-scar positions in annual growth-rings was also evaluated graphically for meadow edge and forest plots.

### Results

From plot sampling, I obtained 375 disks providing 244 scar and 368 pith dates. Fire-scarred trees were uncommon around some meadows, and particularly uncommon on cool aspects on all meadows. Plot burn years (Figure 3.3) were most common after 1850 for study areas in main transportation corridors (e.g., Hillsdale and Prairie de la Vache). In more remote study areas such as Clearwater River or Willow Creek, burn years occurred primarily before 1850. Historic logging (<100 years) appeared to have removed many firescarred trees around the three meadows in the Bow Valley (Sibbald Flats, Ribbon Creek, and Hillsdale).

The overall time-since-fire as of 1950 (a(t)) distribution (Figure 3.4*a*) followed a consistent pattern of an exponentially declining distribution that was interrupted about 50 years prior to 1950 (i.e., 1900). From 1900 to 1950, the overall number of plots burned declined in most meadows, with almost no evidence of fire years after 1950 (Figure 3.3).

Time-since-fire, grouped by meadows (Table 3.2), reflected the pattern of historic burn years described above, with the remote Clearwater meadow having longest overall mean time-since-fire (135 years). Meadows in main transportation corridors (e.g., Ribbon Creek, Prairie de la Vache and Hillsdale) had short overall mean time-since-fire (<50 yrs). Overall time-since-fire data for meadows (Table 3.2, Table 3.4, Figure 3.4*a*), tested with factorial analysis (Table 3.5), indicated that that downwind ends of meadows had significantly shorter time-since-fire than upwind ends (66 years versus 88 years, P = 0.026). Warm aspects near meadows had marginally significant shorter time-since-fire than cool aspects (67 years versus 89 years, P = 0.158). Overall, plots on meadow edges had burned approximately 10 years more recently than those in forests (Table 3.2), but this was not significant (P = 0.259).

Because of few fire-scarred trees, fire interval observations (Table 3.3) were uncommon around some meadows, and particularly uncommon on cool aspects in forests. No quadrants, and no meadows had mean fire intervals indicative of frequent burning (i.e., <10 years). Relative magnitudes of overall interval means, grouped by edge, aspect, and wind factors, were similar to those of time-since-fire observations (compare Table 3.2 to Table 3.3, Table 3.4 to Table 3.5, Figure 3.5*a* to Figure 3.5*b*).

Fire interval data for meadows (Table 3.3, Table 3.5, Figure 3.4*b*), tested with factorial analysis (Table 3.7), showed that meadow edges had shorter fire intervals than adjacent forests (40 years versus 53 years, P = 0.059). Warm aspects had shorter fire intervals than cool aspects (40 years versus 57 years, P = 0.061). Unlike time-since-fire observations, fire intervals were not significantly shorter on downwind ends of meadows than on upwind ends (43 years versus 47 years, P = 0.959). However, the factorial analysis results should be interpreted cautiously due to unequal sample sizes (Underwood 1997).

Table 3.2. Means  $\pm$  SEM and sample size (in brackets) for time-since-fire as of 1950 (years) for plots grouped by study area, meadow quadrant, and plot position. E is edge of meadow, F is forest, up is upwind end of meadow, down is downwind end of meadow, warm is warm aspects (136° to 315°), and cool is cool aspects (316° to 135°).

								~			
Study Alea		Quadrant					,	Over all c	luadrants	Over	
											All
	T T		5								Area
	Up-warm	_	Down-w	arm	Up-cool Down-co			lol			
	м	F	M	F	М	F	М	F	М	F	
Clearwater	171	282	81±18	90±24	117±19	222±57	118	118	107±13	163±32	135±18
River (CW)	(1)	(1)	(5)	(5)	(5)	(5)	(1)	(1)	(12)	(12)	(24)
Hillsdale	52±9	65±0	65	41	14	14	39±13	34±10	42±7	48±7	45±5
(HD)	(5)	(5)	(1)	(1)	(1)	(1)	(5)	(5)	(12)	(12)	(24)
Panther River	108±33	161±117	65±21	94±55	195±75	165±69	91	278	111±25	145±39	129+23
(PR)	(3)	(3)	(5)	(5)	(3)	(4)	(1)	(1)	(12)	(13)	(25)
Prairie de la	43±0	52±8	24±7	27±6	43±8	58±9	57±13	78±34	39+5	50+8	44+5
Vache (PV)	(2)	(2)	(4)	(4)	(4)	(4)	(2)	(2)	(12)	(12)	(24)
Ribbon Creek	32±18	29±15	11±3	23±9	80±54	38±24	14±0	14±0	38+19	25+6	32+11
(RC)	(2)	(2)	(4)	(4)	(4)	(2)	(2)	(2)	(12)	(10)	(22)
Sibbald Flats	48±5	42±14	47±5	60±17	46±7	62±6	77±15	73±0	51±4	58±7	55+4
(SF)	(3)	(3)	(4)	(4)	(4)	(4)	(2)	(2)	(13)	(13)	(26)
Willow Creek	56±15	89±8	89±12	111±14	109±19	86±10	152±44	150+19	102+13	105+9	104+8
(WC)	(2)	(2)	(3)	(4)	(4)	(4)	(2)	(2)	(11)	(12)	(23)
Ya Ha Tinda	69±10	67±12	56±8	84±15	50±15	121±46	66±5	68+18	58+5	85+12	71+7
(YH)	(3)	(5)	(10)	(7)	(4)	(4)	(2)	(2)	(19)	(18)	(37)
Over all study	65±7	82±18	54±6	72±10	86+14	113+19	67+11	78+17	68+5	87+8	77+5
areas	(21)	(23)	(36)	(34)	(29)	(28)	(17)	(17)	(103)	(102)	(205)
	(~~)	(23)	(30)	()	(29)	(20)	(17)	<u>(17)</u>	(105)	(102)	(203)

Table 3.3. Means  $\pm$  SEM and sample size (in brackets) for fire intervals (years) for plots grouped by study area, meadow quadrant, and plot position. E is edge of meadow, F is forest, up is upwind end of meadow, down is downwind end of meadow, warm is warm aspects (136° to 315°), and cool is cool aspects (316° to 135°).

Study Area	Quadrant Over all quadrants								uadrants	Over All	
	Up-warm		Down-warm		Up-cool		Down-cool				Ліса
	M	F	Μ	F	M	F	М	F	М	F	
Clearwater	140	•	123±31	106±28	111±25	120±26	-	-	117±17	$110\pm 20$	114±13
River (CW)	(1)		(4)	(7)	(8)	(3)			(13)	(10)	(23)
Hillsdale (HD)	30±13	31±0	43±12	21±10	15±5	18±5	24±10	70±19	28±6	34±8	31±5
	(5)	(3)	(2)	(2)	(2)	(2)	(4)	(2)	(13)	(9)	(22)
Panther River	40±8	97 <del>±6</del> 9	42±8	25±5	39±20	83±18	56±12	-	44±5	61±15	49±6
(PR)	(6)	(2)	(12)	(5)	(5)	(5)	(7)		(30)	(12)	(42)
Prairie de la	23±2	16 <del>±6</del>	28±4	-	25±3	35±5	-	-	25±2	25±6	25±2
Vache (PV)	(9)	(2)	(6)		(4)	(2)			(19)	(4)	(23)
Ribbon Creek	25.±5	35±2	47±17	35±2	34±3	-	-	-	34±7	35±2	34+5
(RC)	(5)	(3)	(4)	(3)	(2)				(11)	(3)	(14)
Sibbald Flats	32 <del>±6</del>	40±1	19±3	35±17	27±4	-	-	-	26±3	37+9	29+4
(SF)	(5)	(2)	(4)	(3)	(3)				(12)	(5)	(17)
Willow Creek	30±5	88	53±18	38±8	-	32±9	61	-	40+7	40+8	40+5
(WC)	(6)	(1)	(3)	(3)		(4)	(1)		(10)	(9)	(19)
Ya Ha Tinda	30±5	52±17	25±3	42±7	75	-	-	-	28+3	43+7	33+3
(YH)	(2)	(3)	(28)	(15)	(1)				(31)	(18)	(49)
Over all study	32±4	49±12	38±4	49±7	57±12	63±12	46±9	57±17	40+3	53+5	44+3
areas	(39)	(13)	(63)	(38)	(25)	(16)	(12)	(3)	(139)	(70)	(209)
Table 3.4. Means $\pm$ SEM (years) and sample size (in brackets) for time-since-fire as of 1950											
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for plots from all meadows grouped by plot position. Warm is warm aspects (136° to 315°),											
and cool is cool aspects (316° to 135°).											

Aspect	W	Vind	Total
	Upwind	Downwind	-
Cool	99±12	73±10	89±8
	(57)	(34)	(91)
Warm	74 <u>±</u> 10	63±6	67±5
	(44)	(70)	(114)
Total	88±8	66±5	77±5
	(101)	(104)	(205)

Table 3.5. Means  $\pm$  SEM (years) and sample size (in brackets) for fire intervals for plots from all meadows grouped by plot position. Warm is warm aspects (136° to 315°), and cool is cool aspects (316° to 135°).

Aspect	V	Wind				
	Upwind	Downwind				
Cool	59±8	48±8	57±6			
	(41)	(15)	(56)			
Warm	37±4	42±4	40±3			
	(52)	(101)	(153)			
Total	47±5	43±3	44±3			
<del>n</del>	(93)	(116)	(209)			

Effect	Sum of Squares	df	Mean-Square	F-ratio	Р
Wind	3.713	1	3.713	5.041	0.026
Edge	1.482	1	1.482	2.012	0.259
Aspect	0.944	1	0.944	1.281	0.158
Wind $\times$ Edge	0.003	1	0.003	0.003	0.953
Wind × Aspect	0.057	1	0.057	0.077	0.782
$Edge \times Aspect$	0.022	1	0.022	0.030	0.864
Wind $\times$ Edge $\times$ Aspect	0.508	1	0.508	0.689	0.407
Error	145.098	197	0.737		

Table 3.6. Analysis of variance for effects and interactions of wind (upwind or downwind), edge (meadow or forest), and aspect (warm or cool) on  $\log_{10}$  of time-since-fire (years) as of 1950 for plots within treatments.

Table 3.7. Analysis of variance for effects and interactions of wind (upwind or downwind), edge (meadow or forest), and aspect (warm or cool) on  $\log_{10}$  of fire intervals for plots within treatments.

Effect	Sum of Squares	df	Mean-Square	F-ratio	Р
Wind	0.002	1	0.002	0.004	0.959
Edge	2.098	1	2.098	3.602	0.059
Aspect	2.074	1	2.074	3.561	0.061
Wind $\times$ Edge	0.000	1	0.000	0.001	0.979
Wind × Aspect	1.434	1	1.434	1.613	0.205
Edge × Aspect	0.006	1	0.006	0.011	0.918
Wind $\times$ Edge $\times$ Aspect	0.156	1	0.156	0.268	0.605
Error	117.089	201	0.583		



Figure 3.3. Frequency of burn year occurrence (counts and proportion of total sample) for plots for individual meadow study areas. Codes for study areas are: Clearwater River (CW), Hillsdale (HD), Panther River (PR), Prairie de la Vache (PV), Ribbon Creek (RV), Sibbald Flats (SF), Willow Creek (WC), and Ya Ha Tinda (YT).



Figure 3.4. Time since fire as of 1950 (a), and fire interval (b) distributions (counts and proportion of total sample) for all sample plots.



Figure 3.5. Geometric means  $\pm$  SEM (years) for time-since fire as of 1950 (*a*) and fire intervals (*b*) of meadow quadrants for meadow edges and forest plots. Quadrants are upwind (UP), downwind (DOWN), warm aspect (WARM), and cool aspect (COOL). See Tables 3.3 and 3.4 for sample sizes.

Fire-scar position in growth rings could be estimated for 191 fire scars. Due to more frequent scars, plots on meadow edges yielded more estimates than forest plots (Figure 3.6). However a similar pattern of frequent fires scars in the earlywood portion of rings was visible for both forest and meadow plots. Relatively few fire-scars occurred in the dormant section of growth rings.

#### Discussion

Results from this study should be interpreted recognizing two key limitations. First, fire history evidence was sporadic around many meadows with low numbers of fire intervals for some sectors, and unequal sample sizes in statistical tests. Secondly, the lack of fire evidence cannot be attributed with complete confidence to few fires. Possibly many historic fires were of low intensities, and did not scar trees. However, this research appeared to corroborate some regional and local patterns of fire history identified by previous research.

## Regional variation between meadows

Meadows in low elevation valleys with intensive human use (e.g., roads and railways) have more frequent fires, and this fire regime persisted until after the year 1900 (Figure 3.3). In contrast, meadows in more remote valleys at higher elevations have less frequent fires, and fire occurrence (number of burn years) began to decline by 1850. The early (<1900) decline in fire frequency in remote areas of Banff National Park was observed by White (1985a) on the basis of historical reports, and Rogeau (1996:41) from stand age mapping data. Similar regional patterns are evident in the Jasper National Park forest stand age distribution map (Parks Canada 1995).



Figure 3.6. Position of fire-scars in annual growth rings for plots grouped by meadow edge (Meadow) or forest locations. Positions are dormant season (D), early earlywood (EE), mid-early wood (ME), late early wood (LE), and latewood (LW).

White (1985a) concluded that the continued high frequency of fire in more developed areas for the period 1900 to 1930 was attributable to human ignitions (e.g., railway, land clearing etc.). On this basis, the early decline of burning in more remote areas could have resulted from the collapse of pre-settlement human use patterns (Kay et al. 1999). Alternative explanations include climate change (Johnson and Larsen 1991) or efficient fire suppression (Tande 1979, White 1985a), but it seems unlikely that these effects would occur only in remote areas.

Further, meadows at lower elevations (Table 3.1) generally had shorter historical fire intervals (Table 3.4). The general pattern of higher fire frequencies at lower elevations in the Rocky Mountains has been observed in numerous studies (reviewed by Arno 1980, Kay et al. 1999). Tande (1979) calculated a mean fire interval (from the f(t) distribution, see Methods) of <40 years for montane forests in Jasper National Park surrounding the Prairie de la Vache study area, with intervals of greater than 70 years in subalpine forests at higher elevation. In Banff National Park, montane forests had a mean fire interval of 42 years, and lower subalpine forest had mean fire intervals of 94 years on warm aspects and 130 years on cool aspects (White 1985b). High fire frequencies at lower elevations have been attributed to dryer and warmer weather conditions (Tande 1979), and higher human use (Barrett and Arno 1982, White 1985a, Kay et al. 1999). In contrast, Johnson and Larsen (1991) estimated that the fire cycle (calculated from the A(t) distribution) was approximately 90 years, with no variation by elevation, for the Kananaskis Valley surrounding the Ribbon Creek meadow.

# Local variation around meadows

Fire history patterns around meadows did not strongly support the hypothesis that meadows were a focus for frequent cultural burning. Most importantly, meadow edges did not have the short mean fire intervals (<10 years, Prediction 1) that would indicate routine human burning (Tables 3.3 and 5, Figure 3.4*b*). The slightly shorter mean time-since-fire (Tables 3.2 and 3.4, Figure 3.5) and fire intervals (Tables 3.3 and 3.5, Figure 3.5*b*) of meadow edges versus adjacent forest plots, and warm aspects versus cool aspects indicate that differential burning patterns around meadows did occur. However, shorter fire intervals on warm aspects has been reported by several fire history studies for the Canadian Rockies

(Tande 1979, Hawkes 1980, White 1985b, Wierzchowski 1995), and is therefore also a more general pattern when fires burn larger areas than just meadows.

Downwind areas of meadows had shorter time-since-fires than upwind edges (Table 3.4), suggesting that, at least for the last fire, some meadows may have been the location of ignition. Since 1880, meadow and shrubland areas in the Canadian Rockies have consistently been a location for spring and fall fires caused by the railroad, highway slash burning, or other unplanned human-caused fires (White 1985a, Johnson and Wowchuk 1993). Behavior of recent prescribed fires (since 1980) in the Canadian Rockies and foothills has clearly demonstrated that meadow areas are highly flammable in spring (e.g., Bork et al. 1996), and that these fires can burn into forests on downwind edges of meadows (Ian Pengally, Banff National Park, personal communication).

The position of the majority of fire scars in the earlywood sections of tree rings (Figure 3.6) strongly suggests cultural burning as a cause of fires. However, contrary to Prediction 4, the timing of scars was similar in both meadow and forested plots, indicating that spring or dormant season fires burned not only meadows, but also major areas of forest. This evidence also contradicts Johnson and Wowchuk's (1993) conclusion that most forest areas of the Canadian Rockies burned historically from lightning-caused fires in July and August. However, their supporting data were written fire reports for the few burns that occurred after 1950. Near the meadows evaluated during my study, fire occurrence post-1950 was virtually non-existent (Figure 3.3), and recent burn area is reported as very low throughout the Rocky Mountains (Tande 1979, White 1985a, Masters 1990, Reed et al. 1998). It is unlikely that conclusions on season-of-burn, derived solely from limited post-1950 fire data, are applicable to earlier time-periods with different fire regimes and human land uses.

# Cultural burning on the Rocky Mountain eastern slope: a revised hypothesis

The hypothesis of a fire regime dominated by human ignitions for the eastern slopes of the Canadian Rockies is supported by the low occurrence and burn area of lightning fire compared to human-caused fires (previous research by White 1985a, Kay et al. 1999, Heathcott 1999), and the predominance of fire scars in earlywood sections of tree-rings (this study). However, the pattern appears to differ from that reported by Lewis (1982) for northern Alberta areas. There, frequent spring burning was reported as carefully contained in meadows or narrow travel corridors. In contrast, human-started fires in the Rockies were less frequent, but dendrochronology evidence near meadows indicates that these fires spread down whole valleys, burning both forests and meadows. The position of fire scars in tree-rings indicates that these fires usually occurred in the early part of the fire season (e.g., May and June). Warm aspects did burn somewhat more frequently than cool aspects. Barrett and Arno (1982), White (1985a), Murphy (1985), and Kay et al. (1999) report a similar regime of widespread human-caused burns in Rocky Mountain valleys and foothills during periods outside the midsummer lightning fire season.

A revised hypothesis is therefore: In the past, humans periodically burned large areas of the Rocky Mountains in the spring season. These burns were relatively more frequent in more heavily human-used lower elevation valleys (mean fire interval <40 years) than in more remote upper elevation valleys (mean fire interval >40 years). Fires often paralleled trails on south aspects of valleys.

If this hypothesis is valid, what motivated this historic cultural practice of relatively large area of burning? One possibility is that historical burning by people long provided open habitats favourable to bison, and after humans obtained horses, fire was also used to improve horse grazing. Bison are the dominant, identifiable bones in eastern slope archaeological sites, and were also the most commonly observed species in explorer journals (Holroyd and Van Tighem 1983, Kay et al. 1999). The relatively high abundance of bison in comparison to other ungulates may have resulted from movements into the mountains of small sub-herds that separated from large, migratory herds of bison historically found on the Great Plains to the east (Kay et al. 1999). First Nations valued bison highly for food, clothing, and shelter, and people were skilled in using habitat manipulation by fire and other techniques to control herd movements (e.g., Haines 1970, Guthrie 1980).

Moreover, it is possible that bison movement into the mountains was not just passively observed, but actively encouraged by hunters. The mouths of many eastslope valleys are often narrow (<2 km in width) as they enter the foothills and plains. First Nations may have used bison-driving techniques, similar to those used for pounding or jumps (Haines 1970) to herd bison into the mountains. Once within most eastern slope mountain valleys, bison were effectively contained in large rock-walled pounds. Escape routes across

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mountain passes were completely blocked by deep snows for over 6 months per year.

Further, bison hunters on the east slopes of the mountains were often people from the Salish cultures of the interior Cordilleran area (Teit 1909). Hunting and processing sites further into the mountains may have minimized conflict with the Piegan, whose culture centred on the Great Plains to the east (Kidd 1986).

Encouraging bison use of mountain valleys could therefore have been of great economic and security value to native peoples. Strong incentive would exist for the use of fire to create grass and shrub corridors into the mountains. These corridors would be used for subsequent drives of bison up valleys from the prairies. Possibly the objective was to burn relatively narrow (e.g., <1 km wide) corridors along trails on south facing slopes as lane-ways for hazing.

However, control of fire in the east slopes is difficult, especially during the spring season. Conifer foliage is highly flammable during the spring period of low moisture content (Van Wagner 1977). In the central Alberta and Banff National Park areas, this occurs in late May or early June (Fuglem and Murphy 1980, Chrosciewicz 1986, Fingland 1987). This phenomenon, combined with relatively frequent periods of widespread fuel drying during May and June caused by blocking high pressure ridges (Johnson and Wowchuk 1993), and high winds associated with the break down of these ridges (Nimchuk 1983) could result in extreme spring fire behavior. For example, in May, 1999 the northern aspect forest adjacent to the Panther River meadow area (Table 3.1) was burned by a human-ignited, independent crown fire (Van Wagner 1977) that spread a distance of >5 km in 2 hours across partially snow-covered ground (Ian Pengelly, Banff National Park, personal communication.).

# Conclusion and Future Research

The preliminary dendrochronological analysis of trees near meadows in the Rocky Mountains provided some evidence that historical fires near meadows were human-caused. However, the meadows themselves were probably not the main focus of burning, but larger areas both upwind and downwind of meadows. Future research should focus on identifying potential objectives for cultural burning at this large area scale. One possibility may be the creation of fire corridors for driving bison from the plains into the mountains.

On the basis of these hypotheses, specific predictions for burning patterns can be developed for subsequent testing with dendrochronology and other techniques. Key evidence for evaluating the cultural burning versus the lightning fire hypotheses is the time of burning as determined by fire-scar positions within tree-rings. Ongoing research of cambial growth phenology (Walker 1995) should be completed to calibrate scar position to the time-of-year.

# CHAPTER 4. INTERACTION OF ENVIRONMENTAL FACTORS AND TREMBLING ASPEN REGENERATION

#### Introduction

Trembling aspen (*Populus tremuloides*) is a species indicative of the low elevation montane ecoregion in Rocky Mountain national parks (Achuff et al. 1996; White et al. 1998a,b). Aspen stands are typically long-lived clones, regenerated by frequent fires (Mitton and Grant 1996, Kay 1997a). In the Rocky Mountains, aspen communities are second only to riparian communities for species richness (Finch and Ruggerio 1993). Aspen stands historically had a range of different age and size classes (Gruell 1979, Houston 1982, Ripple and Larsen 2000). However, since the late 1800s to 1930s (depending on the location), aspen stands have generally failed to grow to heights >1 m on low-elevation elk (*Cervus elaphus*) winter ranges in several national parks and wildlife refuges (Packard 1942, Cowan 1947, White et al. 1998a) including Yellowstone National Park (Houston 1982, Kay 1990, Romme et al. 1995), near Jackson Hole, Wyoming (Gruell 1980, Boyce 1989), in Rocky Mountain National Park, Colorado (Olmsted 1979, Baker et al. 1997), Banff and Jasper national parks in Alberta (Kay et al. 1999), and Yoho and Kootenay national parks in British Columbia (Kay 1997b).

Hypotheses for aspen decline include high browsing rates by elk (Packard 1942, Cowan 1947, Olmsted 1979, Kay 1990, White et al. 1998a), fire suppression (Loope and Gruell 1973, Gruell 1980, Houston 1982), or combinations of these factors interacting with climatic change (Romme et al. 1995, Huff and Varley 1999). For Yellowstone National Park, Romme et al. (1995) hypothesized that aspen trees originated episodically during periods when moist climatic conditions, high fire frequency, and low elk densities interacted to create numerous aspen suckers that grew rapidly to heights immune to elk damage (e.g., >4 m). Hereafter, I refer to this as the interaction hypothesis.

My objective in this study is to test the interaction hypothesis for aspen decline with time-series and spatial comparisons of aspen, forest disturbance, herbivory, and climate conditions from Bow Valley in Banff National Park, Alberta (BBV). This area provided two useful conditions to evaluate the interaction hypothesis. First, the time period when tree-

sized aspen began to fail to regenerate in BBV is relatively recent (1930s). The period is bracketed in time by detailed information on fire history (White 1985a, Rogeau and Gilbride 1994), weather observations (Feunekes and Van Wagner 1995), and elk populations (Woods 1991). Secondly, recent fencing and tree-clearing (1983 to 1987) of the Trans Canada Highway right-of-way in Banff National Park protected wildlife from high speed vehicle traffic (Woods 1990), and also provided a large wildlife exclosure with recent forest disturbance. Exclosures are a useful experimental technique to contrast wildlife effects on aspen (Olmsted 1979, Baker et al. 1997, White et al. 1998a) and other ecological communities (Krebs et al. 1999, Stohlgren et al. 1999). However, they are frequently undisturbed, small areas, that do not cover a broad range of site conditions. In contrast, the BBV highway exclosure is a transect of over 20 km in length enclosing recently disturbed aspen on a wide range of site types.

# Predictions from the interaction hypothesis

Two sets of predictions from the Romme et al. (1995) interaction hypothesis can be tested with time-series and exclosure data from the BBV:

Climate, disturbance, and elk herbivory effects over time. According to the interaction hypothesis, aspen regeneration reached tree height (>4 m) only during episodic events created by the interaction of three factors: favourable climate, frequent fires, and low elk density. For Yellowstone National Park, Romme et al. (1995) concluded that the climate favourable for aspen was cool, moist summers that enhanced stem regeneration and growth rates. In contrast, for other areas, warm temperatures that stimulate root suckers (Maini and Horton 1966, Hungerford 1988) and drought that kills larger, apically-dominant stems (Bailey and Wroe 1974) may be important factors for aspen stand regeneration. If the interaction hypothesis is applicable to the BBV over time, aspen regeneration to tree height should be correlated with periods of frequent fire, low elk density, and depending on which climatic effect is important for aspen, time periods of either warm-dry climate or cool-moist climate.

Site conditions and herbivory effects over space. Along the Trans Canada in the BBV, three conditions could influence aspen sapling (stems 1 to 4 m) abundance. First, different site moisture conditions, as indexed by plant community type (Archibald et al.

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1996) could approximate different climatic effects. Secondly, the recent (<20 years) clearing of the highway right-of-way would create a disturbance effect. Thirdly, the wildlife exclosure fence protecting the highway would create a variable herbivory effect. If the interaction hypothesis is valid over space in the BBV, then the density of aspen saplings would depend on significant interaction between three site moisture conditions (moist, mesic, dry), and three disturbance-browsing regimes (unbrowsed-disturbed, browseddisturbed, and browsed-undisturbed). Depending on which climate factors are most favourable for aspen, interactions with browsing could increase the relative density of aspen on either disturbed cool-moist or warm-dry sites. For example, cool-moist, unbrowseddisturbed sites should have highest sapling densities if disturbed, moist sites stimulate aspen regeneration. Due to interaction, sapling densities would also remain relatively high on moist-disturbed and moist-undisturbed sites, but decline rapidly on drier sites, particularly in the absence of disturbance. If interaction effects were not significant, then main effects of site moisture level, or disturbance-browsing regime could be significant independently (Underwood 1997).

### Study Area and Methods

The BBV study area is approximately 100 km<sup>2</sup> in the Bow River valley of Banff National Park, Alberta, with an elevation of 1350 m to 1700 m. It lies in the montane ecoregion on the eastslope of the Rocky Mountains, with forest cover types of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), and Douglas-fir (*Pseudotsuga menziesii*) (Achuff and Corns 1982, Archibald et al. 1996). A small portion of the area (<10%) is grassland and almost pure aspen stands (Achuff et al. 1996). Small aspen stands and individual trees are found in coniferous forests. The montane ecoregion was historically subjected to frequent fires (Tande 1979, Arno 1980, Kay et al.1999) but since the 1930s the area burned has declined precipitously due to modern fire suppression and lack of Native American ignitions (White 1985a). Parks Canada used prescribed fires to burn approximately 3000 ha of the area from 1983 to 1995 (Achuff et al. 1996).

Elk were infrequently observed in the BBV prior to 1880 (Kay et al. 1999). They were reported extremely rare or absent from then until reintroduction of 235 elk from

Yellowstone National Park in 1918 and 1920 (Holroyd and Van Tighem 1983, Woods et al. 1996). By 1943, however, Banff National Park began culling elk in the BBV to reduce elk herbivory effects on vegetation, competition on moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (O. *hemionus*) and bighorn sheep (*Ovis canadensis*), and to reduce the probability of an elk die-off (Cowan 1947, Flook 1964, Woods 1991). The culling program ceased in 1970 after at least 3900 elk were removed from the BBV (Holroyd and Van Tighem 1983). The number of elk killed on the highways and by the railway in the BBV increased steadily over time, but decreased as major portions of the Trans Canada Highway were fenced between 1985 and 1997 (Woods 1990, Woods et al. 1996). After 1990, elk population distribution changed from relatively evenly distributed throughout the BBV to a high concentration around Banff townsite (Woods et al. 1996). Potential causes include elk habituation to humans, recolonization of less developed areas by wolves, and decreased highway-caused mortality (Paquet et al. 1996, White et al. 1998a, Parks Canada 1999).

### Time series analysis

Long-term temporal datasets of fire history, elk population, and weather variables were compared to the yearly per cent of aspen regeneration.

Aspen regeneration year. I sampled the diameter at breast height (DBH) for aspen stems >2 m height in 60 plots in the BBV with  $4 \times 50$  m belt transects in open canopy stands, or the point-quarter technique (Mueller-Dumbois and Ellenberg 1974) in moderately closed or closed stands. Plots were located in 20 subunits of approximately 1 km<sup>2</sup> in area randomly selected from a total of 110 mapped across the BBV. In each subunit, I selected three plots, one from each of 3 canopy closure classes: open canopy (<100 trees/ha of all species), moderately open (500 to 1000 trees/ha), and closed canopy (>1000 trees/ha). Assuming a relatively similar fire history in a subunit, this sampling design balanced the number of plots in various canopy competition and time-since-fire conditions. In addition, I sampled aspen stem DBH in ten  $4 \times 50$  m belt transects located in aspen stands burned in the BBV from 1985 to 1990.

I calculated the age of sampled stems with a regression equation (Age = 15.456 +3.748 DBH (diameter and breast height),  $r^2 = .71$ ) from disks of 576 aspen stems (>2 m

height) cut from the BBV and adjacent east slope watersheds (Chapter 5). This regression was applied to 542 aspen trees (>4 m) sampled in BBV plots to calculate tree age, which was then subtracted from the sample year to determine the year of regeneration.

<u>Area burned.</u> The time-since-fire area per year for the BBV was derived from the Banff National Park time-since-fire map for the lower Bow River watershed (Rogeau and Gilbride 1994:18). This method underestimates the area burned for the early period (e.g, <1880) of the time-series because subsequent fires burned over earlier fires.

<u>Elk population</u>. Surveys of elk population numbers in the BBV for the period 1945 to 1975 were inaccurate (Woods 1991). These were fall ground-counts done prior to the late-winter period when the majority of elk were in the valley. Further, counts were confounded by large culls that likely altered elk behaviour and habitat use patterns (Woods 1991). Therefore, I constructed a population model for the 1920 to 1990 period. That simulation calculates the annual population with the equation

$$N_{(t+1)} = N_t + (cow_t^*(b^*1 - (N_t/K)^R)) - (Nt^*(m+d)^*(N_t/K)^R) - M_t$$

where N is the total population, or the summation (calf, cow, spike and bull sex/age classes) in the spring census (April 15 to May 15 prior to calving). These data are available from recent (>1985) classified counts where calves are <1 year old, cows are female elk >1 year old, spikes are male elk 1 to 2 years old, and bulls are >2 years old (Woods et al. 1996). The birth rate (b), natural (from predation and other non-human causes) mortality rate (m), and dispersal rates (d) are estimated maximum rates derived from Woods (1991) and current research (J. McKenzie, pers. comm.). In the model, these rates are density dependent through the multiplier  $(1-(N_t/K)^R)$  where K is the ecological carrying capacity, or the population level where elk are resource-limited (Caughley and Sinclair 1994:117). In this model, the exponent R determines the form of the density dependence function (Richards 1959). Where R is >1, population growth is rapid at low and moderate densities, and declines rapidly as K is approached. Where R = 1 population growth follows a logistic curve with gradual density dependent effects. Houston (1982) and Coughenour and Singer (1996) described density dependent processes in birth and natural mortality rates for Yellowstone National Park. Differential dispersal rates in male and female elk in

Banff National Park may be important for population regulation (Flook 1970:59, Woods et al. 1996).  $M_t$  is human-caused mortality in the BBV tracked for calves, cows, spikes and bulls, which is available from the annual culling, road, and rail-kill records (Flook 1970, Woods 1991). Where only a total human-caused kill record for a year was available, this was apportioned to each population class based on the sex-age ratio of animals at time t.

For comparison, I did two runs of the model ("A" runs) using b, m, and K parameters (Table 1) from Woods (1990). In the A-series of runs, m and d are fixed for all elk population levels, and b is density dependent following a relationship developed by Woods (1990) based upon Houston's (1982) data for Yellowstone National Park. The K values represent the estimated likely lower limit (2200) and upper limit (6400) for ecological carrying capacity in the BBV (Woods 1990). I also did 3 iterations of the model ("B" runs) for low, moderate and high values of K, estimated maximum values of b, m, and d, and I varied R values such that two conditions were met. First, the simulated population remained >200 through the culling period, as observed in all surveys. Secondly, the simulated population approximated the more accurate population estimates (number and sex/age class) obtained after 1984 (Woods 1991). The elk population was assumed as 0 for the period 1885 to 1920 for all model runs. The starting 1920 population was set as 225 females and 25 males (Lloyd 1927, Woods pers. comm.).

<u>Climatic variables</u>. Long-term weather data for the valley (since 1887) were available from the Banff townsite weather station. Summer drought by year was quantified with the drought code (DC) index of the Canadian Forest Fire Weather Danger Rating System (Stocks et al. 1989). Feunekes and Van Wagner (1995) calculated the DC for the period 1891 to 1995 from the Banff townsite weather station data. The maximum DC value for each summer was used as an indicator of relative drought. The higher the DC value, the more extreme the drought level. Overwinter precipitation (November to May), and mean monthly temperatures (May, June, July, August) were also calculated. Table 4.1. Parameters used for 5 runs of a population simulation model for Banff Bow Valley elk for the period 1920-1990. Parameters are b (birth rate), m (mortality rate), d (dispersal), K (food-regulated carrying capacity), and R (Richards Multiplier). For "A" runs b is approximated by a relationship developed by Houston (1982) as modified by Woods (1990), and m, and d are fixed. For "B" runs, the b, m, and d parameters are estimated maximum values multiplied by the Richards (1959) function.

Run No.	Description		Parameter Values Used in Elk Model Runs						
		b	Calf m	Cow m	Spike m	Bull m	d	К	R
A- 2200	From Woods (1990), b is density dependent based on relationship from Houston (1982), with a low estimate of K	b <sub>t=1</sub> =0.624 – .164Nt (b=March calf: cow ratio)	0.0	0.07	0.07	0.07	0.0	2200	I
A- 6600	From Woods (1990) as above with high estimate of K	As above	0.0	0.07	0.07	0.07	0.0	6600	1
B- 2200	From Woods 1990, b from Woods 1991, low estimate of K	0.80	0.5	0.2	0.5	0.3	Calves and cows: 0.1 Spikes: 0.4 Bulls 0.3	2200	2.487
B- 4300	As above, moderate estimate Of K	0.80	As Above	As Above	As Above	As Above	As above	4300	1.044
B- 6400	As above, high estimate of K	0.80	As Above	As Above	As Above	As Above	As above	6400	0.743

Analysis. Time-series statistical procedures followed Wilkinson and Balasanov (1997). For graphical analysis, aspen age, burn area, and weather series were plotted with a 5-year moving binomial mean (*cf.* Van Wagner 1988). This reduced annual variation due to measurement error or other factors, but accentuated high and low values. Statistical relationships between potential causal variables and aspen age (unsmoothed) were analysed with Pearson correlation coefficients for lag periods of 0 to 4 years prior to the dated age. Correlation of variables for each time lag was evaluated for statistical significance with Bonferroni multiple comparison tests (P < 0.05).

### Spatial analysis

I mapped and numbered 117 areas where aspen stands on the same site were bisected by the wildlife exclosure fence along the Trans Canada Highway between the Banff National Park east gate and the Sunshine Village interchange (Figure 4.1). Based on site characteristics and vegetation community type (Archibald et al. 1996), each area was classed as dry, mesic or moist (Table 4.2). I then randomly selected 10 areas of each type for detailed sampling. In 1998,  $2 \times 30$  m belt transects were laid through the stands of highest aspen stem density for each area, both inside the exclosure and at a nearby location (<100 m away) outside the fence with a similar plant community type. All transects were parallel, but >3 m from the fence. Further, I located a  $2 \times 30$  m transect in a similar community type in an area >0.5 km from the fence (Stohlgren et al.1999). Within each belt transect, aspen stems were tallied by size class: short suckers (0 to 1 m height), short saplings (1 to 2 m height), tall saplings (>2 m but less than 5 cm DBH), and trees >5 cm DBH (by 5 cm DBH size classes). On plots outside the wildlife exclosure fence, elk pellet groups were counted on two  $2 \times 200$  m belt transects parallel to the aspen transect. Pellet groups were counted during April and May, 1999, prior to green-up of the herbaceous vegetation (Huggard 1993a).



Figure 4.1. Highway wildlife fence through an aspen stand in the Bow Valley in Banff National Park. The area on the left is exclosed from ungulate use.

Table 4.2. Plant community codes, common plant species, and site conditions for exclosure plots grouped by site type classes used in this study.

Site type	Plant community type code and common vegetation species (from Archibald et al. 1996)	No. of plots	Moisture regime	Nutrient regime	Topographic position and aspect
Dry	a1, Douglas-fir, limber pine (Pinus flexilis), ground juniper (Juniperus communis)	4	Subxeric	Poor to medium	Upper slope, southerly
	b1, lodgepole pine, Douglas-fir, bearberry (Arctostaphylos uva- ursi)	3	Subxeric	Poor to medium	Midslope, southerly
	b2, aspen, bearberry	3	Subxeric	Medium to poor	Midslope, southerly and westerly
Mesic	b3, aspen, white spruce, lodgepole pine, bearberry, buffalo berry ( <i>Shepherdia</i> canadensis)	5	Mesic	Medium	Level, easterly
	c2, lodgepole pine, white spruce, buffaloberry	3	Mesic	Medium	Midslope, variable aspects
	c3, aspen, buffalo-berry, hairy wild rye ( <i>Elymus innovatus</i> )	2	Mesic	Medium to rich	
Moist	c4, aspen, Douglas-fir, white spruce, prickly rose ( <i>Rosa</i> <i>acicularis</i> ), cream-coloured vetchling ( <i>Lathyrus</i> <i>ochroleucus</i> )	3	Mesic	Medium to rich	Lower slope to midslope, variable aspects
	e2, aspen, prickly rose, snowberry ( <i>Symphoricarpos</i> albus), saskatoon (Amelanchier alnifolia)	2	Mesic	Rich to medium	Midslope and lower slope, variable aspects
	f1, balsam poplar ( <i>Populus balsamifera</i> ), aspen, white meadowsweet ( <i>Spirea betulifolia</i> ), prickly rose	4	Subhygric	Rich to medium	Valley bottom, variable aspects
	g1, white spruce, balsam poplar, dogwood ( <i>Cornus stolonifera</i> ), meadow horsetail ( <i>Equisetum</i> pratense)	1	Subhygric	Rich to very rich	Valley bottom, variable aspects

Factorial analysis was used to evaluate the effects of 3 plot locations (unbrowseddisturbed inside exclosures, browsed-disturbed adjacent to exclosures, and browseddisturbed distant from exclosures) × 3 site types (dry, mesic, moist) on the combined stem density of short and tall aspen saplings. Sapling density was not normally distributed, and was square-root transformed for analysis (Underwood 1997). I added a value of 0.5 to stem density to eliminate zero values.

#### Results

### **Time-series** analysis

Aspen regeneration mostly dated to a broad pulse centered on approximately 1910, with few stems originating before 1850, or after 1935 (Figure 4.2). Burn years in the BBV were sporadic, with the most recent large burns dating to fires between 1880 and 1895 (Figure 4.2, Rogeau and Gilbride 1994). Aspen regeneration was not significantly correlated to burn area for most time periods and time lags tested (Table 4.3). Significant positive correlation was observed for the 1893 to 1990 period for the 1 and 4 year time lags. However, burned area was not essential for aspen regeneration. As much as 1% per year of the total number of aspen stems regenerated in years after fire activity had declined (Figure 4.2).

Elk populations were simulated (Figure 4.3) with several alternative parameter values. The A-2200 and A-6400 runs, based on Woods (1990) parameter estimates (Table 4.1), and a logistic form of the model (R = 1), approximated 1940s population estimates, but resulted in extinction of the modeled population by 1950. With these parameters, simulated populations were not large enough to sustain the culling reported for the period 1943 to 1950 (Woods 1991). In the B-series of runs, the population was sustained throughout the culling period, and approximated >1980 surveys. For the lowest value of K (3200 elk), this required R to be set at <1. For all the B runs, >1500 elk were required in the BBV in the spring of 1943 to maintain an elk population >200 during the period of culling (1943 to 1970).

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Figure 4.2. Time series of the current per cent of Bow Valley aspen trees (>4 m height) by stand origin year (MMASP), overall Bow Valley area stand age per cent by year (MMBURN), surveyed elk population for several years (ELKSURV), simulated elk population (ELKMOD), maximum summer drought code (MMDC), and spring (May, June, July) temperature (MMSPR). Variables prefixed by MM are moving binomial means (see text).

Table 4.3. Pearson correlation coefficients for variables potentially influencing regeneration of aspen for 5 time lag periods (0 to 4 years), and 4 time periods. Asterisks indicate values significant at the P < 0.05 level with the Bonferonni multiple comparison test across rows.

Time Period	Years	Variable		Time	Lag (years	s)	······,,
	of data		0	1	2	3	4
1803 to 1990	187	Burn area	0.159	0.149	-0.069	0.088	0.125
1803 to 1925	122	Burn area	0.131	0.130	-0.089	0.055	0.113
1893 to 1990	97	Winter precipitation	0.133	0.003	-0.055	0.011	0.124
		Drought	-0.030	-0.128	-0.125	-0.181	-0.129
		May temperature	-0.024	-0.094	-0.128	-0.011	-0.022
		June temperature	0.030	0.169	-0.256	-0.155	0.186
		July temperature	-0.035	0.004	0.139	0.033	-0.020
		August temperature	-0.044	-0.203	0.018	0.197	-0.156
		Burn area	0.202	0.372*	-0.033	0.201	0.334*
		Elk population	-0.145	-0.157	-0.169	-0.175	-0.164
1893 to 1925	32	Winter precipitation	0.317	0.125	-0.189	0.135	0.041
		Drought	-0.026	-0.182	-0.030	-0.057	-0.209
		May temperature	0.017	-0.183	-0.337	0.196	0.333
		June temperature	0.069	0.223	-0.574	-0.370	0.338
		July temperature	-0.138	-0.079	0.201	0.002	-0.202
		August temperature	-0.051	-0.456	0.075	0.470*	-0.318
		Burn area	0.009	0.337	-0.153	0.024	0.332



Figure 4.3. Select iterations of an elk model to simulate historic (1920-1990) population in the Bow Valley, recorded human cull numbers, and population estimates from ground surveys. Parameters for iterations are listed in Table 4.1.

I could not simulate the high 1960s population survey estimates (Figure 4.3) with any parameters reasonable for elk demographics in the BBV and reported culling statistics (Woods 1991). The B-4300 run appeared to be the most realistic for BBV conditions, and was used for time series analysis (Figure 4.2).

In contrast to elk survey estimates, the period when the modeled elk population exceeded about 750 elk (about 1935) graphically appears to correspond with the period of declining aspen regeneration (Figure 4.2). However, the number of aspen stems did not increase in response to the major reduction in elk populations that occurred after 1945. Further, a minor pulse of aspen regeneration in about 1985 occurred when modeled BBV elk populations were generally increasing (Figure 4.2). However, these stems regenerated predominantly near the Trans Canada Highway (C. White pers. obs.), which in the early 1980s was a major cause of elk mortality (Woods 1990), and may have caused locally reduced elk densities. The lack of a consistent aspen response to elk density was demonstrated by no significant correlation of modeled elk population to aspen stem age at any time lag (Table 4.3).

Climatic parameters varied widely during periods of different elk abundance (Figure 4.2). No strong correlation was apparent between winter precipitation, drought, or monthly temperature for almost all time lags and periods (Table 4.3). During the period of very low elk numbers (1890 to 1925), a significant positive correlation was observed for August temperature at a 3-year time lag (P < 0.005). June temperatures were weakly inversely correlated (P < 0.1) with the number of aspen stems regenerated at 2 and 3-year time lags.

#### Spatial Analysis

Aspen saplings were abundant on unbrowsed-disturbed plots inside the BBV highway wildlife exclosure (Figures 4.1 and 4.4). Factorial analysis results (Table 4.4) showed that the browsing-disturbance regime significantly influenced BBV aspen sapling density (P < 0.005), but that site type was not a significant factor (P = 0.138). Aspen saplings were relatively abundant on all 3 site types within the highway wildlife exclosures, and almost absent outside, but adjacent to the fence, and outside and distant

from the fence (Figure 4.4). There was a marginally statistically significant interaction between site type and browsing-disturbance regime (P = 0.051). Mesic, browsed plots that were adjacent to the fence had very low aspen sapling densities, but mesic exclosed plots had highest aspen densities (Figure 4.4). However, Bonferroni multiple comparison tests showed no significant difference (at the P = 0.10 level) in aspen saplings between site types for any browsing-disturbance treatment.

One factor that could influence aspen sapling density was differential elk use near the highway exclosure fence compared to plots away from the fence. Plots away from the fence had mean distances of  $2.8 \pm 0.6$  SEM km,  $2.6 \pm 1.0$  SEM km, and  $2.5 \pm 0.05$  SEM km from the fence for warm-dry, mesic, and cool-moist sites respectively. Elk use, as indexed by pellet group counts, was lower for plots away from the fence (browsedundisturbed) than for plots adjacent to the fence (browsed-disturbed) for all site classes (Figure 4.5).

#### Discussion

## Aspen regeneration over time

Time series analyses of aspen regeneration by year and potentially related factors provided only a weak test of the interaction hypothesis for several reasons. The year of aspen regeneration, as determined by a stem DBH-age relationship, only approximated the actual year of regeneration. Aspen stem diameters were sampled in stands across a range of elevations and aspects that likely responded differently to climatic variations. For the 1880 to 1990 period there was likely only 1 period of high elk abundance (c. 1940), so there were no temporal replications on the effects of high elk populations on aspen during the time series. Finally, during the period of recent low elk abundance, (e.g., 1950 to 1975), no large burns occurred in the Bow Valley (Figure 4.2, White 1985a, Rogeau and Gilbride 1994).



Figure 4.4. Geometric means  $\pm$  SEM of aspen sapling density (stems/100 m<sup>2</sup>) as a function of plot browsing-disturbance regime and site moisture class. Browsing-disturbance classes are unbrowsed-disturbed in the highway exclosure (Unbr-Dis), browsed and disturbed adjacent to the highway fence (Br-Dis), and browsed-undisturbed away from the fence (Br-Undis). Sample size is 10 per group.

Source of variation	SS	Df	MS	F-ratio	Р
Site moisture condition	11.4	2	5.7	2.02	0.138
Browsing-disturbance regime	207.9	2	103.9	37.09	0.000
Site moisture × browsing-disturbance	27.8	4	6.9	2.48	0.051
Error	227.0	81	2.8		

Table 4.4. Results of the analyses of variance of the effects of site moisture and browsing - disturbance regime on the square-root transformed density of aspen saplings (squared multiple R: 0.521).



Figure 4.5. Geometric mean  $\pm$  SEM of elk pellet counts (groups/100 m<sup>2</sup>) for browsedundisturbed plots away from highway wildlife exclosure fence, and for browsed-disturbed plots adjacent to the highway fence.

Disturbance effects- When elk abundance was low in the BBV (before 1920), aspen regenerated after years with high burn area, but also regenerated in the absence of fire (Figure 4.2). Fire was not essential for aspen regeneration, and was only significantly correlated to the age of aspen stems for the period 1893 to 1990 (Table 4.3). These results are supported by research from other areas in Alberta with low fire occurrence and low elk density. In the absence of fire, aspen regeneration covered grasslands areas at reported yearly rates of 0.05 % (Bailey and Wroe 1974) to 0.75% (Johnson and Smoliak 1968). It is difficult to evaluate disturbance effects during the period when elk numbers were moderate to high (e.g., after 1920) because few areas burned in the BBV (Figure 4.2, White 1985a).

<u>Elk population effects</u>- The population simulation model suggested that estimates of BBV elk numbers derived from ground surveys during the 1940s and 1950s were inaccurate, similar to Wood's (1991) conclusion. The model also suggested that elk likely numbered nearly 2000 in the years 1940 to 1943. Cowan (1947) provided a similar estimate for BBV numbers for this period. An elk population <1500 could not have sustained the known numbers of elk culled after 1943 (Figure 4.3).

Aspen regeneration declined substantially after 1935 when the modelled BBV population increased to >800 elk (Figure 4.2). However, it did not increase substantially when the simulated elk population declined <800 (1950 to 1970). Thus, there appeared to be no simple linear relationship of aspen regeneration to varying historical levels of elk density in the BBV. Pearson correlation coefficients for elk density and aspen regeneration are negative, but statistically insignificant (Table 4.3). Similarly, aspen failed to regenerate prolifically after elk population reductions in Rocky Mountain National Park, Colorado (Olmsted 1979, Baker et al. 1997), and in Yellowstone National Park (Houston 1982, Kay 1990, Huff and Varley 1999).

<u>Climatic effects</u>- Aspen regeneration was correlated significantly to only one climatic variable (August temperature 3 years prior to tree regeneration) during only one period (1893 to 1925) when elk were virtually extinct in the BBV (Table 4.3). This may support previous work in Alberta where Bailey and Wroe (1974) found that pulses of abundant aspen regeneration in grasslands with low elk density were correlated with above average temperatures during June, 1 and 2 years before tree establishment, and with low

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precipitation 2 years prior to establishment. They concluded that these warm dry periods killed apically-dominant older stems, thus stimulating sucker regeneration.

However, for the BBV time periods with moderate and high elk numbers (1925 to 1990), there was no consistent, identifiable correlation of aspen regeneration pattern with mean monthly temperature, summer drought, or overwinter precipitation for any time lag periods (Table 4.3). This result may be partially attributed to grouping aspen stem regeneration dates from all aspects and elevations. For example, warm June temperatures might stimulate aspen suckering on north aspects with cooler microclimates, but retard it on south aspects. However, if interaction of elk density and climatic factors were important, some major, consistent trend in temperature or precipitation should have occurred during the periods of moderate elk densities (e.g. 1945 to 1975). No major trends were evident during this period for the variables used in this study (Figure 4.2). This did not support the interaction hypothesis prediction that moderately dense elk populations interacted with variable climate and disturbance to regenerate aspen (Romme et al. 1995).

Luckman (1998) and Luckman and Kavanagh (2000) utilized weather records combined with dendrochronology (>800 year tree-ring record) to develop long-term climatic patterns for the Banff townsite and Canadian Rockies areas. Relatively high levels of precipitation occurred during the 1950s, and spring and summer temperatures since 1950 may be higher than any time in the last 900 years (Luckman 1998). But these temporal changes do not correspond with the period of aspen decline in the BBV. No consistent relationship of aspen regeneration with climate was also found for Rocky Mountain National Park, Colorado (Baker et al. 1997), and for Jackson Hole and Yellowstone National Park in Wyoming (Hessl 2000).

## Site, disturbance, and browsing interaction

Aspen saplings protected from elk browsing in exclosures were relatively abundant on all site types, and rare on all site types in disturbed or undisturbed areas with elk (Figure 4.4). This suggested that current climate, site moisture, or disturbance levels did not limit sapling regeneration, but browsing did. No observations supported the interaction hypothesis that the browsing-disturbance regime interacted with either dry or moist site conditions to differentially increase or reduce aspen sapling density on browsed-disturbed or browsed-undisturbed sites. Instead, there was a relatively significant interaction for unbrowsed-disturbed sites where for mesic conditions, aspen saplings were more abundant than on dry or moist sites. These results are not unexpected given that aspen has the broadest geographic and environmental ranges of any North American tree (Mitton and Grant 1996). Numerous studies (reviewed in Kay 1997a, White 1998a) report that aspen saplings remain abundant on a wide range of site conditions where elk densities are very low (in exclosures), or low to moderate (outside park boundaries). These include research in Rocky Mountain National Park (Olmsted 1979, Baker et al. 1997, Suzuki et al. 1999), Yellowstone National Park (Kay 1990), Yoho and Kootenay national parks (Kay 1997b), other locations in Banff National Park (Cowan 1947, Kay et al. 1999), and Elk Island National Park in central Alberta (Bork et al. 1997).

Although the exclosure results reported here corroborate other research, they should be evaluated cautiously. Given the significant effect of elk browsing on aspen sapling density, and the evidence from pellet group counts that areas near the highway fence had higher elk density than areas away from the fence (Figure 4.5), confounding could have occurred. Possibly higher elk densities and resulting browsing effects near the fence masked any interaction effects of disturbance and site.

# Conclusion and Future Research

This research from the Bow Valley in Banff National Park supported the hypothesis that elk herbivory is the most significant factor causing the decline of trembling aspen in Rocky Mountain national parks (White et al. 1998a). Variable climate or site conditions did not appear to be important singularly, or through interaction with disturbance or herbivory, in significantly influencing aspen sapling density. However, three weaknesses in the experimental data limit the robustness of this conclusion. First, only one period of high elk density occurred in the time-series analysis. Second, few areas were disturbed by fire during the periods when elk were at moderate numbers. Third, spatial comparisons in this study were possibly confounded by higher elk use near the highway exclosure fence, and consequent higher browsing effects on aspen in the browsed-disturbed treatment area.

Findings of this research and other studies provide direction for further research on

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elk herbivory impacts on aspen. Temporal analysis showed that culling and highway mortality substantially reduced elk populations during the period 1945 to 1975. Although this elk population level was similar to that of the late 1920s, when aspen tree regeneration was still occurring, very little regeneration to tree-size occurred in Banff after 1945. A similar lack of results from elk culling in Rocky Mountain National Park (Baker et al. 1997), and Yellowstone National Park (Houston 1982, Huff and Varley 1999) suggested the climate-disturbance-herbivory interaction hypothesis (Romme et al. 1995). However, the present study and other research (Baker et al. 1997, Hessl 2000) do not support the interaction hypothesis.

Clearly, aspen response to elk browsing is significant, but does not follow the traditional, Clementsian "range management" model for herbivore effects on plants (Stoddart et al. 1975). The traditional model predicts linear, continuous effects of herbivory where incremental changes in herbivore density result in incremental change in vegetation (Ellison 1960). Further, evidence is lacking that climate or disturbance could be significant factors, either singly or interactively with herbivory, in aspen's decline. Aspen response to browsing may be better approximated by more complex state-and-transition type models (e.g., Noy Meir 1975, Walker et al. 1981, Westoby et al. 1989) where transitions between states may be rapid and have different mechanisms and pathways depending on the direction of change. These mechanisms will not likely be apparent in areas with high elk-low aspen, or low elk-high aspen abundance such as the inside-outside exclosure comparisons used in this study. Instead, as recommended by Schmitz and Sinclair (1997) for eastern forest herbivory research, further studies should evaluate herbivory and disturbance effects over a wide range of elk and aspen densities. Research should focus on elk-aspen herbivory processes at intermediate elk densities where the transitions between vigorous to declining aspen states appear to occur.

# CHAPTER 5. THE FUNCTIONAL RESPONSE OF ELK-ASPEN HERBIVORY

#### Introduction

Trembling aspen (*Populus tremuloides*) stands are an important component of the montane ecoregion in the Rocky Mountains (Achuff and Corns 1982). Although the spatial extent of aspen is limited in northern areas of the Canadian Rockies, aspen communities have high biodiversity, are valued wildlife habitats, and are important for aesthetics and recreation (DeByle and Winokur 1985). Aspen is often described as a seral species, but a clone's root system can be thousands of years old (Mitton and Grant 1996). Frequent fires in low elevation areas (Arno 1980) historically played an important role in maintaining aspen. Fires killed competing conifers, top-killed aspen stems, and stimulated prolific suckering from long-lived aspen root systems (DeByle et al. 1987, Peterson and Peterson 1992).

Land managers of many areas of the Rocky Mountains, but particularly national parks, have observed a trend in declining health of aspen stands (Kay 1997a). The number of older trees (>5 cm diameter at breast height, DBH), has decreased due to disease, bark damage from herbivores, or shading from increasing density of conifers (DeByle and Winokur 1985). Although sucker (<1 m height) sprouting from the underground aspen root mass may occur in stands, few stems survive through the sapling phase (>1 m height, <5 cm DBH) to reach tree size. Inside parks, repeated browsing and bark stripping by elk (*Cervus elaphus*) are important factors in the decrease of sapling numbers (Kay 1997a), but overall causes of aspen decline remain controversial (Houston 1982, Romme et al. 1995, Singer et al. 1998, Huff and Varley 1999).

Four hypotheses have been proposed to explain the long-term persistence of aspen in the Rocky Mountains (White et al. 1998a). Options are based upon whether, over the long-term, herbivore populations (particularly elk) were generally high (one main hypothesis with 2 variants), or generally low (Kay 1997a, Keigley 1997).

<u>High-herbivory hypothesis.</u> This holds that the long-term stable state of montane areas occurs when aspen is heavily browsed by abundant, food-regulated elk. In

Yellowstone National Park, this is termed "natural regulation" (Cole 1971, Houston 1982, Boyce 1991, Coughenour and Singer 1996). Heavily browsed aspen are predicted to persist in the ecosystem at low density due to regeneration after fire (Gruell 1979, Houston 1982, Boyce 1989), varying chemical defence of aspen suckers against herbivory (Despain 1991), or a complex interaction of factors such as fire, elk starvation, winter severity and climate change (Houston 1982, Romme et al. 1995, Huff and Varley 1999). Aspen were abundant in the late 1800s due to elk reductions by a rare event of intense human hunting. The current decline of aspen is due to an increase in elk populations to an equilibrium where numbers are regulated by competition for food (Coughenour and Singer 1996). Wolf (*Canis lupus*) or other predation on elk is considered a "non-necessary adjunct" (Cole 1971), which removes animals that would die anyway due to starvation. According to this hypothesis, predation cannot substantially lower elk populations below food-regulated levels (Boyce 1996).

Disturbance hypothesis. A variant on the high-herbivory hypothesis is based specifically upon the effects of fire. Loope and Gruell (1973), Gruell (1979) and Houston (1982) proposed that the lack of fire was the primary reason for aspen's continued decline. Fires remove competition from coniferous trees and cause extensive aspen suckering. Large fires could theoretically "swamp" herbivory effects in areas with moderate or greater elk densities, and some areas of regenerating aspen would be lightly browsed, and reach tree form (Bartos and Mueggler 1979, Romme et al. 1995, Suzuki et al. 1999).

<u>Climate change hypothesis.</u> A further elaboration of the high-herbivory hypothesis maintains that a warmer and dryer climate since the 1930s has been a significant factor in aspen regeneration failure because aspen existence was already marginal on dryer sites (Houston 1982, Romme et al. 1995). This hypothesis is not generally supported because of the consistent regeneration and growth of aspen in numerous wildlife exclosures in the Rocky Mountains under a variety of site conditions (White et al. 1998a, Chapter 4). However, climate change could interact with disturbance to increase herbivory effects in areas with low disturbance (Romme et al. 1995).

Low-herbivory hypothesis: According to this hypothesis, heavily browsed aspen is not a long-term state. It is a recent phenomenon due to high elk populations (Packard 1942; Cowan 1947; Olmsted 1979; Kay 1990, 1997a; Baker et al. 1997; White et al. 1998a,
1998b; Ripple and Larsen 2000). These authors suggest that the current die-back of aspen clones is due to recent human-caused changes in long-term ecological conditions which historically favoured aspen's survival. These changes include: 1) increased elk populations due to release from intense additive predation from humans, wolves and other carnivores, 2) habituation of unhunted elk to human presence, 3) decrease in fire occurrence by elimination of native cultural burning and suppression of current human- and lightning-caused fires.

However, previous studies exploring the effects of elk herbivory and disturbance are often limited to simple two-treatment level comparisons of aspen stands that are highly-browsed to those that are lightly-browsed (e.g., Olmsted 1979, Kay 1990), and to single study areas (e.g., Baker et al. 1997). Site-specific measurements of elk density have not been made that allow comparisons between studies or areas. Further, two-way comparisons of aspen under various productivity and herbivory levels have not been attempted, although interaction effects between disturbance, climate, and herbivory might be apparent only at moderate levels of elk herbivory (Romme et al. 1995, Chapter 4). More general conclusions on the effects of browsing on plant communities require analysis through a range of herbivore, vegetation density, and site conditions (Schmitz and Sinclair 1997).

My objective in this study was to evaluate the effects of elk herbivory and aspen productivity across a quantified range of elk density and tree cover conditions in multiple study areas. I used predation theory (Solomon 1949, Holling 1959) to develop graphical models (Messier 1995, Pech et al. 1995) of elk herbivory on aspen saplings (>1 m height, <5 cm DBH). These models were used to make specific predictions relevant to the optional hypotheses for long-term elk and aspen relationships described above. Predictions for each of these models were then evaluated with data from aspen stands sampled under varying tree cover and elk herbivory levels in 9 study areas on the eastslopes of the Rocky Mountains in Alberta, Canada. The most robust model was selected, and used to evaluate patterns in the elk-aspen herbivory process and to make recommendations for aspen conservation.

#### **Theoretical Models and Predictions**

Predator-prey theory was initially developed to describe animal predation processes (Solomon 1949; Holling 1959), and was later adapted to herbivory (Noy-Meir 1975, Caughley 1976). For plants, the approach is applied through prey density, as quantified through measures such as vegetation biomass or individual ramet density, and the effects on herbivore density and biomass consumption rates. The theory has been applied to species including aspen, European aspen (*Populus tremula*) and birch (*Betula* spp.) herbivory by moose (Lundberg and Dannell 1990) and beaver (Fryxell and Doucet 1993, Fryxell 1999).

The theory reduces the interaction between populations of a predator (or herbivore) and its prey into the product of a numeric response and a functional response (Figure 5.1). In more complex situations, predator aggregation and developmental responses to prey may also be important (Murdoch and Oaten 1975, Krebs 1994). The numeric response is the density or rate of increase of the herbivore population as a function of prey density. Previous research has demonstrated that although aspen is a high quality browse species (e.g., Hobbs et al. 1982, Jelinski and Fisher 1991), it makes up only a small portion (<5%) of elk diets in the Rocky Mountains (Hobbs et al. 1982, Canon et al. 1987, Woods 1991). Yellowstone National Park's high density elk population, for instance, is regulated by grassland forage production (Coughenour and Singer 1996). Therefore, the numeric response of elk is generally set by factors other than aspen and will remain relatively constant over the range of aspen density (Type 0 in Figure 5.1).

The functional response is the relationship between the percent prey killed per predator (kill rate) and the population density of the prey. Kill rate is determined by the "search time", or the time it takes to locate prey, and "handling time", or the time associated with capture and feeding. Holling (1959) described three types of functional response (Figure 5.1). A Type 1 functional response occurs in the rare situations where handling or search time is minimal, and the kill rate increases linearly with prey density until the predator is satiated.



Figure 5.1. Relative changes in the percentage of a prey population killed by predators as a function of prey density for a Type 0 numeric response and three types of functional response (modified from Messier 1995).

The Type 2 functional response is more common and occurs when the kill rate increases at a decreasing rate with prey density. Search time determines the rate of increase in the response, while handling time is the factor that often determines the upper limit of the function. The sigmoidal Type 3 response reflects more complex biological conditions. At low prey density, per capita predator kill rate decreases due to factors such as prey-switching to alternative prey, difficulties in detecting prey, or prey refugia (Holling 1965, Murdoch and Oaten 1975, Taylor 1984). At high prey densities, the Type 3 response is similar to Type 2.

The total response, or predation rate, is the product of the numeric and functional responses. The total response is depicted in Figure 5.1 for a Type 0 numeric response and the three alternative, potential functional responses. In Figure 5.2, the alternate total response curves are in turn superimposed on the percentage recruitment of the prey population as a function of prey density (Ricklefs 1990, Sinclair and Pech 1996). Prey recruitment rates are presumed to be high and constant until resources or space become limiting. In the absence of predation, recruitment decreases to 0 at high prey densities (K).

The graphical models presented in Figure 5.2 are central to developing predictions from the each of the multiple hypotheses for long-term aspen-herbivore relationships (Table 5.1). I make three key assumptions in developing predictions related to this browsing predator-prey system. First, aspen saplings (>1 m height, <5 cm DBH) are the primary prey of herbivores, and their density may influence functional response. Second, aspen saplings are also important for aspen stand recruitment. Regenerating aspen stands with low canopy competition have sapling densities of about 30 to 50 sapling stems/100 m<sup>2</sup> (Figure 4.4, Peterson and Peterson 1992). Third, I assume that the overall predation rate may be a more valid indicator of the functional response (Trexler et al. 1988, Marshal and Boutin 1999) than measures of the kill rate per predator used in previous herbivory research (Noy-Meir 1975, Augustine et al. 1998). For woody vegetation, the predation rate can be relatively easily estimated for multiple samples by estimating browse removal at different herbivore densities.



Figure 5.2. Potential dynamics for optional models (*a* to *d*) of elk-aspen interactions (modified from Pech et al. 1995). Stable equilibria (A and C), and unstable equilibria (B) occur where the recruitment of aspen balances the mortality due to browsing. The corresponding densities of aspen are  $N_A$ ,  $N_C$ , and  $N_B$ , and K is the maximum density of aspen in the absence of browsing. See text for descriptions of models.

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Hypothesis and Graphical Model	Functional Response	Elk Density Effect	Disturbance Effect	Elk x Disturbance Interaction Effect
High elk herbivory (Figure 5.2 <i>a</i> )	Type 3 functional response, single equilibrium state. Declining herbivory rates at low elk density	Low but stable aspen sapling density at high elk density	Slight increase in sapling density with > disturbance	Low to moderate increase in sapling density with < elk and > disturbance
Disturbance (Figure 5.2b)	Type 3 functional response with 2 equilibrium states. Declining herbivory rates at low aspen density	Major shift from low sapling density state to high sapling state at moderate elk densities.	Major shift from low to high sapling density aspen density and from single low to 2 state system	Potential major increase in sapling density with < elk and > disturbance
Climate Change (Figure 5.2 <i>b</i> )	As above	As above. Climatic fluctuations (e.g. periodic deep snows) could cause local elk density reductions, and shifts to high sapling density state	Disturbance, combined with climatic conditions that reduce elk herbivory, could allow aspen saplings to reach high density equilibrium	As above
Low elk herbivory (Figure 5.2 <i>c</i> , 5.2 <i>d</i> )	Type 2 functional response with increasing herbivory rates at low sapling density and single equilibrium state equilibrium, or Type 1 functional response with consistent herbivory rates and single equilibrium state	Aspen saplings persist only at low elk density	No effect at high elk densities, incremental increase at moderate and low elk densities	Low to moderate increase in sapling density with < elk and > disturbance

Table 5.1. Predictions from optional hypotheses for the type of functional response and effects of elk density and disturbance on aspen sapling density. See Figure 5.2 and text for detailed description of models.

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High herbivory with Type 3 functional response (Figure 5.2a). This pattern is predicted by the "High Herbivory" hypothesis for elk-aspen interaction. An equilibrium occurs at A where browsing rates decrease sufficiently to permit sapling survival. Elk regulate aspen saplings at a relatively low density, but aspen should persist indefinitely. At lower densities of saplings than  $N_A$ , elk reduce their per capita browsing rate by switching to other forage. Causes of prey-switching by elk might include the difficulty of finding sparse aspen in coniferous forests (Suzuki et al. 1999), or aspen saplings remaining at low densities may be unavailable for browsing in local refugia such as patches of deep snow.

High herbivory, disturbance and Type 3 functional response (Figure 5.2*b*). This pattern is predicted when disturbance factors such as fire remove overstory tree competition, and stimulate aspen suckering rates. The increase in sapling recruitment rates, relative to elk herbivory rates, results in two stable equilibria (Points A and C) with a boundary at B. At A, aspen sapling density remains low ( $N_A$ ) and is regulated by density-dependent elk herbivory. However, a factor that allows aspen sapling density to increase (e.g., fire or a series of deep snow winters that temporally reduce herbivory) would allow aspen densities to increase, escape the "predator pit" at boundary B, and move to a higher equilibrium point at C with high elk density and high aspen density ( $N_C$ ). This predation function is predicted by the "Disturbance" (Suzuki et al. 1999) and "Climate Change" (Romme et al. 1995) hypotheses for elk-aspen coexistence.

Low herbivory with Type 2 functional response (Figure 5.2c). This is the pattern predicted by the "Low-Herbivory Hypothesis" (e.g., Kay 1997a, Ripple and Larsen 2000). Elk depend primarily on other forage, but aspen saplings are preferred, consistently used forage. In this case, browsing rates vary inversely with aspen density. Provided sapling densities do not drop below a minimum threshold (B), aspen should survive across a range of densities (N<sub>B</sub> to N<sub>C</sub>). The range of sapling densities for aspen survival increases as elk abundance declines from Level 2 to Level 1, thus reducing the risk of extinction. However, if aspen sapling densities drop below N<sub>B</sub>, elk herbivory will drive aspen towards extinction.

Low herbivory with Type 1 functional response (Figure 5.2*d*). This case is similar to Figure 5.2*c*, except the browsing rate does not decrease with increased sapling density. Elk

exist primarily on other forage. They have no preference for aspen, but consume it in proportion to its availability. If the total response increases above Level 2, aspen extinction will rapidly occur. If it is instead reduced to Level 1, aspen equilibrium density would occur at C.

# Methods

Predictions from these models (Table 5.1) should be tested by observing prey recruitment and mortality at different prey productivity and predation (herbivory) levels (Taylor 1984, Boutin 1992, Schmitz and Sinclair 1997). For this study, I sampled aspen sapling density and browsing rates under a range of aspen sapling recruitment conditions (as influenced by disturbance and tree cover), and different elk density levels. I recognized that the analysis would ideally require that plant recruitment and herbivory rate should be measured in the same units, such as the percent of the population (e.g., Noy Meir 1975, Augustine et al. 1998), or per cent of total biomass produced and browsed (Figure 5.2). With similar measures, the relative positions of the recruitment and predation rate curves could be used to directly determine theoretical prey density at equilibrium (Pech et al. 1995, Sinclair and Pech 1996, Sinclair et al. 1998). Previous studies have measured aspen recruitment and herbivory offtake in terms of current annual growth in biomass of twigs (e.g., Basile 1979, Olmsted 1979). However, these volumetric measurements are complex, and thus infeasible for the large number of samples required by my study design. Instead, I approximated aspen production by measuring sapling density (Kay 1990), and herbivory with a visually-estimated browse index.

# Study areas and plot location

The experimental design was a two-way factorial (4 tree cover levels  $\times$  3 elk density levels) replicated in 3 areas for each elk density level. The nine sample areas were interspersed along 150 km of the Rocky Mountains eastslope in Alberta (Figure 5.3, Table 5.2). I selected study areas by compiling 1991 Parks Canada and Alberta Fish and Wildlife estimates of elk populations on winter ranges (White et al. 1995). Population

estimates were divided by the area of winter range <1800 m elevation to calculate elk density (White et al. 1995:21). Three winter range areas were selected for each of three elk density classes: low (<2 elk/km<sup>2</sup>), moderate (2 to 4 elk/km<sup>2</sup>), and high (>4 elk/km<sup>2</sup>). All study areas were in the montane ecoregion (Strong 1992), characterized by valley bottoms with low slope angles (<15°), with a cover of small grasslands interspersed with forests of Douglas-fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), and trembling aspen (Achuff and Corns 1982, Archibald et al. 1996, Beckingham et al. 1996). Common ungulate species are elk, white-tailed deer (*Odocoilius virginianus*), mule deer (*O. hemionus*) and moose (*Alces alces*).

Within each study area it was necessary to sample browsing rates and sapling density under a range of potential recruitment rate conditions (Taylor 1984). This was achieved by choosing different tree cover classes, which are a primary determinant of sapling recruitment rates (Peterson and Peterson 1992). Disturbances that reduce tree cover (e.g., fire or cutting) stimulate aspen recruitment, and dense tree stands suppress recruitment (DeByle and Winokur 1985). In each study area, I sampled 10 plots containing aspen in each of 4 tree cover classes for all species > 4m high. Cover classes were: 1) recently (<25 years) disturbed (>75% killed) by fire, windthrow, mountain pine beetle (*Dendroctonus ponderosae*), or mechanical cutting; 2) low tree density (<750 trees/ha, 3) moderate tree density (750 to 1500 trees/ha), and 4) high tree density (>1500 trees/ha). Aspen trees were included in tree density class estimations under the assumption that canopy domination by large aspen inhibits young aspen regeneration similarly to competition from balsam poplar (*Populus balsamifera*) or conifer species (DeByle and Winokur 1985, Peterson and Peterson 1992).

Plots were located by the following procedure. I took oblique aerial photographs of study areas in late September and early October when aspen leaves were turning colour. On the photographs, each study area was mapped into subareas (15 to 65 per area) of approximately 0.5 to 1 km<sup>2</sup> that contained visible aspen stands. Ten subareas were randomly selected for sampling in each study area. In the field, each selected subarea was traversed on foot, and a plot was subjectively selected in each of the low, moderate or high tree cover classes.



Figure 5.3. Study areas of elk-aspen functional response. From north to south, areas are: Willow Creek (WC), Athabasca-Jasper (AJ), North Saskatchewan (NS), Ya Ha Tinda (YH), Bow-mid (BM), Bow-Banff (BB), Kananaskis-Bow (KB), Eastslopes (ES), and Waterton Lakes (WL). See Table 2 for description of areas.

Study Area	Code	Description	Elk Density
Athabasca-Jasper townsite area	AJ	Jasper townsite area in Jasper National Park. Valley bottom from Prairie de la Vache east to Palisades Training Centre; 100-200 ha (5%) recently disturbed by forest thinning for fire fuel breaks	High: > 5 elk/km <sup>2</sup> of human habituated elk (Parks Canada 1998)
Bow-Banff townsite area	BB	Bow Valley in Banff National Park from Castle Junction east to park boundary. Highly human habituated elk, mostly non-migratory (Parks Canada 1999); <100 ha (<1%) recently disturbed by forest thinning, powerline maintenance	High: >5 elk/km <sup>2</sup> near Banff townsite (White et al. 1995, Paquet et al. 1996, Parks Canada 1999)
Ya Ha Tinda	ҮН	Ya Ha Tinda Ranch and Red Deer River valley from Eagle Pass west to Scotch Camp warden cabin; >800 ha (10%) recently disturbed by prescribed fire and logging cutblocks	High: >10 elk/ km <sup>2</sup> , rapid increase since 1983 (White et al. 1995, Morgantini 1995)
Bow-Mid	BM	Middle elevation areas of Bow watershed in Banff National Park outside of Banff townsite; >3000 ha (15%) recently disturbed by prescribed fire	Moderate: 2 to 4 elk/km <sup>2</sup> ; >50% recent decline in elk numbers with wolf recolonization (Paquet et al. 1996)
Kananaskis- Bow	KB	Bow Valley from Canmore to Exshaw, and Kananaskis Valley from Barrier Lake south to Evans Thomas Creek; 300-500 ha (<2%) recently disturbed by powerline maintenance and cutblocks	Moderate: 2 to 4 elk/km <sup>2</sup> (White et al. 1995)
North Saskatchewan	NS	North Saskatchewan River valley bottom near Kootenay Plains; < 100 ha (<1%) recently disturbed by highway right-of-way maintenance	Moderate: 2 to 4 elk km <sup>2</sup> (White et al. 1995), increasing in last 5 years (Parks Canada 1999)
Eastslopes-South	ES	Lower Kananaskis River, Morley First Nation, Jumping Pound, Elbow, Sheep, and Highwood valleys; >5,000 ha (20%) recently disturbed by cutblocks	Low: <2 elk/km <sup>2</sup> (White et al. 1995)
Willow Creek	WC	Snake Indian River valley from Shale Banks to Welborne blow down; 500-1000 ha (<5%) recently disturbed by wind blow down and prescribed fire	Low: <1 elk/km <sup>2</sup> after period of high wolf predation (Carbyn 1974) and deep snow winters (Dekker et al. 1995)
Waterton Lakes	WL	Waterton Lakes National Park: Blakiston Brook, Belly River; 2000-3000 ha (<10%) recently disturbed (1970- 1980) by mountain pine beetle infestation	Low: <1 elk/ km <sup>2</sup> in most areas (Van Tighem, Parks Canada, pers. comm.). Area of >5 elk/km <sup>2</sup> on adjacent lower winter range grassland area excluded from sampling

Table 5.2.	Description	of study a	reas for	functional	response	of elk-aspen	herbivory.
	<b>L</b>	•			-	L .	

Plots selected for sampling had the highest aspen regeneration (height <4 m) observed in the subarea for that tree cover class. When no plots were found for a tree cover class within a subarea, an adjacent subarea was chosen for sampling of that class. In all study areas, the disturbed tree cover class plots were opportunistically sampled in the largest disturbed areas found during sampling (Table 5.2). I did not sample aspen found on unique terrain features such as steep slopes (>20%), road cuts, or in boulder fields because these areas may be infrequently used by elk (Suzuki et al. 1999).

# Data collection

At each plot, a  $2 \times 30$  m belt transect was placed perpendicular to the slope across the area of densest aspen regeneration (<4 m height). Similar to Kay (1990, 1997b), each aspen stem in the transect was tallied by size class (0 to 1 m height, 1 to 2 m height, >2 m and <5 cm diameter at breast height (DBH), 5 to 10 cm DBH, 10 to 15 cm DBH, 15 to 20 cm DBH, and >20 cm) and as live or dead. Stems 0 to 1 and 1 to 2 m in height were recorded by browsing class (4 levels): <20% twigs browsed (BC1), 20 to 50% browsed (BC2), 50 to 80% browsed (BC3), and >80% browsed (BC4). Stems >2 m and <5 cm DBH were recorded by class (4 levels) of black, scarred bark caused by elk stripping bark from trees with their lower incisors (DeByle 1985a). Classes were: <20% stem barked (BC1), 20 to 50% barked (BC2), 50 to 80% barked (BC3), and >80% barked (BC4). I aged 1 to 2 aspen trees of each size class tallied in 115 plots in seven study areas by cutting disks from stems at 60 cm above the ground and counting annual growth rings. Tree disks were not collected in two areas (Waterton Lakes and North Saskatchewan) due to research permit conditions.

Tree cover was estimated by two methods. For relatively open stands (<1000 trees/ha), all live trees (>4 m height) in a  $4 \times 50$  m transect centred over the aspen belt transect were counted. For dense stands, I used the point quarter distance method (Mueller-Dombois and Ellenberg 1974) with sample points at the 5, 15, 25, 35, and 45 meter sample points on a 50 m transect centred over the aspen transect. For each tree tallied in both methods, I recorded species, DBH, height, height to live crown, and width of live crown.

Ungulate use was estimated by counting pellet groups (Neff 1968, Collins and Urness 1979). Two  $2 \times 200$  m pellet-group transects laid on diagonals across the slope from the aspen belt transect were used to record pellets on each sample plot. Transects were surveyed from April 15 to June 15, prior to herbaceous vegetation growth, when pellets deposited over winter were most visible. The dominant vegetation cover type along 50 m segments of the transects was recorded as: grass, aspen, mixedwood (conifer and deciduous), or conifer (lodgepole pine, Douglas-fir and spruce).

# Data analysis

I quantified (geometric mean and standard error) tree density (stems/ha for all species), basal areas (m<sup>2</sup>/ha for all species), and wildlife use (pellet groups/100 m<sup>2</sup>) by sample area. I developed a regression of tree age to DBH for comparisons of aspen age distributions between study areas. For predation (herbivory) response and factorial statistical analyses, I used the density of live aspen saplings, which is the combined density (stems/100 m<sup>2</sup>) of the tall sucker (1 to 2 m height) and sapling (>2 m height and <5 cm DBH) size classes. Although frequency count data typically follows a negative binomial distribution, simulations by White and Bennetts (1996) showed that analysis with ANOVA is relatively robust to violations of normality. In addition, ANOVA provided the increased power and efficiency of multi-factorial analyses (Zar 1996). I minimized the effects of violations of parametric assumptions (normal distribution and equal variance) by balancing sample sizes for groups (Underwood 1997), comparing results of alternative data transformations of sapling counts on normal probability plots (Zar 1996), and using the square root transformation ( $\sqrt{(count + .5)}$ ). I added 0.1 stem per 100 m<sup>2</sup> to plot aspen sapling density to eliminate zero values in logarithmic graph plots.

An overall index of browse utilization (B) for each plot was estimated by the midpoint of the browse index class weighted by the number of stems in each class with the equation:

B = ((.1\*BC1) + (.35\*BC2) + (.65\*BC3) + (.9\*BC4))/N

where BC1, BC2, BC3 and BC4 are the density of stems in the respective browse classes, and N is the total density of sapling stems. The overall browse utilization index is equivalent to the total predation response (Figure 5.1) and was estimated only from plots where elk pellet groups constituted >70% of the total for all ungulate species (n = 222). I graphed B index values against sapling density for 3 levels of aspen sapling density (< 5, 5 to 50, and >50 stems/100 m<sup>2</sup>) for the 3 elk use levels to plot the total predation response.

The general linear model (Underwood 1997) used to test for main canopy competition and herbivory effects, and interactions was:

$$D_{ecwn} = u + E_e + C_c + EC_{ec} + W(E)_{e(w)} + CW(E)_{ce(w)} + e_{n(ecw)}$$

where D is the square root transformation of aspen sapling density, E is elk density effect (3 levels), C is the tree cover effect (4 levels), EC is the interaction effect between elk density and tree cover, W(E) is the effect of different watershed study areas nested within elk density levels, and CW(E) is the interaction between watersheds and tree cover, nested in the elk density. I then used the total response and values from the factorial analysis to develop a model of elk herbivory as a function of elk pellet group and aspen stem density.

#### Results

Overall elk pellet group counts for plots (Figure 5.4) indicate that the relative elk density estimates of low, moderate, and high were valid for study areas. Counts had geometric means >2.8 groups/100 m<sup>2</sup> in the high elk density areas, and <1 group/100 m<sup>2</sup> in the low elk density areas.

Geometric mean pellet counts for tree cover types (Figure 5.5*a*) are the overall average, for all vegetation cover types, for the tree cover type class in the centre of the plot. These means showed generally similar counts for each elk density level, reflecting the averaging of vegetation and forest cover classes surrounding the plot. However, disturbed and high tree cover classes, particularly at low elk density levels, had lower pellet counts.



Figure 5.4. Plot geometric mean  $\pm$  SEM for elk pellet groups (counts/100 m<sup>2</sup> for two 2 x 200 m transects per plot) for study areas (n = 40 plots/study area). See Table 5.2 for study area codes.





A more site-specific pattern of pellet counts is available from individual 50 m segments of transects when grouped by cover type and elk density class (Figure 5.5b). The grass cover type had highest pellet counts, while aspen, mixed wood and conifer types had lower counts.

There was a consistent pattern of differences for the two measures of tree cover (basal area and tree density) between the four tree cover classes (Figure 5.6). These ranged from geometric mean basal areas of  $<1 \text{ m}^2$ /ha and tree densities of <100 stems/ha in recently disturbed sites to geometric mean basal areas of  $>30 \text{ m}^2$ /ha and tree densities >1000 stems/ha in stands classified as high forest cover.

The aspen sapling browse utilization index (Figure 5.7) showed a consistent pattern with elk density class. Saplings in high elk density areas were heavily browsed for all tree cover levels types (browse utilization index > 0.7). In contrast, saplings in low elk density areas were lightly browsed (index < 0.3) except for stems in low tree cover areas (index >0.3). The browsing utilization index had intermediate values ( $\equiv$ 0.5) for tree cover classes at moderate elk densities. The total herbivory response to increased aspen sapling density, as measured by the browse utilization index, decreased sharply with increased sapling density at all three elk densities (Figure 5.8). At low sapling densities, most aspen saplings were highly browsed, even at low elk densities. As stem density increased, the degree of browsing on individual stems declined markedly, even at moderate elk densities.

Factorial analysis (Table 5.3, Figure 5.9) revealed that aspen sapling density was dependent on the two main effects of elk density class and tree cover class. However, elk density class explained more of the variance in aspen sapling density than tree cover. An interaction effect between elk density and tree cover was also apparent, with highest sapling densities in disturbed plots with low elk density (Figure 5.9). In addition, there was a significant effect of study area and tree cover nested within elk density class, suggesting other sources of variance tied to individual study areas, and not explained by the three general elk density classes.



Figure 5.6. Geometric mean  $\pm$  SEM of (a) trees/ha and (b) basal area (m<sup>2</sup>/ha) for tree cover classes (n = 40 plots/group).



Figure 5.7. Mean  $\pm$  SEM of browse utilization index values for tree cover classes by elk density class (n = 30 plots/group).



Figure 5.8. Mean  $\pm$  SEM, and sample sizes (number of plots) of browse utilization index values for 3 levels of aspen sapling density by elk density class. Low aspen sapling density is <5 stems/100 m<sup>2</sup>, moderate is 5 to 50 stems/100 m<sup>2</sup>, and high is >50 stems/100 m<sup>2</sup>.

Source of variation	SS	df	MS	F-ratio	Р
Elk density	853	2	426	90.49	0.000
Tree cover	292	3	97	20.64	0.000
Elk density $\times$ tree cover	78	6	13	2.76	0.012
Study area within elk density	357	6	59	12.62	0.000
Study area within elk density $\times$	288	18	16	3.39	0.000
tree cover					
Error	1527	324	5		

Table 5.3. Results of the analyses of variance of the effects of elk density and tree cover on the density (square-root transformed) of aspen saplings (squared multiple R: 0.464).



Figure 5.9. Geometric mean and standard error of aspen sapling density for tree cover classes by elk density class (n = 30 plots/group).

Aspen age as a function of DBH was estimated by regression equation (Age (years) = 15.456 + 3.748 DBH (cm),  $F_{1,574} = 1432.7$ , P < 0.001,  $r^2 = 0.71$ ). Aspen tree (>4 m height) age distributions (Figure 5.10) had a consistent pattern. Low elk use study areas such as Willow Creek (WC) and Waterton Lakes (WL) had higher proportions of aspen trees in relatively young age classes (<50 years old) than areas with high elk densities such as Bow-Banff and Athabasca-Jasper. However, there was variation in aspen age distributions between areas, particularly within the moderate elk density class.

### Discussion

### Predation model evaluation

The high aspen herbivory, disturbance and climate hypotheses (Table 5.1) all predict a sigmoidal Type 3 functional response with decreased browsing rates at low and high aspen sapling density (Figure 5.2*a*, 5.2*b*). A low, but stable, abundance of saplings should be evident if any of these models is valid. If the disturbance hypothesis is valid, sapling densities could have 2 stable states (high or low abundance) at similar elk densities. Therefore, this hypothesis predicts a highly significant interaction effect should occur between elk density and disturbance that would result in a major increase in aspen sapling density when the upper equilibrium point (C in Figure 5.2*b*) occurs. In contrast, if the low herbivory hypothesis is applicable, a Type 1 or 2 functional response should be evident with consistent or increasing browsing rates at low aspen densities, and only one state where aspen saplings persist. This equilibrium range that maintains aspen saplings would only occur if elk densities were low (Level 1 in Figure 5.2*c*, 5.2*d*), because sapling recruitment rates are never high enough to provide a broad equilibrium range above Level 2. Further, for the low herbivory hypothesis, no major interaction effect between elk density and tree cover (e.g., disturbance) should occur.

Data from this study for the functional response, and the interaction and main effects of elk density and tree cover, all supported the low herbivory hypothesis (Table 5.1, Figure 5.2c). I discuss this evidence below.



Figure 5.10. Stand age distributions of aspen trees (>4 m height) for study areas. Codes are: Willow Creek (WC), Athabasca-Jasper (AJ), North Saskatchewan (NS), Ya Ha Tinda (YH), Bow-mid (BM), Bow-Banff (BB), Kananaskis-Bow (KB), Eastslopes (ES), and Waterton Lakes (WL).

### Functional response

The browse utilization index values as a function of aspen sapling density (Figure 5.8) follow an exponentially declining (depensatory) function at all elk densities. This must result from a Type 2 functional response (Figure 5.1) where elk consume a decreasing proportion of aspen with increasing aspen density. Type 2 responses are common in simple one-predator and one-prey species herbivory systems (Lundberg and Dannell 1990). In the multi-prey situation of this study, where numerous alternative plant forage species are readily available, the Type 2 response indicates that aspen is relatively high priority prey. Aspen will be used even at low sapling densities, and on the valley-bottom sites sampled, does not appear to have a refuge from predation. Analogous multi-prey systems are described for carnivores by Pech et al. (1995) and Sinclair et al. (1998), and for herbivores by Augustine and McNaughton (1998) and Augustine et al. 1998.

Suzuki et al. (1999:236) suggest that aspen saplings might persist in low densities in gaps created by small-scale disturbances in the canopy of mixed aspen/conifer forests that are tending, through succession, towards conifer dominance. However, I found that even though elk use tends to decrease as forest tree cover increases (Figure 5.5), browsing rates generally increase in these stands at moderate and high elk densities as elk search for increasingly sparse suckers and saplings (Figure 5.7). The high value of aspen as ungulate forage has been noted in other studies (e.g., Nelson and Leege 1982, Hobbs et al. 1982, Dannell et al. 1991). DeByle (1985a) described increased browsing rates when stem aspen densities are low. In Yellowstone National Park, Kay and Wagner (1996) found that ongoing high herbivory had reduced most aspen clones to low stem numbers of heavily browsed stems, and approximately one-third of aspen stands shown in early photographs had completely died out.

Two recent studies (Suzuki et al. 1999, Barnett 2001) described the persistence of aspen saplings on or near Rocky Mountain winter ranges with high elk density. However, these studies did not evaluate site-specific elk use or quantify the sapling abundance. Apparently sites with aspen sapling occurrence were limited areas of very steep slopes, or rocky terrain that are lightly used by elk (Suzuki et al. 1999). Aspen survival to tree-

height in these locations could be ecologically relevant to long-term persistence of aspen on adjacent valley-bottom winter ranges, but mechanisms remain undetermined.

The assumption of no numeric response by elk to increasing aspen density made in this study might be questioned as to how alternative numeric responses could interact with the total and functional responses. My study lies along a gradient of elk winter ranges dominated by stable grasslands in the south, and a more boreal-like environment in the north (Strong 1992). In boreal habitats, twigs and leaves from species such as aspen, willow (*Salix* spp.), rose (*Rosa* spp.), raspberry (*Rubus* spp.) and buffalo berry (*Shepherdia canadensis*) are important sources of elk forage (Rounds 1979; Hunt 1979; Gates and Hudson 1981, 1983; Woods 1991). However, if increased density of aspen does result in an increasing numeric response by elk (e.g., Type 2 with Y intercept), Messier (1995) demonstrated that an overall depensatory predation rate is still expected, similar to the results obtained with the Type 0 numeric response assumed here.

# Interaction and main effects of herbivory and tree cover

The linear interaction pattern between tree cover and herbivory levels (Figure 5.9) demonstrated that disturbance could regenerate increasingly higher densities of aspen saplings as elk density decreased. These results are most consistent with the Type 2 functional response where a single equilibrium range for prey (Figure 5.2c) occurs for any density of predators (Sinclair et al. 1998). Increased aspen sapling density through disturbance and decreased browsing rates at low elk density simply interact to incrementally broaden this equilibrium range (e.g., from Level 2 to Level 1 in Figure 5.2c). Under these conditions, it is unlikely that climate is a significant factor influencing aspen saplings, unless it facilitated increased carnivore predation which in turn caused a major, long-term reduction in elk numbers. Post et al. (1999) reported that the North Atlantic Oscillation caused increased snow depths, which favoured increased wolf kill rates of moose on Isle Royale, Michigan. Reduced moose density, in turn, was reflected in increased growth rates of balsam fir (*Abies balsamea*), the primary browse species in winter. However, Kiffney et al. 2001 found no statistically significant difference in

precipitation in southwestern British Columbia between El Nino and non-El Nino/La Nina years, and no significant trend in precipitation during the last 50 years.

Further, the interaction effect has lower, but still relatively high statistical significance (Table 5.3). Thus, it is unlikely that disturbance or climate alone could cause major shifts from a low-density sapling state to a high-density state at moderate or high elk density (e.g., Figure 5.2b). Instead, low-density sapling stands will likely continue to decline, even at moderate elk densities, and this may be accelerated by disturbances such as fire. Thus, these results agree with other studies of disturbance effects on aspen in areas of moderate or high elk density (>5 elk/km<sup>2</sup>) reviewed by White et al. (1998a). Fire failed to create aspen stands with stems >1 m near Jackson Hole Wyoming (Bartos et al. 1994) where elk pellet counts averaged approximately 10 groups/100 m<sup>2</sup> (Basile 1979). Similarly, aspen failed to successfully produce new stems >1 m high in Yellowstone National Park after the large 1988 wild fires (Romme et al. 1995), or after large (>500 ha) prescribed fires in Banff National Park (Kay et al. 1999). In Elk Island National Park, Alberta, Bork et al. (1997) found that prescribed fires did not stimulate regeneration of small trees (<5 cm DBH) in areas of high ungulate density. Olmsted (1979) and Bartos et al. (1994) predicted that fire might even accelerate the decline of aspen in areas of high elk density by killing the residual older trees that are above browsing height. Ongoing high elk utilization of sprouting suckers would then eventually reduce the biomass of the surviving root system. Post-burn monitoring in Yellowstone and Banff national parks (Kay and Wagner 1996, White et al. 1998a) located declining densities of shrub aspen and dead aspen clones that indicated that fire, in combination with long-term high herbivory, could eliminate aspen stands.

As predicted by the low herbivory hypothesis (Table 5.1), elk density was the factor best correlated with aspen sapling density (Table 5.3). Although tree cover was also a significant predictor, it explained a smaller portion of the variation in sapling density and was most important only at low elk density (Figure 5.9).

The important main effect of elk herbivory impact on Rocky Mountain aspen is well documented (e.g., Packard 1942, Cowan 1947, Olmsted 1979, Kay 1990, White et al 1998a). However, my study specifically measured an index of elk habitat use (pellet group

counts) to quantify elk densities, and also measured an index of browse use over a range of these densities. In Alberta's Rocky Mountains, aspen saplings were only abundant at low elk densities (Figure 5.9) where pellet group counts averaged <1 per 100 m<sup>2</sup> (Figures 5.4 and 5.5) and the browse utilization was <0. 4 (Figure 5.7). At moderate (1 to 3 groups/100 m<sup>2</sup>), and high (>3 groups/100 m<sup>2</sup>) elk densities, the browse index was >0.4, and the abundance of saplings decreased exponentially (Figure 5.9).

Similarly, the main effect of tree cover on the abundance of aspen regeneration, most apparent at low elk density (Figure 5.9), is also well known (DeByle and Winokur 1985, Peterson and Peterson 1992). Recently disturbed and lightly browsed stands may have over 1000 stems (< 1 m height)/100 m<sup>2</sup> that rapidly thin to 90 stems/100 m<sup>2</sup> by 17 years after disturbance (from Canadian studies reviewed by Peterson and Peterson 1992). The relatively high density of saplings at moderate and high tree cover and low elk density shown in Figure 5.9 may have resulted from the bias created by sampling the densest patches of sapling regeneration in subareas (see Methods section).

Romme et al. (1995) concluded that the peak of a bell-shaped distribution of aspen tree ages in Yellowstone National Park corresponds to an episodic event of interacting climatic, disturbance, and herbivory conditions. For my study areas, the main effect of long-term, high browsing rates (Figure 5.7) which causes low survivorship of aspen saplings in areas of high elk densities consistently (Figure 5.8) resulted in bellshaped, older stand age distributions. These distributions are different from the dominantly young-aged distributions occurring in low-density elk areas (Figure 5.10). It is not necessary to invoke a more complex interaction hypothesis for this contrast between high and low elk density areas. However, the variable patterns of stand ages in moderate elk density areas likely results from transitional herbivory conditions between low and high elk density. For example, the Bow-mid (BM) area has only recently had a major reduction in elk density due to wolf predation whereas the North Saskatchewan (NS) area historically had low elk densities which are now increasing (Table 5.2).

# Elk habitat use and the functional response

Aspen stands in the Canadian Rockies often lie in the ecotone between small grassland areas (<50 ha) and adjacent mixedwood and conifer types (Achuff and Corns 1982). Spring pellet counts provide an index of relative elk use of these areas during the previous fall and winter seasons. The pattern of higher elk use in grasslands and open areas relative to nearby forests (Figure 5.5b) is a characteristic trait of this herbivore in most locations (Geist 1982:224). High use of areas dominated by grass and short shrub cover has been reported for numerous Rocky Mountain areas including northern British Columbia (Peck and Peek 1991), Alberta national parks (Cowan 1947, Flook 1964), the Rocky Mountains in Montana (Jenkins and Wright 1988), Yellowstone National Park (Houston 1982, Coughenour and Singer 1996), and areas in Utah (Collins and Urness 1979). I found pellet group counts in high elk use areas that were similar to Holroyd and Van Tighem's (1983: 412) results for the montane ecoregion in Banff and Jasper national parks. Their study reported means of 10 to 15 groups/100  $m^2$  for grassland types compared to 2 to 4 groups/100 m<sup>2</sup> for forest types. However, highest use of open cover areas is not ubiquitous in the Rocky Mountains. East of the continental divide in Montana, Lyon and Jensen (1980) reported higher pellet counts in forested habitats (1.45 groups/100 m<sup>2</sup>) than in adjacent clearcuts (0.91 groups/100 m<sup>2</sup>). They attribute the reversed habitat use pattern to elk security requirements in human rifle-hunting areas near roads.

For herbivores, the Type 2 response of reduced proportional use of forage species at increasing forage density could be attributed to a complex set of interactions between searching, biting, cropping and chewing activities (Spalinger and Hobbs 1992). Results from this study, though, suggest the hypothesis that risk-sensitive habitat use patterns by elk may be important for aspen persistence (White et al. 1998a, Ripple and Larsen 2000). At low elk densities, elk pellet group counts were very low (<0.5 groups/100 m<sup>2</sup>) in recently disturbed areas with dense aspen sapling thickets (>50 stems/ 100 m<sup>2</sup>, Figure 5.9) compared with other tree cover classes (Figure 5.5*a*). In the Waterton Lakes and Willow Creek areas, disturbed stands also contained numerous downed logs (C. White personal observations), which made movement difficult. In contrast, elk pellet counts were highest in plots classed as having low tree cover (Figure 5.5*a*), or in pellet transects classed as grassland (Figure 5.5*b*). Higher elk use in winter of open vegetation cover areas could be linked to high intake rates of quality forage when open areas have low snow-depths compared to forests (Gates and Hudson 1981, 1983). Furthermore, elk may pursue predation-sensitive foraging strategies, utilizing open vegetation areas where they can forage in groups with higher individual probabilities of successful detection and flight from predators (Huggard 1993a, 1993b; Bender and Hauffler 1996).

These observations suggest that changing elk distribution patterns between adjacent habitat patches may be partially the cause of the Type 2 functional response reported here. Elk use patterns shift over time within a relatively small area (e.g., <1 ha) as elk respond to patch-level changes in aspen sapling density, forest cover, or amount of deadfall (Ripple and Larsen 2000). Possibly, herbivore foraging patterns at the habitat patch level, rather than at the grain level (e.g., aspen ramet) determine the functional response, in contrast to alternative, grain-scale models (Lundberg and Dannell 1990, Spalinger and Hobbs 1992, Fryxell and Doucet 1993, Kie 1999). This hypothesis requires further testing because elk foraging patterns may be critical for long-term aspen persistence.

# A preliminary model of elk herbivory and disturbance effects

A Type 2 functional response is consistent with predictions of the low herbivory hypothesis for long-term coexistence of elk and aspen. The low herbivory hypothesis is supported by numerous lines of evidence including archaeological data, historical journal analysis, repeat photography, fire-scar dendrochronology, fire effects, aspen stand analysis and wildlife exclosure data (Kay 1990, 1997a; Baker et al. 1997; White et al. 1998a,b; Kay et al. 1999; Ripple and Larsen 2000). Recent studies of recolonizing wolves (Paquet et al. 1996, Kunkel 1997) have also concluded that wolves, in combination with other predators and sources of mortality, could dramatically reduce elk densities in the Rocky Mountains. The role of predators in limiting abundance of vertebrate herbivores may be a general factor in the persistence of many ecological communities (Krebs et al. 1999). Further, long-term community stability and persistence likely result from not only the numeric results of

predation, but also from the behavior patterns of individual organisms interacting at multitrophic levels (Fryxell and Lundberg 1998).

Figure 5.11 synthesizes disturbance and herbivory interactions with trembling aspen. To develop this model, I used 222 plots where elk pellets were >70% of the total plot counts for all ungulate species. I fitted a negative exponential curve, which results from the Type 2 functional response, to the per capita (pellet group) level of browsing (Bcap) as a function of aspen sapling density (a), yielding the equation:

Bcap =  $0.211 e^{-0.002a}$  (r<sup>2</sup> = .56)

I then solved the equation for pellet group and aspen sapling densities that resulted in a browse index isoline of 0.3, assuming a linear increase in browsing rate with elk density. The 0.3 browse isoline approximated the twig-browsing threshold of 30% of current annual growth that Olmsted (1979) estimated was critical for successfully regenerating aspen in Rocky Mountain National Park. For example, in northwestern Wyoming, elk browsing of 43% of current annual growth (Basile 1979) resulted in the demise of all aspen suckers in recently burned areas (Bartos et al. 1994).

The 0.3 isoline is plotted in Figure 5.11 in combination with the 95% confidence interval ellipses of the geometric means of elk pellet group and aspen sapling density observations for each of the 9 study areas. Areas to the left of the 0.3 isoline in Figure 5.11 have abundant aspen saplings with low browsing. Those to the right have few saplings that are heavily browsed.

This model captures the salient points of elk and aspen interaction in the Canadian Rockies. Aspen's response to browsing does not follow the traditional, Clementsian, rangemanagement model of herbivore effects on plants (Stoddart et al. 1975) which predicts a monotonic herbivory effect where incremental changes in herbivore density result in continuous, incremental changes in vegetation (Ellison 1960). Instead, aspen's response to browsing may follow more complex state-and-transition type models (e.g., Noy-Meir 1975, Walker et al. 1981, Westoby et al. 1989, Dublin et al. 1990, Augustine et al. 1998).



Figure 5.11. A state and transition model of aspen sapling density as a function of elk density (as indexed by pellet group counts), showing confidence interval ellipses (P = 0.95) for geometric means of observations from study areas (n = 40/study area). Study areas near A have abundant aspen saplings. Areas near C have no aspen saplings. Herbivory-driven transitions between states occur near the 0.3 browse index isoline, and are shown by solid arrows at B and D. Potential effects of forest disturbance (e.g., fire) within each state are shown with open arrows.

Aspen stands have two general alternative states— abundant saplings (around A in Figure 5.11), and no saplings (around C). The no sapling state could eventually lead to aspen clone death if stem survival past the sucker stage is required to maintain viable root systems (Sheppherd and Smith 1993), and as older trees die and are not replaced. The transitions (at B and D) between states have different pathways and mechanisms depending on the direction of change. At high aspen sapling density in state A, elk density can be relatively high (2 to 3 pellet groups/100 m<sup>2</sup>) with aspen sapling survival because the per capita elk foraging rate is lower in denser sapling stands. The transition towards no aspen saplings probably occurs around B at >3 pellet groups/100  $m^2$ . Herd sizes are larger and elk, that are less predation-sensitive and increasingly competitive for food, forage more frequently in aspen stands. North Saskatchewan (NS) area aspen stands were likely transitional during this study due to recently increasing elk densities (Table 5.2). Ya Ha Tinda (YH) stands also appeared to have also recently shifted states (Figure 5.11) due to a rapidly increasing elk population since 1983 (Morgantini 1995), as numerous dead or heavily browsed saplings were still visible in this area. At low aspen sapling densities, per capita elk foraging rates on suckers and saplings are high (Figure 5.8). Elk density must be very low (indexed as <1 pellet group/100 m<sup>2</sup>) for the browse utilization to be low enough for aspen to cross the transition at D towards abundant aspen saplings. At this density, elk are foraging in small herds, and individuals are likely highly sensitive to predation. Forage is relatively abundant in grasslands, and elk may not even search for food inside remnant aspen stands.

The diverse pattern of aspen sapling density between study areas near the 0.3 browse index isoline explains the significant statistical effects of study areas nested within elk density levels (Table 5.3). Further, the apparently different elk density at which aspen clones decline (B in Figure 5.11) versus when they recover (D) would explain the failure of aspen to reach tree size when elk populations are reduced to moderately low numbers. For example, once aspen stands were browsed to low densities in Yellowstone National Park, even a relatively major elk reduction program in the 1960s did not allow aspen to outgrow herbivores (Houston 1982, Huff and Varley 1999). Similarly, elk culling programs in Banff National Park between 1940 and 1970 (Woods 1991) and high rates of highway mortality

until 1985 (Woods 1990) reduced elk to relatively low densities (Chapter 4), but did not result in a substantial number of aspen reaching tree size (Figure 5.10).

The model predicts that disturbances such as fire could have diverse outcomes. depending on aspen sapling and elk density. At low elk density, disturbance maintains dense aspen through two mechanisms. First, apically-dominant aspen trees are top-killed which stimulates prolific suckering and development of dense sapling thickets (DeByle and Winokur 1985, Peterson and Peterson 1992). Secondly, elk use declines in recentlydisturbed, dense sapling stands (Figure 5.5a) which reduces browsing rates (Figure 5.7), further maintaining dense aspen recruitment. Reduced elk use will be even more pronounced if disturbance causes many downed logs similar to conditions I observed at Willow Creek (WC) and Waterton Lakes (WL), and Ripple and Larsen (2001) studied in Yellowstone National Park. In the low density aspen sapling state (around Point C in Figure 5.11) disturbance will have the opposite effect. Disturbance reduces tree cover, the more open cover conditions favour increased elk use, and elk browse off all young aspen suckers before they reach sapling size. For example, recolonizing wolves recently reduced elk density in Banff National Park (Paquet et al. 1996) from levels similar to Banff townsite (BB) to current levels observed in the mid Bow valley (BM) (Figure 5.11). However, after 50 years of high herbivory (Table 5.2), aspen stem densities were low in the BM area, and four large prescribed burns (areas of 500 to 1000 ha) failed to create dense sapling stands. even though elk density was relatively low.

In the absence of disturbance, some individual aspen stands may self-thin (DeByle and Winokur 1985) towards a condition of widely-spaced mature stems and fewer saplings (<20 saplings /100 m<sup>2</sup>, Figure 5.9). These stands, which were previously relatively resistant to herbivory, could be browsed more heavily when elk pellet groups are >1 group/100 m<sup>2</sup>.

A prediction of the low-herbivory model described here is that disturbance may also play an important role in redistributing elk. In this study, the grassland cover type was the most highly used by elk at all density levels (Figure 5.5). Grasslands and shrublands currently cover <10% of most study areas (Achuff and Corns 1982, Achuff et al. 1996). If disturbance increases the area of grassland, and predators limit the numeric response of elk (e.g., more grassland does not result in more elk), existing elk numbers should, to some degree, redistribute themselves across the increased area of preferred grassland habitat. Elk density would then decrease in areas of less preferred habitat (e.g., aspen, mixed wood and conifer types). The importance of disturbance in maintaining low forest cover areas is exemplified by data from the Athabasca River valley area of Jasper National Park (AJ study area in Figure 5.3), where reduced fire occurrence (Tande 1979) has increased coniferous forest cover. Through comparison of 1915 and 1997 photographs, Rhemtulla (1999:48) measured a 50% decline in the area of grassland and herb cover types, and a 64% decline in shrubland area. The magnitude of the predicted elk redistribution by forest disturbance would result from complex interactions between predators, elk, and vegetation cover types. These processes remain poorly understood and depend on scale of disturbance. For example, when disturbed areas are relatively small, ungulates may move from adjacent undisturbed areas into the disturbed area, and inhibit aspen regeneration (Basile 1979, Bork et al. 1997).

# **Conclusions and Research Needs**

Analysis of the functional response of elk herbivory to aspen sapling density, and of two main factors important to aspen density (tree cover and elk density level) support the low herbivory model for the long-term persistence of elk and aspen in the Canadian Rockies. The low herbivory model predicts that aspen historically persisted in the montane ecoregion because elk were limited to low numbers, presumably by humans and carnivore predation, and these areas were burned frequently, often through human ignitions (Kay 1990, 1998; White et al. 1998a). In some areas, reduction of predators and human hunting, elk habituation to humans, and fire control have provided conditions for elk numbers to increase while their preferred grassland habitat has been decreasing (White et al. 1994, 1998a, Kay et al. 1999, Parks Canada 1999). Increasing elk herbivory results in a relatively rapid transition from a regenerating aspen state to a declining state, where few stems survive beyond the sapling age class. In this state, high herbivory levels combined with disturbances such as fire will not create increased densities of young aspen, and may even kill long-lived aspen clones (Kay and Wagner 1996, White et al. 1998a). Continued high browsing rates maintain aspen stands in an open state that further encourages elk use. Restoration to the

regenerating aspen state may require low densities of risk-sensitive elk that avoid foraging in developing thickets of aspen regeneration (White et al. 1998a, Ripple and Larsen 2000).

Due to the intensifying human land use in the Rocky Mountains, it may not be possible for recolonizing wolves (Paquet et al. 1996, Kunkel 1997), in combination with other non-human predators, to reduce elk populations in many areas to the historic low densities necessary for long-term aspen persistence (White et al. 1998a). Where biodiversity maintenance is a land management objective, conservation of aspen will increasingly require the prediction of the effects of predation (in this case herbivory) on declining prey populations (Sinclair et al. 1998). The issue will be made more complex in many parks and wilderness areas by programs to maintain long-term forest disturbance regimes (e.g., fire, insects and disease) to achieve "ecological process", "ecological integrity", or "ecological baseline" management objectives (Parks Canada 1997, Arcese and Sinclair 1997, Boyce 1998, Huff and Varley 1999). For example, prescribed burning to maintain long-term ecological conditions (Morgan et al. 1994) in areas of high elk density will likely only accelerate the demise of aspen (Bartos et al. 1994). In many national park areas, aspen stand fencing, and averse conditioning and translocation programs for elk may be an important option to achieve biodiversity management objectives (White et al. 1998a, Parks Canada 1999).

A major limitation in this study was that the measures used for aspen recruitment (sapling density), and mortality (the browsing index) are not directly comparable. Thus more complex analyses of predation (e.g., Sinclair et al. 1998) in general, and herbivory processes (e.g., Noy Meir 1975, Augustine et al. 1998) specifically, were not possible. Future research should explore easily measured, but comparable indicators of aspen recruitment and browsing. One option may be to quantify the density of aspen stems by browsing class at a fine resolution of stem heights and browsing classes around the 1m height class.

The Type 2 functional response for elk herbivory on aspen reported here may result from predation sensitive foraging that governs elk browsing rates at the habitat patch, not the individual plant scale (White et al. 1998a, Ripple and Larsen 2000). Understanding the functional response of elk requires additional research on elk movement, group size, and
vigilance behaviour patterns while foraging in various aspen stem densities, distributions of cover types, and with different risk levels and types of predation (e.g., wolves, cougars, humans, or bears (*Ursus* spp.)).

Finally, most studies of aspen herbivory are short-term. Given that longevity of aspen clones may exceed thousands of years (Mitton and Grant 1996), mechanisms for aspen long-term persistence over a wide range of herbivory, climate, and disturbance conditions should be deduced, and appropriate research conducted. For example, persistence of multi-aged aspen stems on steep, rocky slopes could, through undetermined mechanisms, be important to the periodic regeneration of aspen clones on adjacent valley-bottom ungulate winter ranges. If these aspen stands are included in analyses (e.g., Suzuki et al. 1999), the functional response of elk-aspen herbivory will likely follow a Type 3 pattern, with a more positive prognosis for long-term persistence of montane aspen stands.

# CHAPTER 6. PREDATION RISK AND ELK-ASPEN FORAGING PATTERNS

## Introduction

Trembling aspen (*Populus tremuloides*) is a characteristic species for low elevation, montane ecoregions in Rocky Mountain national parks (Achuff et al. 1996, White et al. 1998a). Aspen stands are typically long-lived clones, usually regenerated by frequent fires (Mitton and Grant 1996, Kay 1997a). In the Rocky Mountains, aspen communities are second only to riparian zones for species richness (DeByle 1985a, Finch and Ruggerio 1993). Aspen stands historically had a range of age and size classes (Gruell 1979, Houston 1982). However, since the late 1800s to 1930s (depending on the location), new aspen stems have rarely growns to heights >1 m on elk (*Cervus elaphus*) winter ranges in several national parks and wildlife refuges (Packard 1942, Cowan 1947, White et al. 1998a) including Yellowstone National Park (Houston 1982, Kay 1990, Romme et al. 1995), near Jackson Hole, Wyoming (Gruell 1980, Boyce 1989), in Rocky Mountain National Park, Colorado (Olmsted 1979, Baker et al. 1997), Banff and Jasper national parks in Alberta (Kay et al. 1999), and Yoho and Kootenay national parks in British Columbia (Kay 1997b).

The factors responsible for aspen decline remain controversial (Kay 1997a, Huff and Varley 1999) but there are three broad theories for long-term aspen condition (White et al. 1998a): 1) Heavily-browsed aspen stands persisted under intense herbivory by abundant, food-regulated elk (Cole 1971, Houston 1982). This is termed ecological carrying capacity (Caughley 1976, 1979). The current decline of aspen is simply a return to long-term conditions as elk populations recover from over-hunting by humans during the late 1800s. Episodic events such as a combination of cool-moist climate and fire could result in pulses of aspen stems periodically reaching tree size (Romme et al. 1995). 2) Aspen was historically vigorous, lightly browsed, and coexisted with moderate to high densities of elk, but has recently degenerated due to the combination of herbivory, fire suppression and possibly climate change (Loope and Gruell 1973; Gruell 1979, 1980; Houston 1982). 3) Aspen persisted under conditions of low elk density and herbivory (Packard 1942, Cowan 1947, Olmsted 1979), maintained by intense predation on elk from humans, wolves, and other carnivores (Kay 1990, 1998; White et al. 1998a,b).

Analysis of aspen abundance, fire effects, and historical and current elk distribution patterns in Rocky Mountain national parks (Kay 1990, White et al. 1998a, Ripple and Larsen 2000) provided support for hypothesis 3— recent (since c.1900) reductions of predation rates on elk have resulted in increased elk herbivory on aspen. If this hypothesis is valid, predators could influence the elk-aspen herbivory interaction in 2 ways. First, the lethal effect of killing elk thus reducing elk density and herbivory. Second, the nonlethal effects where predation risk alters elk behaviour in ways that reduce herbivory on aspen (see Figure 1.1, Chapter 1). Direct effects on aspen due to general elk density and browsing levels are significant (Olmsted 1979, Kay 1990, White et al. 1998a, Chapter 5). However, nonlethal consequences of predation risk are also important influences on animal foraging behaviors (Lima and Dill 1990, Lima 1998, Kie 1999). After reviewing historical conditions in Yellowstone National Park, Ripple and Larsen (2000) hypothesized that elk behavioral responses to wolves could have influenced aspen herbivory levels in riparian areas of Yellowstone National Park.

In this study, my objective was to evaluate two possible effects of predation risk on elk foraging patterns on aspen during winter (October through March): 1) Effects of travel routes used by predators (humans and wolves) on elk habitat use; and 2) Effects of aspen stand structure (thicket versus open-grown) and predation or hunting risk on elk foraging behavior. I test the general hypothesis that these nonlethal effects are important determinants of aspen condition.

### Theory and Predictions

Plants and large mammalian herbivores have two-way interactions (Noy-Meir 1975, Caughley 1976, Schmitz and Sinclair 1997). Plants provide food, shelter and cover for herbivores and their predators. Herbivores alter plants or their habitats directly by feeding and trampling on plant parts, and indirectly by nutrient additions through defecation and urination (Hobbs 1996, Augustine and McNaughton 1998).

# Predation theory

Elk browsing rates on aspen appear to increase with decreasing stem density (Debyle 1985a, 1985b; Kay and Wagner 1994; Chapter 5). In predation theory, this is described as a Type 2 functional predation response (Holling 1959, Taylor 1984). Type 2 functional responses are common in simple one predator-one prey herbivory systems (Lundberg and Dannell 1990). However, in the multi-prey, elk-aspen situation, where numerous alternative plant forage species are readily available, the Type 2 response indicates that aspen is highly preferred by elk. High priority prey will be used even at low densities, and may have few refuges from predation (Pech et al. 1995, Sinclair et al. 1998, Augustine and McNaughton 1998). The high value of aspen as ungulate forage has been noted in other studies (e.g., Nelson and Leege 1982, Hobbs et al. 1982, Dannell et al. 1991). DeByle (1985b) described increased browsing rates when stem aspen densities are low. In Yellowstone National Park, Kay and Wagner (1994) found that ongoing high herbivory had reduced most aspen clones to low numbers of heavily browsed stems, and for approximately one-third of aspen stands shown in early photographs, both the stems and roots appeared to have completely died out.

Olmsted (1979) estimated that the twig browsing threshold between viable and declining aspen stands occurred when approximately 30% of current annual growth was browsed. Theoretically, the Type 2 functional response will cause this threshold to be a curved isoline for a range of aspen and elk densities (see Figure 5.11, Chapter 5). At high aspen stem densities, per capita elk twig consumption declines, and aspen can sustain a higher density of elk. The curvilinear response could result in elk-aspen herbivory being approximated by a state-and-transition type model (e.g., Noy-Meir 1975, Walker et al. 1981, Westoby et al. 1989). Aspen would have two general alternative states (Chapter 5)— dense sapling (stems 2 to 6 m height) thickets (around A in Figure 5.11), and declining aspen stands with no saplings (around C). The transitions (at B and D) between states could be rapid, but have different pathways and mechanisms depending on the direction of change. When densities of aspen saplings are high (A), elk density could be moderate (e.g., 1 to 3 elk/km<sup>2</sup>, White 1998a) with aspen sapling survival because the per capita elk foraging rate

is lower in denser sapling stands. The transition towards declining aspen stands with no aspen saplings probably occurs around B at 3 to 5 elk/km<sup>2</sup>, or 2 to 3 elk pellet groups/100 m<sup>2</sup>. In declining aspen stands at C, per capita elk foraging rates on suckers and saplings would be high (DeByle 1985a,b). Elk densities might have to be very low (e.g., <1 elk/km<sup>2</sup> or < 1 pellet group/100 m<sup>2</sup>) for stands to cross the transition at D towards more abundant aspen saplings (White et al 1998a, Chapter 5).

A Type 2 response could be attributed to the limitations imposed by handling time (Holling 1959), which for herbivores is a complex set of interactions between the competing activities of searching, biting, cropping and chewing (Spalinger and Hobbs 1992). Alternatively, aspen could be regarded as a secondary prey taken at a constant number as "bycatch" (Sinclair et al. 1998). A third explanation is reduced herbivore foraging rates when higher vegetation density increases predation risk, and the herbivore avoids dense vegetation (Fritz 1992, Hare 1992).

#### **Risk sensitive foraging**

Three-level trophic communities (predators-herbivores-plants) are influenced by multi-way interactions (Price et al. 1980, Hunter and Price 1992, Fryxell and Lundberg 1998, Krebs et al. 1999) that may change herbivore abundance or behavior, and hence regulate community structure (Hairston et al. 1960). Predation-sensitive foraging models are based on trade-offs between the benefits of energy intake and the costs of a shortened reproductive life due to predation (Sih 1987, Lima and Dill 1990, Lima 1998). Successful herbivores should utilize their environments in ways that balance safety with feeding. In situations where predation risk is low, animals should forage in high-resource habitats where energy intake is maximized. If predation risk is high in these habitats, however, safer locations with less forage availability may be used. In situations where low-resource habitats are risky, animals should concentrate in better habitats until resources are greatly depleted (Fryxell and Lundberg 1998). Where 3-level trophic systems have co-evolved, development of plant structures that increase the risk of predation on herbivores, thus providing "enemy-free space" with low herbivory, could increase plant fitness (Price et al. 1980, Jeffries and Lawton 1984, Fritz 1992).

# Elk and predator behavior patterns

Previous research provides several areas of knowledge for potential elk-aspen foraging patterns under predation risk. First, studies of elk habitat use in the Rocky Mountains report a general cover type preference of grassland > aspen > conifer (Collins and Urness 1979, Houston 1982, Holroyd and Van Tighem 1983, Chapter 5). Numerous studies rank aspen as a highly favored elk forage species (Nelson and Leege 1982). Aspen twigs, leaves and bark have relatively high concentrations of important nutrients (Jelinski and Fisher 1991), and at northern latitudes they are a valuable food source for elk, particularly during winter (Hunt 1979, Rounds 1979). Second, wolves (Canis lupus) and humans, two of elk's dominant predators (Cowan 1947, Huggard 1993a, Kay 1994), have consistent travel corridors in the Rocky Mountains. Both species usually follow valley bottom trails or lightly used roads, and in winter may utilize ice-covered streams (Carbyn 1974, Huggard 1993a, Paquet et al. 1996, Kunkel 1997). Wolves prefer trails with snow depths <20 cm (Huggard 1993c), and often follow routes packed or plowed by humans (Paquet et al. 1996). Third, in areas with low herbivory, recently disturbed aspen stands and the edges of older stands often have dense patches (<1 m spacing) of young stems (DeByle 1985a, Shepperd and Fairweather 1994). These thickets could provide cover for stalking carnivores such as cougar (Felis concolor, Kunkel et al. 1999), and impede elk escape if predator attack does occur (e.g., Lima 1992). Finally, an important elk defense against predation may be group foraging in open areas where stalking predators such as cougars are more detectable (Kunkel et al. 1999), and elk have running room to escape (Geist 1982). Also, in the Rocky Mountains, snow depths are often lower in wind-swept open areas which increases elk's ability to forage (Skovlin 1982, Lyon and Ward 1982) and escape predation (Huggard 1993c).

These previous observations suggest that patterns of elk and predator foraging could occur in spatially-nested scales (Senft et al. 1987, Bailey et al. 1996), which for this study I characterized as landscapes, corridors, and patches (Figure 6.1). At a macro-scale (>10 km<sup>2</sup>), human land-use structures elk habitats into high predation risk and low predation risk landscapes. High-risk landscapes could have wolves and human hunters. A low risk landscape could be a busy national park where elk are unhunted and predators are few such as the Bow Valley in Banff National Park, Alberta, or Rocky Mountain National Park in Colorado (White et al. 1998a). The landscape level defines general elk population densities and behavior patterns. At the meso-scale corridor level (1 to  $10 \text{ km}^2$ ), trails, roads, and streams provide corridors for human and predator travel. Depending on the rates of human hunting and predator control, elk and predators may either be attracted to or avoid corridors near these travel routes (Shultz and Bailey 1978, Lyon 1979, Dekker et al. 1995, Ripple and Larsen 2000). At the micro-scale (0.01 to 1 km<sup>2</sup>) patch level, macro- and meso-scale phenomena determine differential elk foraging strategies within patches. For this study, these patch types include grass, aspen and conifer cover types, or dense aspen thickets versus open stands.

#### Predictions on effects of human and predator travel routes

Given predator travel patterns, I predicted that in high predation landscapes (Figure 6.1), elk will trade-off food availability for safety, and forage relatively less in corridors next to trails used by wolves and humans than at distances further from trails (Table 6.1). For example, in studies of human-hunted elk, significant reduction in elk use (>60%) was found up to at least 500 meters from roads in Montana (Lyon 1979), and within 200 meters from roads in Colorado (Rost and Bailey 1979). In contrast, in low predation risk landscapes, elk are often unhunted and human-habituated (White et al. 1998a). They should be attracted to corridors next to busy roads avoided by wolves (Dekker et al. 1995, Paquet et al. 1996). The differential effect of trails or roads on elk use should be evident as an interaction (Table 6.1) between the effects of landscape type (high or low risk), and distance from road or trail (close, moderate, or far).



Figure 6.1. A spatial model of elk-aspen distribution patterns at 3 scales: macro-scale (high and low predation risk landscapes), meso-scale corridors (distance from road or trails), and micro-scale (aspen stand habitat patches). The stylized locations of the predation risk transects used in this study are shown with dotted lines.

At the patch level, nested within corridors, I expected a response of elk use to interactions between region, distance from road or trail, and cover type (Table 6.1). As risk increases, elk use of grasslands which are most preferred by elk and could offer the safest foraging areas, should increase while low resource-value conifer habitats should most rapidly be abandoned (Houtman and Dill 1998, Fryxell and Lundberg 1998). Aspen habitats, with intermediate value, should have intermediate trends.

#### Predictions on effects of aspen stand structure

At the micro-scale level, elk use of aspen patches in comparison to the surrounding matrix of grassland can be viewed as an integrator of local habitat preference, competition, and predation risk (Brown 1988). In landscapes with high predation risk, low elk density, and abundant forage in grasslands (A in Figure 5.11, Chapter 5), I predicted that dense aspen sapling thickets, which could provide cover for predators, would rarely be entered by risk-sensitive elk (Table 6.2). Under low browsing pressure, thickets persist because regeneration of aspen remains continuous at the edge of clones, inhibiting herbivore use. If predation risk decreases, and elk density increases (towards the 30% twigs browsed isoline between B and D, Figure 5.11), elk use should increase most rapidly in grasslands next to aspen. If thickets continue to discourage elk use, this will create a maximum difference in elk use between grasslands and aspen. As elk densities increase further in low risk landscapes (toward C), the risk-sensitive foraging tradeoff should result in strong pressure for elk to utilize areas within aspen thickets. Higher elk browsing of thickets will in turn, over time, reduce thicket density. Where thickets are removed, elk should have similar use levels in aspen and grassland cover types.

Distance from main	Landscape Risk				
valley bottom trail or highway	High predation risk with trail used by wolves	Low predation risk with busy highway avoided by wolves			
Close	Lowest	Highest			
(<100 m)	Grass >>> Aspen >>> Conifer	Grass > Aspen > Conifer			
Moderate	Moderate	Moderate			
(100 to 500 m)	Grass >> Aspen >> Conifer	Grass >> Aspen >> Conifer			
Far	Highest	Lowest			
(500 to 1000 m)	Grass > Aspen > Conifer	Grass >>> Aspen >>> Conifer			

Table 6.1: Predictions for elk corridor and patch use for high predation and low risk predation landscapes at 3 distances from trails used by predators.

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Table 6.2: Predictions for elk patch use and browsing rates for grasslands on the edge of aspen stands, and the interior of stands for 3 predation risk levels.

Predation risk	Relative elk habitat use and browsing rates	Remarks
High	Edge > Interior	Heavily hunted area, or area near trail used by wolves, elk use low in both edge and interior patches
Moderate	Edge >> Interior	Elk use increases first at edge of aspen stands
Low	Edge = Interior	Aspen thickets removed, elk use all areas

### Study Areas and Methods

I tested predictions by evaluating elk use (indexed by pellet counts) and browsing effects in aspen stands and adjacent grasslands and forests on five valley-bottom elk winter range areas of the Canadian Rockies in Alberta (Table 6.3). The Jasper-Willow Creek area is a  $\approx 30 \text{ km}^2$  area in Jasper National Park where wolf predation on elk has been frequently observed (Carbyn 1974, Dekker et al. 1995). In 1999, about 20 to 40 elk utilized the area during winter (W. Bradford pers. comm.). These elk may periodically leave the park onto Alberta provincial lands where they are hunted during the fall hunting season, or year-round by Treaty Indians (Dekker et al. 1995). The Ya Ha Tinda Ranch is a  $\approx 100 \text{ km}^2$  area along the Red Deer River adjacent to Banff National Park where approximately 1000 to 2000 elk winter on grasslands within 3 to 5 km of the ranch buildings (Morgantini 1995).

During the study, wolf use was relatively high in areas further away from the ranch, and bull elk were hunted during a fall rifle-hunting season. Three study areas (Kananskis Golf Course, Bow Valley Provincial Park, Banff-Bow Valley) were in the lower Bow Valley on Alberta provincial lands and in Banff National Park. The Bow Valley has several areas of different wolf and human predation rates on elk (Paquet et al. 1996). The  $\approx 100 \text{ km}^2$  Banff-Bow Valley area is bisected by a fenced highway, and provides habitat for over 500 elk. Near Banff townsite, human mortality rates on elk (from roads and the railroad) were 2%/year on roads and the railroad, and <4%/year caused by wolves (Paquet et al. 1996, Woods et al. 1996). Elk also concentrated on unhunted zones in Bow Valley Provincial Park, 50 km east of Banff, and the Kananaskis Golf Course complex, 60 km southwest of Banff (Alberta Environment Protection files, Canmore Office).

Study Area	Road and trail corridor	Paired edge-interior	Model thickets
	pellet count transects on	aspen stand transects on	
	risk gradients	risk gradients	
Jasper National Park-	5 transects – running	1 transect – running	
Willow Creek	from 500 to 800 m from	from 600 m away from	
	trail to edge of trail,	trail to the trail in Mud	
	plus >15 km of wolf scat	Creek meadow	
	counts on trails		
Ya Ha Tinda Ranch		1 transect – running	
		across ranch boundary	
		from east at Eagle Creek	
		_	
Banff National Park-	5 transects – running	1 transect – running	5 - located from .3 to 5
Bow Valley	from 500 to 1000 m	across east park	km from Banff townsite
	from Trans Canada	boundary near Harvey	at Recreation Grounds,
	Highway to edge of	Heights, Alberta	Hoodoos, Golf Course,
	highway fence, plus >15	-	Indian Grounds and
	km of wolf scat counts		Duthill
	on trails		
Bow Valley Provincial		1 transect - running from	
Park		Kananaskis River to	
		center of park at Many	
		Springs Pond	
Kananaskis Golf Course		1 transect – running	
		from clearcuts east of	
		Boundary Ranch to	
	*	powerline through golf	-
		course	

Table 6.3. Predation risk study areas and data collected in each area.

All study areas are in the montane or lower subalpine ecoregions of the Canadian Rockies (Strong 1992). Vegetation cover is predominantly lodgepole pine (*Pinus contorta*) forests interspersed with stands of trembling aspen, Douglas-fir (*Pseudotsuga menziesii*), and white spruce (*Picea glauca*), and grass meadows, and shrub birch (*Betula spp.*) and willow (*Salix spp.*) shrublands (Achuff and Corns 1982, Archibald et al. 1996, Beckingham et al. 1996). The study areas have a continental climate with peak precipitation in June, and winter snow depths generally less than 50 cm (Holland and Coen 1982).

### Ungulate and wolf habitat use

I used pellet and scat counts on belt transects to index relative winter habitat use by wolves and ungulates (Neff 1968, Edge and Marcum 1989). Elk defecate most frequently when active, so pellet counts are likely biased towards areas where elk are feeding or moving as opposed to bedding (Collins and Urness 1979). Transects were measured in April and May, immediately after the winter snowpack melted. I evaluated wolf and elk habitat use by cover type and distance from trails and roads (Table 6.3) at Jasper-Willow Creek (low human use, high wolf use, low elk density) and Banff-Bow Valley area (high human use, low wolf use, high elk density). From air photographs, I identified 5 transect locations (Figure 6.1) perpendicular to the main valley bottom trails (Jasper area) and the Trans Canada Highway (Banff area) where a mix of aspen, conifer, and grassland habitat patches was found at 10 to 100 m, 100 to 500 m, and 500 to 1000 m from the road or trail, and aspect and elevation were relatively similar along the transect. On the air photographs, I selected locations for five  $2 \times 50$  m plots in each cover type at each of the 3 distances from the trail or road for each transect. All scats and ungulate pellet groups with centers within plots were counted by species.

I used a factorial analysis (2 study areas  $\times$  3 cover types (grass, aspen, conifer)  $\times$  3 distances from trail/road (close, moderate, far)) to test for main and interaction effects on the elk pellet group counts. Although frequency count data typically follows a negative binomial distribution, simulations by White and Bennetts (1996) showed that analysis with ANOVA is relatively robust to violations of normality. I minimized the effects of

violations of parametric assumptions (normal distribution and equal variance) by balancing sample sizes for groups (Underwood 1997), comparing results of alternative data transformations of pellet counts on normal probability plots (Zar 1996), and using the square root transformation ( $\sqrt{(\text{count + .5})}$ ).

I tallied all wolf scats within 1 m of the main trail centers in the Willow Creek area of Jasper National Park for 3 years (1997, 1998, 1999), on side trails in Willow Creek for one year (1999), and on side trails near the Trans Canada Highway in the Banff-Bow Valley for 2 years (1998, 1999). Each trail was surveyed once in April or May, immediately after snowmelt. Trail distances by cover type were measured by wheelodometer.

To evaluate effects of aspen stand structure and predation risk on elk habitat use (Table 6.2), I identified 5 transects (Table 6.3) across areas where elk likely had welldefined and rapid increases in risk (<2000 meters across). For example, the elk predation risk from wolves likely decreased further from wolf-used trails in the Jasper-Willow Creek area, or the predation risk from humans decreased when entering national or provincial parks in the Bow watershed from hunted, multiple use lands. Along each transect, I located three risk level zones (high, moderate, and low risk of predation or hunting) to approximate points A, B (on the 0.3 browse index isoline) and C respectively in Figure 5.11 (see Chapter 5). At 5 sample points in each zone, I counted pellet groups on a  $2 \times 50$  m plot in the interior of an aspen stand paired to a stand edge plot in grasslands 10 to 30 m away. Where possible, aspen interior plots were established in thickets, defined as a dense stand (<1 meter spacing, >50 stems/100  $m^2$ ) of stems predominantly 2 to 6 meters in height. Where no thickets were found (low risk-high elk density areas), I paired edge plots to plots in the interior of aspen stands with the highest stem densities in the area. The moderate risk zone on each transect was recognized as the zone where saplings were relatively dense in and near aspen stands, but rare in adjacent grasslands. Predictions of elk use of aspen patches versus adjacent grassland patches at 3 risk levels (Table 6.3) were tested with a one-way analysis of variance of the ratio of paired values (aspen stand interior/edge of stand) of elk pellet group counts.

# Elk browsing effects on aspen

I estimated elk aspen browsing levels on aspen at 5 points (10 m spacing) within each of the five  $2 \times 50$  m paired plots at the low, moderate, and high risk points along each risk transect (see above). At each point, the nearest 2 aspen stems in each of three height classes (suckers (0 to 1 m), tall suckers (1 to 2 m), and saplings (2 to 6 m)) were tallied by live or dead condition, and four browsing classes: < 20% twigs browsed and/or stem debarked (BC1), 20 to 50% twigs browsed and/or stem debarked (BC2), 50 to 80% twigs browsed and/or stem debarked (BC3), and >80% twigs browsed and/or stem debarked. For analysis, an overall browsing index was calculated for saplings from the midpoint of each browse class, weighted by the number of stems in each class (BC 1 to BC4), and divided by the total number of stems (n), with the equation:

# B = (0.1\*BC1 + 0.35\*BC2 + .65\*BC3 + 0.9\*BC4)/n

Predictions (Table 6.2) of elk browsing intensity of aspen stems inside patches versus stems adjacent to grassland patches, at 3 risk levels were tested with a one-way analysis of variance of the ratio of paired values (interior of aspen stand/edge of stand) of browse index values.

Few aspen thickets of stems 2 to 6 m in height occurred at the high elk density and low predation/hunting risk end of transects. To evaluate over-winter elk herbivory effects on sapling stands under these conditions, I constructed 5 artificial sapling thickets in the Banff-Bow Valley area (Table 6.3). Methods followed Lundberg and Dannell (1990) and Edenius (1991). Unbrowsed aspen stems were cut during winter dormancy in December and early January from the nearby fenced, highway wildlife exclosure. Each artificial thicket consisted of 36 stems (2 to 5 m in height) set 20 cm into frozen ground to form a thicket  $4 \times 4$  meters (approximately 0.75 m spacing between stems), and a further 10 stems were placed with 5 m spacing in the grassland area around the thicket. Thickets were built around 1 to 3 mature, single aspen stems (>5 m height). I measured the browsing condition class (see above) for each stem every 8 to 12 days after construction (early January, 1999) until spring (late March).

For analysis of browsing effects in and near thickets, the browsing index (see above) was calculated for each sample date for stems grouped as open (in the meadow), edge (on edge of thicket), interior (0.5 to 1 m inside the thicket), and core (center of thicket).

#### Results

#### Patch types and travel corridors

Wolf scat abundance on main and side trails was different between the Banff-Bow and the Jasper-Willow Creek areas (Table 6.4). Fencing prevents wolves from using the Trans Canada Highway in the Bow-Banff area, and wolf use, as indexed by scat counts, was relatively low along side trails within 1.5 km of the fenced highway. For the Jasper area, wolf scats were abundant on the main valley bottom trail, and less common on side trails.

Factorial analysis results of elk pellet counts (Table 6.5, Figure 6.2) showed significant main effects of landscape area (Banff or Jasper), distance from trail or road, and patch type. Banff had higher pellet group counts than Jasper. For both areas, the pattern of elk pellet counts was grass > aspen > conifer. The interaction effect between landscape area and distance from trail road was significant, demonstrating an opposite pattern of elk use in Banff and Jasper corridors near roads and trails. In Banff, elk use was highest near the highway, with consistently less elk use in all patch types with increasing distance classes. In Jasper, elk use was lowest near the trail, but was more variable with distance from the trail (Table 6.6). Contrary to predictions, there was no significant interaction between landscape, distance from trail or road and patch type. The relative number of pellet groups within grass, aspen and conifer patches was fairly consistent with distance and landscape area (Figure 6.2).

Туре	Attribute	Jasper-Willow Creek			Banff-Bow Valley		
	Patch Type	Grass	Aspen	Conifer	Grass	Aspen	Conifer
Main trail	Distance (km)	9.5	0.6	12.5			
or	Scat Count	46	1	62	Fenced		
highway	Scats/km	4.8	1.6	5.0			
Side trail	Distance (km)	1.7	.4	2.3	7.9	1.2	21.2
	Scat Count	8	0	1	5	0	13
	Scats/km	4.7	0	.4	0.63	0.0	0.61

Table 6.4. Trail and highway distances sampled and mean spring (May, June) wolf scat counts by cover type on trails for the Banff townsite area, Banff National Park, and Willow Creek area, Jasper National Park.

Table 6.5. Results of the analysis of variance of the effects of landscape area (Banff-Bow Valley, Jasper-Willow Creek), distance from road or trail (near, moderate and far), and patch type (grass, aspen, and conifer), on the square-root transformation of elk pellet group counts (multiple  $R^2 = 0.555$ ).

Source of variation	SS	Df	MS	F-ratio	Р
Landscape	390.66	1	390.66	387.81	0.000
Distance from Road/Trail	50.63	2	25.32	25.13	0.000
Patch Type	202.86	2	101.43	100.69	0.000
Landscape × Distance	68.34	2	34.17	33.92	0.000
Landscape × Patch	6.81	2	1.70	1.69	0.151
Distance × Patch	53.48	4	26.74	26.55	0.000
Landscape $\times$ Distance $\times$ Patch	5.42	4	1.36	1.35	0.252
Transect (Landscape)	95.20	8	11.90	11.81	0.000
Error	427.11	424	1.01		



Distance from Trail or Road

Figure 6.2. Geometric means  $\pm$  SEM of elk pellet group counts for grass (G), aspen (A), and conifer (C) cover types at 3 distances from trails or roads in the Banff (B) and Jasper (J) study areas. The 1 pellet group/100 m<sup>2</sup> threshold line indicates the level above which aspen saplings are rare (see Chapter 5). For each sample, n = 25.

Table 6.6. Mean pellet group counts/100 m<sup>2</sup>  $\pm$  SEM for patch cover types within study areas. Column means with different superscript letters within areas and row means with different superscript numbers are significantly different (see text) at P < 0.05(Bonferroni test on square root of elk pellet counts). Samples sizes are n = 25 for plots grouped by landscape, distance and patch type; n = 75 for plots grouped by patch types, n= 225 for each landscape, all distances and patches; n = 150 for plots grouped by cover for all distances; and n = 450 for all plots.

Landscape	Distance		Patch Type	For all	For all	
	from trail or road	Grass	Aspen	Conifer	Patches	distances
Banff-Bow	Close	38.6± 6.3	$14.2\pm 2.0$	7.9±1.4	20.3±2.8 ª	12.7±1.2
Valley	Moderate	19.6±3.0	7.5±1.0	4.7±1.0	11.2±1.5 <sup>b</sup>	
	Far	13.9± 2.8	$3.5 \pm 0.7$	2.7±0.7	6.7±1.1 °	
Jasper-	Close	2.2±0.4	$0.6 \pm 0.2$	0.0±0.0	1.0±0.2 <sup>d</sup>	
Willow	Moderate	3.9±0.7	$1.4 \pm 0.3$	0.4±0.1	2.0±0.3 °	$1.4\pm0.1$
Creek	Far	2.4±0.5	1.3±0.2	0.3±0.1	1.3±0.2 <sup>d</sup>	
For both landscapes	All distances	13.7± 1.7 <sup>1</sup>	$4.7\pm0.6^{2}$	2.7±0.4 <sup>3</sup>		7.0±0.6

## Aspen stand structure and predation risk

Elk pellet group counts and browsing index values for paired aspen stand interior and edge plots varied significantly between plots that had different predation and hunting risk (Figure 6.3). There were few elk pellets in both edge and aspen interior plots in highrisk areas. Pellet numbers increased more rapidly in edge plots than in aspen interior plots as risk decreased (Figure 6.3*a*). Areas at moderate risk had a statistically significantly lower (P = 0.03, Bonferroni adjusted) ratio of interior to edge pellet group counts (Figure 6.3*c*) than did low risk areas. Aspen sapling browsing index values had a corresponding pattern (Figure 6.3*b*). The stand interior to edge ratio of browsing (Figure 6.3*c*) was significantly lower in moderate than in high risk areas (P = 0.04, Bonferroni adjusted) or low risk areas (P = 0.001, Bonferroni adjusted).

Elk use patterns corresponded with changing aspen stand structure. Aspen stands in moderate and high risk areas were dense and multi-aged (Figure 6.4*a*). However, in lower risk areas where pellet counts were >1 group/100 m<sup>2</sup>, stands had low sapling densities and were much more open (Figure 6.4*b*).

## Model thickets

Over-winter (approximately January 10 to March 20) browsing by elk was intense on the model aspen stands constructed in the Banff-Bow area. All thickets were browsed within 10 days of construction (Figure 6.5). Browsing index values, decreased for stem placements in the following order: isolated stems in open areas, stems on the edge of  $4 \times$ 4 m thickets, stems 1 m in from thicket edge, and stems in center of thickets (Figure 6.5). By the end of winter, the mean browsing index was greater than 0.7 for all stem placements.



Figure 6.3. Means  $\pm$  SEM of (a) elk pellet groups (groups/100m2), (b) browsing index values for paired plots on the edge and in the interior of aspen stands on transects from high to low predation or hunting risk to elk, and (c) the ratio of interior to edge pellet count and browse index. For each sample, n = 25.



Figure 6.4 Dense stand of aspen saplings near a trail heavily used by wolves at Willow Creek in Jasper National Park, Alberta (*a*), and a heavily browsed, low stem-density stand approximately 500m from the trail (*b*).



Figure 6.5. Mean  $\pm$  SEM of browsing index values of aspen stems in and near model thickets. See text for location of stems. Sample sizes are open stems (n = 50), edge stems (n = 100), interior stems (n = 60), and for core stems (n = 20).

#### Discussion

#### Patch type and travel corridors

General elk use by patch type (grass > aspen > conifer), as indexed by pellet group counts (Figure 6.2, Table 6.6), was consistent for the Jasper and Banff areas. High elk use of grass and short shrub habitat patches has been reported for numerous Rocky Mountain areas including northern British Columbia (Peck and Peek 1991), Alberta national parks (Cowan 1947, Flook 1964), Montana (Jenkins and Wright 1988), Yellowstone National Park (Houston 1982, Coughenour and Singer 1996), and lodgepole pine and meadow areas in Utah (Collins and Urness 1979). Pellet group counts were comparable those from earlier research (1975 to 1980) in the montane ecoregion in Banff and Jasper national parks where means of 10 to 15 groups/100 m<sup>2</sup> for grassland types and 2 to 4 groups/100 m<sup>2</sup> for forest types were reported (Holroyd and Van Tighem (1983: 412).

The different patterns of elk pellet groups near valley bottom trails in a wilderness area of Jasper National Park in contrast to near a busy 4-lane highway in Banff National Park (Figure 6.2) were in accordance with predictions (Table 6.1). In the Banff area, there were consistently fewer elk pellet groups as the distance from the highway increased (Table 6.6). This may be the result of predator avoidance (Dekker et al. 1995). In Banff wolves cannot use the highway as a valley-bottom travel vector due to highway fencing (Table 6.4), and only infrequently use areas near the fence due to high traffic volume. Paquet et al. (1996) found from tracking and radio telemetry studies that wolves avoided areas within 500 m of the highway in Banff. Dekker et al. (1995) described a similar pattern of relatively low wolf use, and high elk use near the main highway in the Athabasca Valley in Jasper National Park. However, in the Athabasca Valley, elk could also be attracted to the highway right-of-ways because of tree clearing and agricultural grass cover (Holroyd and Van Tighem 1983). In the Banff area, highway fencing blocks elk use on most of the right-of-way area (Woods 1990), thus reducing the effect of this confounding factor.

In the Jasper-Willow Creek area, the valley bottom trail was a main winter travel vector for wolves (Table 6.4). This corroborated the findings of several other studies of wolf movements in undeveloped areas of the Rocky Mountains (Carbyn 1974, Paquet et

al. 1996, Kunkel 1997). In winter at Willow Creek, wolves maintain runways through snow along trails by repeatedly using the same route (Carbyn 1974). In addition, Jasper National Park wardens make infrequent winter patrols on the main trail by snow machine (G. Antoniuk pers. comm.). Trails where the snow is packed, but are only lightly used by people are often preferred winter travel routes for wolves (Paquet et al. 1996). There was significantly less elk use within 100 m of the Jasper trail, but elk use was more variable with distance than in Banff (Figure 6.2, Table 6.6). In contrast to Banff where wolves predictably avoid areas close to the highway (Paquet et al. 1996), Jasper wolves may use main trails heavily, but they still utilize side trails and areas away from trails (Table 6.4). Further, predators such as cougar, black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*) are likely more common at all distances from trails in the remote Jasper area compared to near the highway in the busy Banff area (Banff Bow Valley Study 1996).

Contrary to predictions for an interaction effect on elk habitat use that included distance from trail or road (Figure 6.2, Table 6.2), there appeared to be similar relative elk use patterns for patch types (e.g., grass >> aspen > conifer for Banff, grass > aspen >> conifer for Jasper) for all distances within landscapes. Possibly elk use of adjacent patch types as sampled with my methods was not independent. Elk often forage in grass patches, but may seek hiding cover in adjacent conifer patches when resting (Lyon 1979, Lyon and Ward 1982, Thomas et al. 1988). However, the low number of pellet groups in the aspen and conifer types closer to trails in the Jasper-Willow Creek area (Table 6.6) suggested that elk avoided forest cover here when foraging or travelling.

The overall patterns of elk use with landscape, distance from trail or road, and patch type had important biological significance for aspen regeneration. In Jasper, aspen saplings within aspen and conifer patches near the trail were often unbrowsed (Figure 6.4*a*). However, in all patch types at all distances from the road in Banff, Jasper aspen patches >500 m from the trail, and all Jasper grasslands, pellet group counts exceeded the threshold of  $\approx 1$  group/100 m<sup>2</sup> (see Chapter 5) where aspen saplings are completely browsed off (Figures 6.2, 6.4*b*).

#### Aspen stand structure and predation risk

Elk pellet group and browsing index values for paired aspen interior and grassland edge across predation and hunting risk gradients (Figure 6.3) followed the predictions from risk-sensitive foraging (Table 6.2). These results support the hypothesis that the Type 2 functional response observed for aspen sapling-elk interaction (Figure 5.11, see Chapter 5) is at least partially caused by relatively less time spent by elk in densestemmed aspen patches. Along risk gradients (Figure 6.3), this interaction was most clearly manifested at intermediate risk levels. At high risk, elk densities were low, and elk browsing was low both on the edge and inside adjacent aspen thickets (Figures 6.3a,b; 6.4a). At low risk, elk were at higher densities, and over time killed aspen saplings (Figures 6.3*a*,*b*; 6.4*b*). The remaining, open-grown stands were again more equitably used by elk in comparison to adjacent grasslands (Figure 6.3c). At intermediate risk, elk densities were moderate in grasslands, but they most clearly avoided using aspen thickets. Further evidence of this fine-scale elk-foraging pattern was provided by browsing over time in the model thickets built in the Banff's Bow Valley. Elk browsed sapling stems in open grasslands near stand edges preferentially (Figure 6.5). However, in this high elk density situation, even stems at the core of aspen thickets were heavily browsed within 90 days of stand construction. Shepperd and Fairweather (1994) observed comparably high elk browsing rates when fences protecting sapling stands in Arizona were removed.

The relatively low rates of browsing of aspen suckers and saplings in multi-aged, high stem density stands compared to those in more open aspen stands has been recognized by previous researchers (DeByle 1985a,b). The low elk use of dense aspen stands I observed could be the result of an interrelated suite of factors. Dense stands may have better cover for stalking predators such as cougars (Kunkel et al. 1999), increased snow depths (Telfer 1978), and decreased forage availability (Bailey and Wroe 1974). In contrast, adjacent open grassland areas provide elk with ease of escape from predators (Geist 1982), and when elk numbers are low, high availability of palatable grasses (Willoughby et al. 1997).

Plant structural characteristics such as thorns, spine, tough leaves and prickles may reduce herbivore use (Harper 1977, Cooper and Owen-Smith 1986, Pollard 1992).

But intuitively, increasing density of highly palatable forage such as aspen saplings would result in higher herbivore use of patches, not lower, if no other factors were operative. However, aspen communities exist in montane landscapes that historically included not just plants and herbivores, but also predators– humans, wolves, cougars, and black and grizzly bears (Mattson 1997, Kay 1998, White et al. 1998a, Kunkel et al. 1999). In 3-level trophic systems, the interaction between vegetation structure, predator hunting behavior, and herbivore response to predation risk is likely profound, variable and complex (Lima and Dill 1990, Hunter and Price 1992, Lima 1998, Kie 1999). Results of the present study suggest the hypothesis that aspen's dense-stemmed thicket trait confers increased fitness to aspen clones in predator-rich environments, but could be detrimental in herbivore-rich situations. This requires further investigation.

# Integration of risk sensitive foraging patterns and aspen stand structure

The three spatial scales of elk density and risk-sensitive foraging patterns (Figure 3) evaluated here (regional, near trails and roads, and habitat patch level) appear to be associated with major structural differences in aspen stands. At the regional level, in high-predation risk areas, such as Jasper's Willow Creek, where elk densities were low (<1 pellet group/100 m<sup>2</sup>, Figure 6.2), aspen were often multi-aged and dense (Figure 6.4*a*). In low predation and hunting-risk areas, such as in Banff, elk densities were usually high (>3 to 5 pellet groups/100 m<sup>2</sup>, Figure 6.2). Under these conditions, all aspen stands were heavily browsed, and dense multi-aged stands did not occur.

At intermediate spatial scales, human and predator travel routes had completely different effects under different risk situations. In high-predation risk ecosystems with low human use, valley-bottom trails were frequented by wolves (Table 6.4). Elk were not attracted to these trails, and may even have avoided some areas near them (Figure 6.2). As a result, in the Jasper Willow-Creek area, aspen stands were multi-aged and densest near the main trail, and more heavily browsed at increased distances from the trail (Figure 6.4). In low-predation risk areas (e.g., near busy national park roadways) the opposite effect occurred. Elk may be attracted to valley bottom travel routes and facilities heavily used by humans, but avoided by wolves (Paquet et al. 1996). This resulted in very high

elk densities in aspen stands (e.g., >10 pellet group/  $100 \text{ m}^2$ ) such as observed in this study for the Banff's Bow Valley (Figure 6.2). This "reversed" pattern of elk use in modern park landscapes makes herbivory impacts acute for aspen stands in valley-bottom areas once heavily used, but now avoided, by predators (Ripple and Larsen 2000).

At the finest scale of the habitat patch, structural conditions of aspen (low density stands versus dense, multi-aged stands) further affected elk foraging behavior. In a highpredator risk region, particularly near routes frequented by predators, aspen stands had high stem densities with low browsing rates (Figures 6.3b, 6.4a). In contrast, a positive feedback mechanism occurred when elk densities were high- browsing reduced stem density, which increased elk habitat use and browsing rates. Most aspen stands in lowpredation risk and high elk density areas in the Rocky Mountains are currently in this condition (Kay 1997a). From 1940 to 1970, several national parks including Jasper. Banff, Yellowstone, and Rocky Mountain culled elk, but achieved no significant response from aspen (White et al. 1998a), even when elk populations were reduced to levels where aspen regeneration had previously occurred (Houston 1982, Huff and Varley 1999). This led to alternative hypotheses that fire suppression or climate change were important causes of aspen decline (Houston 1982, Romme et al. 1995). However, results of my study suggest that aspen regeneration would not be expected at the same elk densities at which it initially declined due to different elk behavioral patterns in remnant open stands (Figure 5.11, see Chapter 5). Only a major decrease in elk density would re-create the dense multi-aged stands that are more resistant to herbivory.

Historically, spatial factors that affected predation on herbivores such as predator travel routes (Carbyn 1974), wolf pack buffer zones (Mech 1977) and denning locations (Dekker et al. 1995), or First Nation intertribal warfare areas (Kay 1994, Martin and Szuter 1999) likely shifted with time. The resulting spatially-dynamic risk sensitive foraging patterns of elk would often provide conditions favorable for creating dense aspen stands that would be resistant to periodic higher densities of elk if predation risk declined. In contrast, many current risk zones (e.g., park boundaries) are spatially-fixed, and may result in long-term high elk density in some areas (White et al. 1998a).

Results of this study should be interpreted recognizing two limitations. First, the landscape analysis, or "natural experiment" technique used here to evaluate hypotheses for risk sensitive foraging by elk on aspen did not control for the relative effects of predation risk versus elk competition for food. For example, in all analyses, areas of higher risk had lower densities of elk, as indexed by pellet groups (Figures 6.2, 6.3*b*; Table 6.6). Relatively low browsing rates on aspen in these areas could be more related to the higher availability of preferred foods (e.g., some grass species) in low elk density areas than risk-driven avoidance of aspen stands. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a relatively consistent result of increased carnivore predation or human hunting rates (Lyon and Ward 1982, Dekker et al. 1995, Paquet et al. 1996, Kunkel and Pletscher 1999). A second study limitation is that few study areas were evaluated, particularly for the trail and road corridor analyses where only one area for each treatment was sampled. Possibly, other factors may have confounded observations, and this research should be repeated in more areas.

#### Conclusion

Patterns of elk herbivory on aspen appear to result from multi-scale factors that include not just general elk density, but also varying risk-sensitive foraging patterns resulting from predator habitat use (Ripple and Larsen 2000) and aspen stem-density conditions. In those areas of the Canadian Rockies national parks that are heavily used by people, the current pattern is one of high-density elk populations attracted to valleybottoms, and intense elk foraging on low stem-density aspen stands. This is the opposite of historical conditions throughout the Rockies, and of the current situation in more remote areas, where elk have lower densities, and are not attracted to valley bottom travel routes that are heavily used by wolves or human hunters.

Low herbivory results in dense, multi-aged aspen stands that are resistant to periodically higher browsing rates by fluctuating populations of elk. This condition is likely similar to the long-term spatially-dynamic conditions that maintained aspen in valley-bottom areas.

Elk-aspen foraging patterns result from complex interactions between predators, herbivores and vegetation. As predicted by Hunter and Price (1992), these interactions are highly influenced by heterogeneity in more natural systems where predators still occur. Neither "top-down" or "bottom-up" influences necessarily prevail. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a consistent result of maintaining the historical range of variability of carnivore predation or human hunting rates. Therefore it may be difficult to isolate the effects of predation from reduced elk competition for food in future research on aspen herbivory.

Results of this study suggest the hypothesis that aspen's dense-stemmed thicket trait confers increased fitness to aspen clones when interactions between predator and herbivore behavior, and vegetation density occur.

# CHAPTER 7. SUMMARY AND INTEGRATION: THE TREMBLING ASPEN CONSERVATION DILEMMA

My enemy's enemy is my friend.

Hebrew Proverb

In this concluding chapter, I summarize my research results on the ecology of aspen, elk and fire in the montane ecoregion of the Canadian Rockies. I describe a potential integrated hypothesis for aspen's long-term abundance, and recent decline. From this basis, management actions and future research for aspen conservation are reviewed.

# Summary of Findings

#### Repeat photography

The top-down hypothesis for long-term condition of Rocky Mountain trembling aspen holds that these communities persisted due to frequent human-caused fires and low herbivory levels caused by predation on ungulates by carnivores and humans (White et al. 1998a, Kay et al. 1999). I repeated the taking of 165 historic photographs (taken in years 1874 to 1949) showing detailed aspen stand conditions in 7 areas along the eastslope of the Rocky Mountains. Historic and current aspen stand conditions (e.g., stem spacing by height class and species, barking, and browse class) were quantified for 195 stands visible in photographs. Analysis of variance of 10 or 15 historic and current observations per area was used to test specific predictions of the top-down hypothesis for stand structure change over time.

Large aspen in historic photographs showed no evidence of bark-scarring from elk browsing, an indication of low elk browsing since at least 1850. Aspen stand ages in historic photographs appeared to increase from the period 1874 to 1889 to the period 1890 to 1904, likely due to declining fire frequency before organized fire suppression programs began. Aspen stands in all areas responded to a known period of low herbivore density (1880 to 1930) by consistently showing an all-aged structure with abundant saplings (1 to 4 m in height). Current repeat photographs in Banff and Jasper national park areas with high elk density (>4 elk/km<sup>2</sup> since 1940) show heavy browsing and few aspen saplings in stands that were historically multi-sized and lightly browsed. Five other areas with low or moderate elk density (<4 elk/km<sup>2</sup>) maintained multi-sized aspen stand conditions similar to those visible in historic photographs. All areas had increased conifer cover and older trees due to reduced fire frequency.

These results are consistent with the top-down model for long-term Rocky Mountain montane ecosystem development. Those conditions changed, though, with reduced burning by First Nation cultures by 1875, and were accelerated in Banff and Jasper national parks where, in addition to fire, hunting and predators were also controlled. Previous repeat photograph studies in the Rocky Mountains (e.g., Gruell 1980, 1983; Houston 1982; Kay 1990) reported similar declines in aspen communities. Gruell (1980) and Houston (1982) concluded that fire suppression, not elk herbivory, was the most important factor. However, these studies did not evaluate changes across a range of elk densities.

### Fire history

Historically, wildland fires frequently burned in the montane ecoregion of the eastslopes of the Rocky Mountains in Alberta, Canada. Recent decreases in fire frequency have been attributed to 2 alternative hypotheses: 1) climate change reducing the number of large lightning fires (Johnson and Larsen 1991, Weir et al. 1995), or 2) reduced cultural burning due to recent changes from long-term First Nation and early settler land use patterns (White 1985a, Kay et al. 1999). I tested historic fire frequency predictions derived from a cultural burning hypothesis that people regularly fired montane meadows in spring (Lewis 1982). Dendrochronology was used on fire-origin or fire-scarred lodgepole pine tree-disks obtained from 10 ha plots at the forest edge, and 200 meters into the forest for 12 sectors around meadows, replicated at each of 8 meadows located in different watersheds. The discrete time-since-fire (a(t)) and fire interval (f (t)) distributions were tested for variation around meadows.

Fire occurrence near most meadows declined after 1900, and virtually ceased after 1950. Fire intervals on the edge of meadows were relatively long (40 years). Factorial analyses of a(t) and f(t) by plot location (3 factors  $\times$  2 levels each) indicated that fire

occurred more frequently on meadow edges than in nearby forests (mean fire interval 40 years versus 53 years), more frequently on warm aspects than on cool aspects (mean fire interval 40 years versus 57 years), and more frequently on downwind ends of meadows versus upwind ends (mean time-since-fire 66 years versus 88 years). Dating the season of burn by fire-scar position within growth rings showed the majority of scars occurred in the early-wood period of growth.

These results should be interpreted with caution due to significant variations between meadows. However, results suggest that cultural burning in spring (outside the lightning season), and partially focussed on meadows, was an important component of longterm fire regimes in the eastslopes of the Rocky Mountains. Contrary to the initial hypothesis, it appears that people may have most often burned warm aspects (south and west facing slopes) along whole valleys, not just in meadows. Similar results were reported by Barrett and Arno (1982) for areas in Montana and Idaho. However, in Alberta these areas were burned at relatively long intervals (>30 years). Motives for human burning could have included maintaining corridors for bison movement or habitats for important plant resources.

# Environmental interaction effects

Although trembling aspen stands were historically multi-aged and vigorous, they currently fail to regenerate to heights >1m in several Rocky Mountain national parks. The interaction hypothesis attributes aspen decline to a combination of several factors including reduced disturbance, changing climate, and increased herbivory by elk (Romme et al. 1995). I used time-series analysis to test the complex interaction hypothesis with long-term (110 to 190 years) time-series data from the Bow Valley in Banff National Park, Alberta, on aspen stand regeneration year, area disturbed by fire, elk population, magnitude of summer drought, and mean spring temperature. Further, I used a factorial design to evaluate response of aspen saplings (density in the 1 to 4 m height class) to 3 site classes (dry, mesic, moist) and 3 browsing-disturbance classes (unbrowsed-disturbed, browsed-disturbed, browsed-undisturbed).

Bow Valley aspen stands continued to regenerate and reach tree height (>4 m) until approximately 1930, which is nearly 3 decades after frequent burning stopped in the Bow

Valley. There is no consistent period of climate change since 1930 that corresponds with failed aspen regeneration. However, elk densities became high at this time. Aspen saplings are abundant in unbrowsed areas on all site classes, and nearly absent in both disturbed and undisturbed areas on all site classes on browsed plots. No interaction effect with moisture conditions (in time or space) was evident in explaining the abundance of saplings. However, these results may have been confounded by high elk use on plots next to exclosure fences.

The results did not support the Romme et al. (1995) interaction hypothesis. In concurrence with past studies (reviewed by White 1998a), and recent research from Yellowstone National Park (Kay 1990, Ripple and Larsen 2000), Rocky Mountain National Park (Baker et al. 1997), and Jackson Hole (Hessl 2000), the single main factor of high elk density appears to be the most significant cause of aspen decline in the Bow Valley.

# The functional response of elk-aspen herbivory

Hypotheses for aspen's current decline in montane ecoregions include long-term high herbivory by elk, decreased disturbance, climate change, and long-term low elk herbivory (White et al 1998a, Romme et al.1995, Baker et al. 1997). Predation theory (Holling 1959, Pech et al. 1995), as applied to herbivores (Noy-Meir 1975) was used to describe alternative herbivore functional responses predicted by each hypothesis. To test predictions, I used elk census data from spatially separate watersheds on the eastslope of the Canadian Rockies to define 9 areas, with 3 areas in each of 3 elk density levels (<2, 2 to 4, >4 elk/km<sup>2</sup>). In each study area, I sampled aspen stand conditions in 10 plots in each of 4 tree cover classes: recently disturbed (<25 years ago), and low, moderate, and high tree cover. Plot elk density was indexed with pellet group counts.

The total herbivory rate on aspen saplings (1 to 4 m height) fitted the browsing pattern that would result from a Type 2 functional response (e.g., increased rate of herbivory with decreased sapling density). Results from a factorial analysis (3 elk densities  $\times$  4 tree cover classes) showed that the main effects of elk density and tree cover on the number of aspen saplings were significant. A weaker, but still significant interaction effect indicated that disturbance acted to incrementally increase the number of aspen saplings, but did not cause a major shift to an abundant sapling state in areas of moderate and high elk density. The results were most consistent with the predictions of

the low elk herbivory hypothesis. Other studies have reported similar effects of high impacts of elk herbivory (DeByle1985a, Kay and Wagner 1994) and fire (Kay and Wagner 1996, White et al. 1998a) in low density aspen stands.

Interactions between elk and aspen sapling density can be described with a state and transition model with two states (low elk density-abundant saplings, and high elk density-no saplings) separated by a curvilinear transition resulting from the Type 2 response. Transitions from low to high aspen sapling states likely occur at very low elk densities (indexed at <1 pellet group/100 m<sup>2</sup>), but the transition from high to low states may occur at higher densities (2 to 3 pellet elk pellet groups per  $100/m^2$ ). Disturbance likely enhances long-term aspen persistence in the high-density sapling state, and retards it in the low-density sapling state. The Type 2 functional response described here may partially result from predation sensitive elk avoiding aspen sapling thickets at low elk density, similar to recent conclusions by Ripple and Larsen (2000).

A limitation in this study was that the measures used for aspen recruitment (sapling density), and mortality (the browsing index) were not directly comparable. Thus, more detailed analyses to determine stability points between predation (herbivory) and recruitment rates (e.g., Noy-Meir 1975, Sinclair et al. 1998, Augustine et al. 1998) were not possible. Further, given the longevity and wide spatial distribution of aspen clones, other factors may be important in long-term aspen persistence and will require further research.

# Predation risk and elk-aspen foraging patterns

Risk-sensitive foraging patterns by elk could be influenced by distance from roads or trails, the type of user on road or trail (Lyon 1982, White et al. 1998a), and condition of aspen stands (see above). In this component of the study, I evaluated the hypothesis that these behavior patterns create 2 states of aspen stand conditions: 1) mature, open stands with no stems in the sapling (1 to 4 m) height class in unhunted or low predator abundance areas, and 2) dense, all-aged thickets with numerous saplings in hunted or high predator abundance areas. I tested specific predictions from this hypothesis in a nested, spatial hierarchy of landscapes, corridors and habitat patches in Banff and Jasper national parks and Kananaskis Country, Alberta. I used elk pellet counts, and classes of stem bark damage and twig browsing as indices of elk use. First, pellet counts were measured in 3 patch types (grass, aspen, conifer) at 3 distances from road or trail on 5 transects near park roads avoided by predators and compared to counts on 5 transects near park trails heavily used by wolves. Wolf use of trails in these landscapes was indexed with scat counts per km of trail. Secondly, I contrasted pellet counts and browsing levels on plots inside aspen stands paired to plots on the edge of aspen stands in adjacent grasslands on 5 transects running across predation or hunting gradients (e.g., across wolf-frequented trails or protected area boundaries). Thirdly, I measured overwinter browsing levels on stems inside, on the edge, and outside of 5 "model thickets" built inside Banff National Park.

Road and trail transects showed that elk use was high near Banff roads heavily used by park visitors and avoided by wolves, as compared to areas more distant from roads. In Jasper, elk use appeared to be slightly less near backcountry trails used by wolves. On all transects, elk pellet densities for cover types followed a pattern of grass > aspen > conifer. Protected area boundary transects showed that in high predation risk landscapes, aspen stands were lightly browsed, dense, and rarely entered by elk. As risk decreased, elk density and aspen use increased proportionally faster on edge plots in grasslands compared to the interior of aspen stands. In low risk landscapes, elk density was high, but proportionally lower in edge plots, and stands had a low density of heavilybrowsed stems. Aspen saplings outside model thickets were completely browsed first (all twigs <1 cm removed, and >50% of bark), but by the end of winter, almost all thicket stems were completely browsed.

These results were generally consistent with predictions from risk sensitive foraging theory (Lima and Dill 1990, Lima 1998), previous work on elk habitat use (Skovlin 1982), and elk response to hunting, roads, and predation (Lyon 1979, White et al. 1998a). Variable elk densities and risk sensitive foraging patterns helped maintain the 2 states of aspen condition. In agreement with recent research by Kay (1990), Kay et al. (1999), Ripple and Larsen (2000) and Hessl (2000), I propose that regeneration of aspen stands in the Rocky Mountains likely requires low densities of risk-sensitive elk. However, this conclusion requires corroboration in additional study areas, and increased knowledge about the effects of spatial distribution and availability of habitat patches on specific use patterns by elk and predators.
## Integration: The Anthropogenic Hypothesis for Montane Aspen Abundance and Decline

My findings are consistent with a hypothesis that long-term historic human use patterns may have helped sustain Rocky Mountain, montane aspen stands, and that different, current human use patterns are an important cause of aspen's recent decline in national parks. Consider that long-term human ungulate hunting and burning of valley bottom corridors maintained vigorous, dense, lightly-browsed aspen stands. Further, the relatively low historical human use of these corridors did not displace carnivores such as wolves, cougars, and bears that were important sources of predation on herbivores such as elk. But the favorable conditions for aspen have recently changed in many parks and wildlife refuges where elk are unhunted, have become habituated to humans, and congregate in high densities (>5 elk km<sup>2</sup>) in heavy human use areas avoided by wary carnivores.

From this viewpoint, aspen is possibly not only a "natural feature", but also a culturally-created component of montane ecosystems. The anthropogenic hypothesis would require that we reconsider some traditional ideas on the ecology of montane areas in the Canadian Rockies. For example, the traditional viewpoint is that aspen communities are largely the result of unique landforms and climatic conditions in the montane ecoregion (Achuff and Corns 1982). Moreover, historic trails and campsites were commonly found in aspen stands (Parks Canada 1989, Kay et al. 1999) because aspen was easy to travel through, and provided the resources necessary for human occupation (Parks Canada 1989). Simply put, aspen communities attracted human use. The cultural resource hypothesis would suggest the opposite– humans were a significant ecosystem component, who through predation and burning, helped maintain aspen communities. In a sense, aspen was attracted to humans. Likely, both cultural factors and ecological factors were necessary for aspen community persistence.

In summary, the anthropogenic hypothesis for montane aspen persistence proposes that an important historical effect of humans was to help provide "enemyfree"space (Jeffries and Lawton 1984) for aspen stems to periodically survive the sapling

stage (1 to 4 m in height) that is highly susceptible to ungulate browsing. Humans served this function in two ways. First, by periodically burning montane landscapes, humans created abundant, dense suckers. Secondly, by hunting, humans provided an additive source of predation that helped maintain low densities of risk-sensitive ungulates near trails and campsites. These herbivores avoided dense aspen stands.

I predict that the anthropogenic hypothesis for historic aspen abundance and current decline is possibly most applicable under 5 conditions in the Rocky Mountains:

1) <u>Valley-bottom, montane areas in relatively rugged mountain terrain</u>. Here, in comparison to more homogenous landscapes, decreases in the numerical and behavioral effects of human and carnivore predation may cause highest concentrations of more sedentary and less risk-sensitive elk on the limited areas of high quality habitat (Baker et al. 1997, Ripple and Larsen 2000).

2) <u>Areas where humans and other predators were historically sustained by other</u> <u>primary resources</u>. Important resources for past human foraging in the Canadian Rockies likely included bison on the eastern slopes, and salmon on the western slopes (Parks Canada 1989). These resources may have partially sustained humans and other carnivores that also heavily hunted secondary prey such as elk and moose (Kay et al. 1999).

3) <u>Areas with low lightning-fire frequency, but high frequencies of historic</u> <u>anthropogenic fire</u>. Although eastslope of the Rocky Mountains lie in a zone of subsiding air mass with few lightning-caused ignitions, historic fire frequencies were relatively high, and likely maintained by humans (Heathcott 1999). Human-caused fires likely most often occurred in the spring and fall seasons (Lewis 1980, Chapter 3 this study), when aspen is most flammable (Quintilio et al. 1991).

4) <u>Low current human-caused rates of ungulate mortality</u>. This will favour ungulate habituation to humans, and higher ungulate densities in comparison to areas with high highway-caused mortality (Woods 1990), or hunting (Lyon 1979, Lyon and Jensen 1980).

5) <u>High current human use</u>. High human use will displace more wary carnivores from areas that may be relatively heavily used by human-habituated elk (Paquet et al. 1996, Woods et al. 1996).

### The Aspen Management Dilemma

Trembling aspen communities in the Rocky Mountain montane ecoregion are often ancient (Mitton and Grant 1996), have high biodiversity (Finch and Ruggerio 1993), and may be an important indicator of ecological conditions (White et al. 1998a, Kay et al. 1999). In many parks, wildlife refuges and other areas aspen is clearly declining in abundance and condition (Packard 1942, Cowan 1947, Olmsted 1979, Kay 1990, White et al. 1998a). Where ecosystem objectives require maintenance of ecological integrity or biodiversity (Woodley 1993, Canadian Heritage 1994, Parks Canada Agency 2000), the decline of aspen must be closely monitored, and restoration activities carefully considered (e.g., Parks Canada 1997).

One of the most useful paradigms for conserving aspen may be the historical or long-term range of variability concept (Morgan et al. 1994, Landres et al. 1999). The principles of the paradigm are: 1) current ecosystems are the product of past conditions and processes; 2) spatial and temporal variability in disturbance regimes are a vital attribute of ecosystems; and 3) maintenance or restoration of long-term ecosystem states and processes will conserve biodiversity (Grumbine 1994, Landres et al. 1999). The approach requires interdisciplinary scientific research to rigorously test predictions for the long-term condition of indicators defining ecosystem states and processes (e.g., Swetman et al. 1999, Kay et al. 1999). In many landscapes, careful, unbiased assessment of human's long-term ecological effects will be important (Vale 1998). For this reason, I have avoided using the phrase "natural range of variability" (Landres et al. 1999) because this describes a preconception of long-term conditions that may not be applicable to some ecosystems.

In this study, I used interdisciplinary techniques such as repeat photography, anecdotal fire history, dendrochronology, climate and site evaluations, predator-prey analysis, and risk-sensitive foraging theory to test alternative hypotheses for historic aspen abundance, and its current decline in the Canadian Rockies national parks. The resulting, redefined, anthropogenic hypothesis for long-term range of variability in ecosystem states and processes provides one scenario for predicting potential techniques for aspen restoration in parks and protected areas in this region. If the hypothesis is correct, modern human land uses and expectations in these areas are virtually opposite of long-term

conditions in such areas in this region. Today's park visitors want to view wildlife species, not hunt them. Visitors want green "park-like" forests, not burned habitats possibly more productive for many ungulate species. And today there are millions of people using park areas, not the few hunter-gatherers of times past. From the viewpoint of the anthropogenic aspen-decline hypothesis, current human land use conditions in many areas of the Rocky Mountains are likely not within the long-term range of variability of ecological conditions that sustained aspen.

#### Current management actions

If the anthropogenic hypothesis is correct, management of aspen through the longterm range of variability approach is confounded by almost contradictory policies in Rocky Mountain national parks and protected areas that require 1) minimal human intervention to maintain wilderness values, and 2) maintenance of ecological integrity and biodiversity in areas increasingly impacted by current human landuses (Boyce 1991, Landres et al. 2000). However, White et al. (1998a) and Parks Canada (1999) make several recommendations that have immediate application to maintain aspen in many Rocky Mountain parks while recognizing that minimal human ecosystem manipulation is necessary to maintain national parks as ecological baselines (Arcese and Sinclair 1997). These recommendations are derived from the Banff-Bow Valley Study (1996), a three-year independent commission which reported to Canada's minister responsible for national parks on the future condition of Canada's first national park, and the Banff National Park Management Plan (Parks Canada 1997). Implementation of these actions in Banff has been controversial (Zinkan and Syme 1997). The implementation plan (Parks Canada 1999) requires an adaptive approach guided by annual evaluation from a scientific advisory group that reviews data from ongoing intensive research on human, wolf, elk, aspen, and willow response patterns (e.g., Hurd 1999, Hebblewhite 2000, Nietvelt 2001, Banff National Park 2001).

<u>Restore carnivores.</u> The weight of evidence supports the importance of top-down, predation processes in the long-term structuring of Rocky Mountain ecosystems. Keystone species (Mills et al. 1993) in these landscapes were likely humans and wolves. Other predators such as cougars and bears may have also been important (Kunkel and Pletscher 1999). Additive predation effects on ungulates may have significantly structured montane ecosystems (Kay 1994, 1998; Kay et al. 1999). In national parks, where human hunting is now largely prohibited, we should, wherever possible, maintain populations of wildlife predators such as the wolf (MacCracken 1996, Clark et al. 1999). Where predation cannot be restored, the Banff-Bow Valley Study (1996:179) recommended that elk culling or translocation may be necessary. Translocation of elk from near Banff and Jasper townsite areas began in 1998 (Parks Canada 1999). Elk are usually moved to low-ungulate density locations outside of the national parks.

<u>Restore "wild" elk behavior patterns.</u> It is difficult to restore the predator-prey relationships when human-habituated ungulates can escape predation by using townsites, roadsides, and other areas avoided by the more wary predators such as wolves or grizzly bears. The Banff Townsite Elk Management Plan (Parks Canada 1999) requires that park wardens routinely apply "aversive conditioning" to any elk remaining in heavy human use areas. This includes use of slingshots, rubber slugs, noisemakers, and dogs. If this is unsuccessful, the habituated elk are trapped and translocated.

<u>Restore bison.</u> In Banff and Jasper national parks, bison, once the dominant large herbivore in low-elevation areas, are now extirpated. Elk now dominate these areas (Kay and White 1995). This is significant ecologically because bison are grazers, but elk can extensively consume woody vegetation. Bison restoration is required if long-term ecological conditions are to be maintained (Kay et al. 1999).

Restore fire, but with caution. Managers have often viewed fire as a panacea for ecological problems in Rocky Mountain national parks. Low elevation ecosystems were usually structured by a long-term regime of frequent (<40-year fire cycle), low intensity fires, probably started mostly by native peoples. However, to simply add fire back into today's herbivore-impacted ecosystems could damage, possibly irrevocably, numerous plant and animal populations. Fire can only be successfully restored in combination with maintenance of herbivore assemblages in their long-term patterns of abundance and distribution.

<u>Carefully manage human use.</u> The Rocky Mountains are one of the world's scenic treasures, and are regional, national, and international attractions driving massive tourism, recreation, and real estate development industries in western Canada and the United States. Cumulative effects modelling indicates that even seemingly benign human activities such as

hiking can displace wary carnivores from key habitats (Weaver et al. 1986, Gibeau et al. 1996, Paquet et al. 1996). Further, in developed areas, complete control of fire and human hunting is required, which further changes ecosystems from long-term ecological conditions. Clearly, careful management of human use in the Rocky Mountains is important for restoring long-term structure and function to these ecosystems (Zinkan and Syme 1997). The Banff National Park Management Plan (Parks Canada 1997) stipulates many actions to reduce human use to restore carnivore habitats.

#### Future aspen management

Aspen restoration in modern park ecosystems will be an adaptive management and research process (Holling 1978, Walters 1986) where managers view actions as treatments to validate predictions for experimental research (Sinclair 1991). This thesis has provided quantification of historic factors such as elk density and fire regimes that can be used to define these treatments. Further, I have suggested the overall anthropogenic hypothesis for long-term aspen persistence that may assist in the deduction of other predictions for historic and current aspen conditions and trends.

The ongoing management actions described above are not fully integrated to sustain aspen, carnivores, and herbivores over broad temporal or spatial scales. Further, their sporadic application will not lead to useful experimental research (Sinclair 1991). In contrast, DeByle (1979) proposed a thoughtful long-term management elk-aspen restoration program for the Gros Ventre watershed in Wyoming that has application in many Rocky Mountain situations. DeByle's (1979) proposal is essentially a landscapelevel rest-rotation system simulated with an elk population growth model. Critical elements of the program are:

1) At a landscape level, ungulate populations in some areas would be at high densities at any given time. DeByle (1979) regarded this as important to maintain hunter support for the program. In areas where large carnivores such as wolves must be sustained, high-density elk populations would also provide an essential prey base.

2) At any given time, some watersheds would be managed for low elk densities (e.g., <25% of food-regulated carrying capacity).</li>

3) During periods of low elk density, intensive burning would be prescribed to

rejuvenate aspen and other woody plant communities.

DeByle (1979) recommended that a 110-year rotation would provide the most elk population stability at a landscape level, and be most consistent with aspen regeneration and longevity requirements. My estimates of the elk densities necessary for aspen regeneration in degraded areas (indexed as <1 pellet group/100 m<sup>2</sup>, Figure 6.11) are likely lower than DeByle's. However, once dense aspen stands are obtained, the moderate elk density levels proposed for the Gros Ventre should maintain aspen stands relatively resistant to browsing.

Banff National Park (1995) proposed the DeByle rotation system for a 3-area system in the Bow Valley of Banff National Park. A serious disadvantage of the proposal is that seasonal fencing of highway crossing structures could interfere with the movements of several wildlife species besides elk. The proposal's key advantage in comparison to the current program of translocating elk out of the park (Parks Canada 1999) is that at any one time, at least 1 area would be managed for moderate to high elk densities, and could receive translocated elk. This would partially maintain a prey-base inside the park for carnivores.

Alternatively, a regional-level rotation system for elk population management could be considered that uses several Canadian Rockies watersheds such as the Athabasca, North Saskatchewan, Red Deer, Bow, Kananaskis, Highwood, Kootenay, and Oldman. This scale of management would require the cooperation of Parks Canada and both the Alberta and British Columbia governments to meet a complex set of ecosystem management objectives for humans, wolves, elk, aspen and fire. A multi-area approach would provide opportunities for a range of experimental approaches including baseline areas where active management actions would be minimal. These areas would likely be within the national parks, and provide the landscape-level scientific controls necessary for research on complex ecosystem interactions (Arcese and Sinclair 1997).

#### Future Research

My research on aspen, elk and fire in the Canadian Rockies has suggested 3 important topic-areas requiring further research.

1) Timing of historical fires- Preliminary dendrochronological analysis of trees near meadows in the Rocky Mountains (Chapter 3) provided evidence that historical fires near meadows were human-caused. However, the meadows themselves were probably not the main focus of burning, but larger areas both upwind and downwind of meadows. Future research should focus on identifying potential objectives for cultural burning at this large area scale. One possibility may the creation of fire corridors for driving bison from the plains into the mountains. On the basis of these hypotheses, specific predictions for burning patterns can be developed for subsequent testing with dendrochronology and other techniques. Key evidence for evaluating the cultural burning versus the lightning fire hypotheses is the time of burning as determined by fire-scar positions within tree-rings. Ongoing research of cambial growth phenology (Walker 1995) should be completed to calibrate scar position to the time-of-year.

2) Herbivory functional response- The Type 2 functional response for elk herbivory on aspen reported in Chapter 5 and 6 may result from predation sensitive foraging that governs elk browsing rates at the habitat patch, not the plant ramet, scale (White et al. 1998a, Ripple and Larsen 2000). Understanding the functional response of elk requires additional research on individual elk movement, group size, and vigilance behaviour patterns while foraging in various aspen stem densities with different risks levels and types of predation (e.g., humans, wolves, cougars, or bears), and different densities of elk. Further, these factors should be studied under a range of forest and grassland cover conditions at a landscape level to improve predictions on the effects of forest disturbance in redistributing elk into grasslands, and away from aspen stands. Comparative measures of aspen productivity and ungulate consumption rates must be developed that allow rapid sampling.

3) Traditional knowledge of montane ecosystems- Current ecological research suggests the hypothesis that humans were an important species in the Rocky Mountains, who through hunting and the use of fire, influenced wildlife habitats and herbivore densities and distributions (Kay et al. 1999). Greater understanding of these human-

effects could be attained by anthropological research, and by land management agencies adopting a more participatory role for First Nations in management and research of montane ecosystems (e.g., Parks Canada Agency 2000).

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### APPENDIX A. HISTORICAL PHOTOGRAPH SOURCES

Centre, Hinton, Alberta
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# Study Area

AJ	Athabasca River Valley, Jasper Townsite Area
BB	Bow River Valley, Banff National Park
BK	Bow Valley (outside of Banff National Park) and Kananaskis Valley
ESN	Eastslope North (North Saskatchewan, Red Deer and Ghost watersheds)
ESS	Eastslope South (Elbow, Sheep and Highwood watersheds)
ОМ	Oldman River Valley
WL	Waterton Lakes National Park

Archive	Photo No.	Year	Sector Analysed	Study Area
DFOR	05807	1913	7	AJ
GBOW	NA-0659-103	1915	9	AJ
GBOW	NA-0915-33	1911	8	AJ
GBOW	NA-0915-33	1911	4	AJ
GBOW	NA-0915-41	1911	5	AJ
GBOW	NA-0915-44	1910	7	AJ
GBOW	NA-2062-01	1915	8	AJ
GBOW	NA-2896-07	1913	7	AJ
GBOW	NA-3658-108	1910	8	AJ
GBOW	NA-3658-53	1915	4	AJ
NAC	PA-011068	1914	4	AJ
NAC	PA-011070	1914	6	AJ
NAC	PA-011111	1914	4	AJ
NAC	PA-011157	1914	4	AJ
NAC	PA-011174	1914	5	AJ
NAC	PA-018490	1921	6	AJ
NAC	PA-020487	1921	9	AJ
NAC	PA-087189	1925	6	AJ
WMCR	V439-123-16	1905	6	AJ
WMCR	V573-281	1920	4	AJ
GBOW	NA-0637-08	1889	6	BB
GBOW	NA-0637-09	1889	8	BB
GBOW	NA-0714-236	1925	5	BB

Archive	Photo No.	Year	Sector	Study Area
			Analysed	
GBOW	NA-0714-236	1925	9	BB
GBOW	NA-0937-03	1930	6	BB
GBOW	NA-1363-04	1910	6	BB
GBOW	NA-2635-22	1920	4	BB
GBOW	NA-2635-22	1920	6	BB
GBOW	NA-3379-16	1925	6	BB
GBOW	NA-3490-16	1920	5	BB
GBOW	NA-3884-29	1925	5	BB
GBOW	NA-3884-29	1925	7	BB
GBOW	NA-3884-29	1925	9	BB
GBOW	NA-4654-16	1902	9	BB
GBOW	NA-4697-14	1885	6	BB
GBOW	NA-4697-30	1885	4	BB
GBOW	NA4654-11	1902	7	BB
GBOW	NC-53-071	1905	5	BB
GBOW	NC-53-071	1905	6	BB
NAC	PA-012105	1901	8	BB
NAC	PA-012108	1901	4	BB
NAC	PA-012126	1901	8	BB
NAC	PA-020449	1902	8	BB
NAC	PA-020451	1902	9	BB
NAC	PA-020585	1905	5	BB
WMCR	BNP-1930-1	1930	4	BB
WMCR	NA66-1716	1910	5	BB
WMCR	NA66-1758	1895	2	BB
WMCR	NA66-1758	1895	4	BB
WMCR	NA66-2149	1930	6	BB
WMCR	NA66-2346	1889	7	BB
WMCR	NA71-4335	1920	8	BB
WMCR	NA71-4491	1920	7	BB
WMCR	NG-04-741	1904	4	BB
WMCR	PD49-1-23	1914	4	BB
WMCR	V177PA364-5	1910	9	BB
WMCR	V219PA146-1	1905	4	BB
WMCR	V428PD1-13	1920	4	BB
WMCR	V497PA51-15	1910	4	BB
DFOR	09686	1915	7	BK
DFOR	14208	1921	6	BK
DFOR	14208	1921	5	BK
DFOR	14844	1921	6	BK
DFOR	16441	1923	8	BK

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DFOR	19524	1927	6	BK
DFOR	19527	1927	7	BK
DFOR	19528	1927	7	BK
GBOW	NA-0714-264	1936	5	BK
GBOW	NA-0714-264	1936	6	BK
GBOW	NA-0714-264	1936	8	BK
GBOW	NA-2814-01	1920	6	BK
GBOW	NA-4093-29	1913	9	BK
GBOW	NA-4093-30	1913	8	BK
GBOW	NA-4697-62	1885	6	BK
GBOW	NC-53-034	1905	7	BK
GBOW	NC-53-034	1905	7	BK
NAC	C-000531	1925	6	BK
NAC	C-000531	1925	5	BK
NAC	PA-037555	1881	7	BK
NAC	PA-037556	1884	8	BK
NAC	PA-037556	1884	9	BK
NAC	PA-037556	1884	6	BK
NAC	PA-037556	1884	4	BK
NAC	PA-037970	1884	7	BK
NAC	PA-037970	1884	9	BK
NAC	PA-057202	1927	9	BK
NAC	PA-058050	1926	4	BK
NAC	PA-058050	1926	9	BK
NAC	PA-50779	1883	5	BK
WMCR	V215-PG16	1907	4	BK
WMCR	V369-PA440	1915	2	BK
WMCR	V428-PD2-11	1920	8	BK
DFOR	04001	1911	2	ESN
DFOR	04005	1911	5	ESN
DFOR	05930	1913	9	ESN
DFOR	05931	1913	5	ESN
DFOR	08952	1915	4	ESN
DFOR	08961	1915	6	ESN
DFOR	09254	1915	5	ESN
DFOR	09257	1915	5	ESN
DFOR	11044	1916	6	ESN
DFOR	11044	1916	4	ESN
DFOR	11049	1916	9	ESN

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Archive	Photo No.	Year	Sector Analysed	Study Area
DFOR	14189	1921	6	FSN
DFOR	14213	1920	4	ESN
DFOR	14215	1920	2	ESN
DFOR	14215	1920	3	ESN
GBOW	NA-1263-24	1908	6	ESN
GBOW	NA-1943-30	1922	6	ESN
GBOW	NA-2657-12	1915	5	ESN
GBOW	NA-2657-34	1915	2	ESN
GBOW	NA-3544-25	1911	6	ESN
WMCR	NA-0065-60	1906	6	ESN
WMCR	NA-0065-61	1906	6	ESN
WMCR	NA-0065-471	1905	7	ESN
DFOR	02222	1920	5	ESS
DFOR	09673	1915	1	ESS
DFOR	11918	1916	5	ESS
DFOR	11918	1916	6	ESS
DFOR	16019	1922	6	ESS
DFOR	16466	1923	4	ESS
DFOR	16466	1923	6	ESS
DFOR	16472	1923	3	ESS
DFOR	16472	1923	4	ESS
DFOR	16474	1923	4	ESS
DFOR	16474	1923	5	ESS
DFOR	16475	1923	5	ESS
DFOR	16476	1923	7	ESS
DFOR	17359	1924	2	ESS
GBOW	NA-0067-18	1935	6	ESS
GBOW	NA-0067-18	1935	8	ESS
GBOW	NA-0695-79	1920	6	ESS
GBOW	NA-2674-48	1935	7	ESS
GBOW	NA-2674-48	1935	6	ESS
GBOW	NA-3471-50	1910	5	ESS
GBOW	NA-4450-08	1941	2	ESS
WMCR	V091-588	1935	8	ESS
WMCR	V091-588	1935	5	ESS
WMCR	V091-598	1935	4	ESS
WMCR	V091-598	1935	6	ESS
WMCR	V091-598	1935	7	ESS
WMCR	V091-600	1931	7	ESS
WMCR	V091-600	1935	9	ESS
Archive	Photo No.	Year	Sector Analysed	Study Area
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DFOR	03470	1912	8	OM
DFOR	03470	1912	6	OM
DFOR	03471	1912	6	OM
DFOR	03858	1912	6	OM
DFOR	03858	1912	7	OM
DFOR	06755	1915	5	OM
DFOR	16164	1922	6	OM
DFOR	16165	1922	5	OM
DFOR	16620	1923	8	OM
GBOW	NA-0586-04	1903	8	OM
GBOW	NA-0586-04	1903	9	OM
GBOW	NA-0586-05	1903	5	OM
GBOW	NA-0586-05	1903	7	OM
GBOW	NA-0670-31	1903	9	OM
GBOW	NA-0670-32	1903	8	ОМ
GBOW	NA-0712-26	1925	5	ОМ
GBOW	NA-0712-26	1925	6	ОМ
GBOW	NA-2252-06	1884	5	ОМ
GBOW	NA-2252-06	1884	7	ОМ
GBOW	NA-2833-34	1914	4	ОМ
GBOW	NA-3490-73	1910	6	OM
GBOW	NA-3903-79	1910	8	OM
NAC	PA-037973	1884	6	ОМ
NAC	PA-38288	1900	6	OM
NAC	PA-38289	1900	7	ОМ
WMCR	PA-460-16	1910	4	ОМ
WMCR	PA-460-16	1910	6	ОМ
DFOR	06477	1913	5	WL
GBOW	NA-0716-23	1886	1	WL
GBOW	NA-0716-23	1886	3	WL
GBOW	NA-4954-33	1907	6	WL
GBOW	NA-4954-33	1907	7	WL
NAC	C-035651	1948	9	WL
NAC	C-06847	1874	7	WL
NAC	C-06867	1874	8	WL
NAC	C-06870	1874	6	WL
NAC	C-07087	1874	6	WL
NAC	C-07377	1874	5	WL
NAC	C-79751	1874	1	WL
NAC	C-79753	1874	4	WL

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Archive	Photo No.	Year	Sector Analysed	Study Area
NAC	C-81774	1874	6	WL
NAC	C-81780	1874	7	WL
NAC	PA-019525	1923	5	WL
NAC	PA-019525	1923	6	WL
NAC	PA-74369	1874	7	WL
NAC	PA-74369	1874	6	WL
WMCR	V428-PD4-2	1920	6	WL
WMCR	V428-PD4-5	1920	5	WL
WMCR	V573-210	1921	5	WL
WMCR	V573-210	1921	8	WL

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