REPEAT PHOTOGRAPHY OF MONTANE TREMBLING ASPEN IN THE CANADIAN ROCKY MOUNTAINS

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ABSTRACT

The top-down hypothesis for long-term condition of Rocky Mountain trembling aspen (*Populus tremuloides*) holds that these stands developed under conditions of frequent anthropogenic fires and low herbivory by ungulates due to intense predation by carnivores and humans. To test predictions of the hypothesis, we repeated 156 historic photographs (taken in years 1874 to 1949) showing detailed aspen stand conditions in seven areas along the east slope of the Rocky Mountains in Alberta, Canada. We quantified historic and current aspen stand conditions (e.g., stem spacing by height class and species, barking, and browse class) for 195 stands visible in photographs. Large aspen in historic photographs have no bark-scarring from browsing by elk (*Cervus elaphus*), an indication of low elk use before 1870. Aspen stand ages in historic photographs appear to increase from the period 1874 to 1894 to the period 1895 to 1914, 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 a multi-aged structure with abundant saplings (1 to 4 m high). Current repeat photographs in Banff and Jasper national park areas with high elk density (>4 elk/km^2 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^2) maintained multi-aged 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 support the top-down model for long-term Rocky Mountain montane ecosystem development. Those conditions changed, though, with reduced burning by First Nation cultures by the 1890s, and were accelerated in Banff and Jasper national parks where, in addition to fire, hunting and predators were also controlled. Maintenance of aspen will likely require restoration of long-term low elk density and wary behavior patterns, followed by prescribed burning.

keywords: Alberta, *Cervus elaphus*, elk, fire history, herbivory, *Populus tremuloides*, repeat photography, Rocky Mountains, trembling aspen.

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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 effects of wildlife, fire, and climate on landscapes and vegetation in various situations from rangelands in 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 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, 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 1985*a*). Evidence of fire, such as recently burned trees and logs, and young

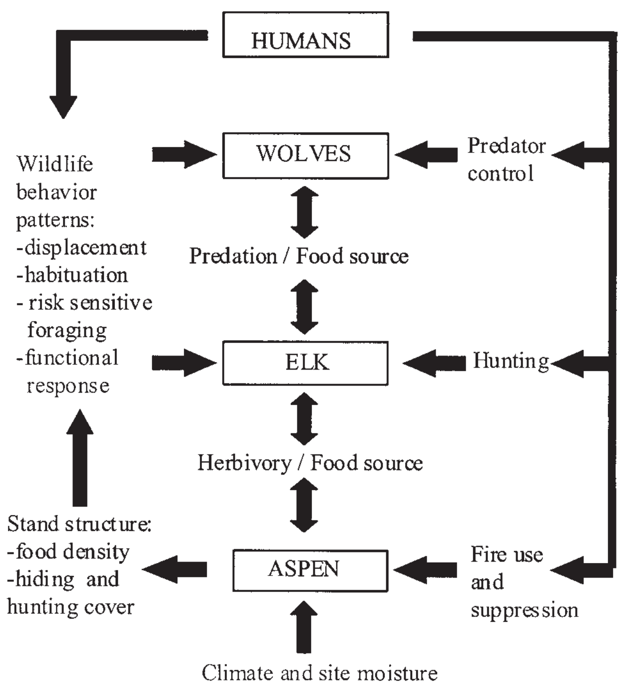

Figure 1. Trophic model linking humans, predators (i.e., wolves), elk, and aspen.

forest regeneration are 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 midsummer 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 dendrochronological 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 four-level trophic model (Figure 1) that links humans, wolves (*Canis lupus*), elk, and aspen through the processes of predation, herbivory, burning, and differential wildlife responses to humans (White et al. 1994; 1998*a*,*b*; 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 U.S. 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. 1998*b*). 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 used 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 east slope of the Rocky Mountains to test predictions made by the top-down hypothesis for aspen decline. We used historic photographs with current retakes to test five specific predictions from the hypothesis (Table 1).

Prediction 1

Long-term elk densities were low and regulated by top-down predation. Because elk at moderate to high density on winter ranges will strip the bark from aspen with their lower incisors (DeByle 1985), older, large-diameter aspen trees visible in historic photographs should therefore 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 affected by predation, and likely regulated by bottom-up processes related to production of forage such as moisture conditions (Coughenour and Singer 1996). 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 ca. 1870 when European land use began to intensify across most the area (Byrne 1968, Kay et al. 1999).

Table 1. Statistical tests and sample sizes for predictions evaluated with attribute data through repeat photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Saplings are aspen stems 2–4 m high, and suckers are 1–2 m high. Sample sizes for montane fire frequency predictions are broken down by north (N) and south (S) regions.

<table>
<tr><th>Prediction</th><th>Statistical hypothesis and null hypothesis</th><th>Statistical test</th><th>Sample size</th></tr>
<tr><td>Long-term low elk herbivory therefore low bark scarring on aspen trees that originated prior to 1870 where visible in historic pictures</td><td>H: mean bark scarring is <35%
H_0: mean bark scarring is ≥35%</td><td>Single sample t-test</td><td>n = 14 from all historical photographs and all areas showing aspen stems that are large enough to have originated prior to 1870</td></tr>
<tr><td>High montane fire frequency reduced by cessation of native burning therefore increasing stand ages as early as 1890s</td><td>H: estimated aspen stand age increases for 20-year periods beginning in 1870s
H_0: estimated stand age equal or less for initial 20-year periods, increases after 1910</td><td>Two-factor ANOVA of estimated aspen stand age in photographs for two areas (north and south), and the three time periods</td><td><table><tr><th></th><th>n</th><th></th></tr><tr><th>Period</th><th>N</th><th>S</th></tr><tr><td>1874–1894</td><td>14</td><td>16</td></tr><tr><td>1895–1914</td><td>25</td><td>21</td></tr><tr><td>1915–1934</td><td>47</td><td>14</td></tr></table></td></tr>
<tr><td>Low herbivory and high fire frequency created a single age class of closely spaced young aspen visible in photographs taken before ca. 1885</td><td>H: mean spacing of saplings is <4 m and suckers is <2 m
H_0: mean spacing of saplings is ≥4 m, suckers is ≥2 m</td><td>Single sample t-tests</td><td>Sectors showing saplings: n = 25
Sectors showing suckers: n = 16
from all photographs taken <1885</td></tr>
<tr><td>High vigor aspen due to low herbivory before 1940; therefore, historic photos in all areas should show numerous aspen suckers and saplings with low barking and low browsing</td><td>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 ≥10 m, barking ≥20%, or browse class ≥2</td><td>Single sample t-tests for historic sapling and sucker spacing (log-transformed) and barking for seven areas, with Bonferroni multiple test adjustment.</td><td>n = 15 for each of seven areas for all attributes except barking where n = 10 per area</td></tr>
<tr><td>Declining aspen vigor in areas of high elk density (1940 to 1999); therefore, substantial increase in spacing of aspen stems in 1–2 m and 2–4 m high classes in Banff and Jasper national parks compared to other areas</td><td>H: significant difference in differences between historic and current spacing of aspen stems between Banff and Jasper parks, and other areas
H_0: no significant difference in differences between current and historic spacing between areas</td><td>One-way ANOVA of difference between current and historic aspen stem spacing for seven study areas</td><td>n = 15 for each of seven areas</td></tr>
</table>

Prediction 2

High montane fire frequency was reduced when First Nation's burning was curtailed due to changing land-use patterns prior to organized fire suppression. Thus early historic photographs should show evidence of young forests with few older stands, due to frequent fires started by native peoples (Kay et al. 1999). Further, the time-since-fire (years), as estimated from vegetation conditions visible in photographs, should increase as early as the 1890s due to reduced burning as native peoples began to utilize treaty lands, and were educated with the European-based fire-prevention doctrine (Murphy 1985). In contrast, the bottom-up model holds that there were minimal effects of native cultural burning on fire regimes (Johnson and Larsen 1991). It therefore predicts no change in fire frequency, or even increased burning due to European settlers, until government-organized fire suppression programs in the Rocky Mountains and foothills became partially effective after ca. 1910 (White 1985*a*, Murphy 1985).

Prediction 3

Aspen stands prior to increasing European influences 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 this time. If tests for these conditions are supported (see above predictions), a group of the earliest photographs (before 1885) of montane aspen in the area should show that almost all have a single young age class with abundant, unbrowsed stems. An alternative hypothesis (Romme et al. 1995) predicts that the age class of aspen stems 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.

Prediction 4

Consistent high vigor, multi-aged aspen should have occurred in all areas due to low herbivory prior 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, Byrne 1968) and nearly extirpated elk (Stelfox 1964). Forests may have aged due to increasingly effective fire suppression (Murphy 1985, White 1985*a*). 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).

Prediction 5

Aspen vigor should have declined in areas of high elk density, 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. 1998*a*). The top-down hypothesis predicts that aspen vigor should decline in those areas, but remain high in other areas of low elk density. Alternative variants of the bottom-up hypothesis (climate change and fire suppression) would predict a general decline of aspen throughout the east slopes 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 inside or outside of protected areas and parks, in environments characteristic of long-term ecosystem states and processes (Banff-Bow Valley Study 1996, White et al. 1998*b*, Kay et al. 1999).

METHODS

Historic and current aspen conditions were evaluated in seven areas along the east slope of the Rocky Mountains in Alberta, Canada (Figure 2, Table 2). All aspen stands were located in the montane ecoregion with relatively low elevations ranging from <1,800 m near Jasper townsite to <2,200 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; K.J. Van Tighem, Parks Canada, personal communication), two national park study areas have relatively high winter elk density (Athabasca-Jasper Townsite vicinity [AJ] and Bow-Banff Townsite vicinity [BB]; >4 elk/km^2). Three areas have moderate elk density (Eastslopes North [EN], Bow-Kananaskis [BK], and Waterton Lakes [WL]; 2–4 elk/km^2), and two areas have low elk density (Eastslopes South [ES] and Oldman [OM]; <2 elk/km^2). Originally, it was planned to include the Ya Ha Tinda Ranch area in the Red Deer valley, but that high-density elk area had to be deleted because few historic photographs of aspen could be located.

We 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). We obtained 20.3 × 25.4-cm (8 × 10-inch) black-and-white prints of all photographs showing trembling aspen stand characteristics. These photographs generally had aspen in the foreground or middle ground and were detailed enough to show 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). When multiple photographs of a view occurred, we chose those with the earliest dates and the clearest visibility of aspen conditions.

From 1996 to 2000, we took repeat images of photographs from the same location at a similar time of year as the original with a 35mm 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 nine sectors (3 × 3). While at the photopoint in the field, we visually estimated historic and current aspen and conifer stand attributes along a subjectively placed transects of approximately 30 m across the historic photograph sectors where aspen was most visible (maximum of three sectors per photograph). A magnifying glass was used to view historic prints and binoculars to view the current scene. Attributes estimated were time-since-fire (years); conifers (>2 m high) spacing and crown width (m); spacing (m), height (m), diameter at breast height (cm), and relative area of black bark (%) for aspen trees (>4 m high) and saplings (2 to 4 m high). For aspen suckers (1 to 2 m high), we estimated spacing (m) and browse class (four levels: <20% twigs browsed [BC1], 20% to 50% browsed [BC2], 50% to 80% browsed [BC3], and >80% browsed [BC4]). The spacing and browse class of suckers <1 m high was not estimated because these were often obscured by shrubs and herbaceous plants. It was often possible to estimate spacing to approximately 0.1 to 0.2 m conifer crown widths and suckers (1 to 2 m high), but only to about 1 m for saplings and trees. Where no individual trees, saplings, or suckers were observed in a transect, the spacing was recorded as 100 m. When an attribute could not be estimated due to poor visibility in the current or historic scene, it was recorded as missing.

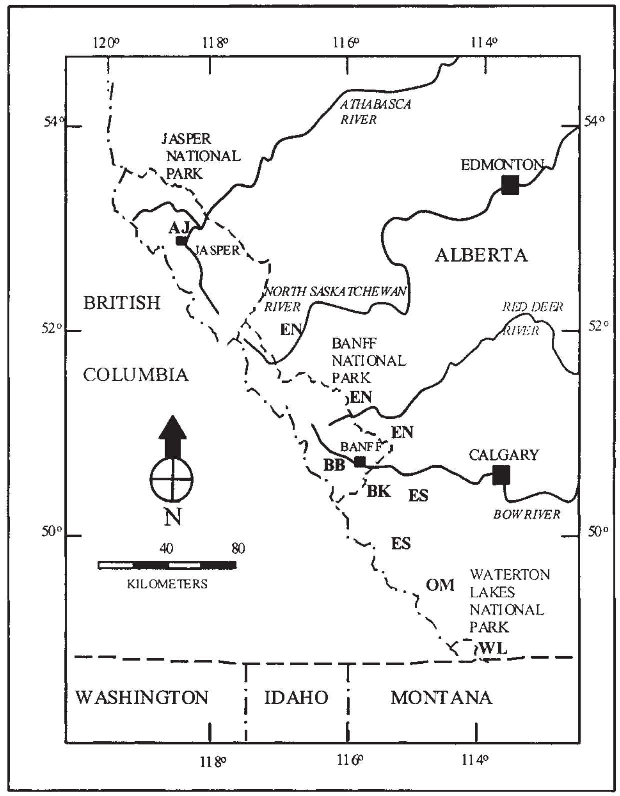

Figure 2. Locations of the seven study areas for repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Study area codes: Athabasca-Jasper (AJ), Bow-Banff (BB), Eastslopes-North (EN), Bow-Kananaskis (BK), Eastslopes-South (ES), Oldman River watershed (OM), and Waterton Lakes (WL).

Ocular attribute estimates were calibrated with other, more quantitative data. Time-since-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 entire province of Alberta (Delisle and Hall 1987), and fire history from a concurrent study (White 2001). Accuracy in estimating aspen stand conditions was improved by reviewing

Table 2. Description of study areas for repeat photography study of trembling aspen stand conditions in the Rocky Mountains, Alberta.

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

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 (White and Feller 2001).

Other data collected included general site location, Universal Transverse Mercator coordinates (from Global Positioning System or 1:50,000 maps), elevation, aspect, and general plant species cover estimates for the selected sectors. We made all current photographs with 35mm color slide film (Kodak Ektagraphic 200 ASA). Slide format provided maximum capability for subsequent viewing of images. Historic prints and current slides were digitally scanned at 300 dpi for report preparation and stored on compact discs for archiving. All materials will be archived at the Whyte Museum of the Canadian Rockies in Banff, Alberta.

For statistical analysis (Table 1), historic and current attributes observed for each sampled photograph sector were entered in a database. As recommended by Underwood (1997), we 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. Then, observations were systematically selected by database number 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 $\log_{10}$ 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 appeared to pre-date 1870. To analyse fire frequency predictions, we combined two study areas to create a "south region" (Waterton and Oldman) and three study areas to create a "north region" (Eastslopes-South, Bow-Banff, and Bow-Kananaskis). Photograph sample size was inadequate to include the Eastslope-North and Athabasca-Jasper areas. This combination of areas provided a minimum of 14 historic photographs per region for each of three periods (1874 to 1894, 1895 to 1914, and 1915 to 1934). The two regions provided the opportunity to contrast fire frequency changes across a relatively broad south-to-north environmental gradient with potentially different First Nation's traditions and occupancy patterns. Because of limited data, unequal sample sizes (Table 1) were used to evaluate the effects of two factors (2 regions × 3 periods of historic photographs) on the variable time-since-fire (years). We used a subset of data, from the earliest photographs (taken from 1874 to 1885) to evaluate tests from Prediction 3 (Table 1) on the combined effects of low herbivory and recent fire on aspen.

RESULTS

In all, we reviewed several thousand historic photographs in the various archival collections. We 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 3; see White [2001] for a complete photograph source listing). 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 (National Archives of Canada, Ottawa, ON) 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 east slope 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 4; Figures 3a, 4a, 5a, 6a). Positions and shapes of the few scars visible in photographs (e.g., Figure 3a) indicated that they originated from pruned branches or fires, not elk browsing. Only 14 images contained trees that likely pre-dated 1870 based upon stem diameter at the time of the photograph (Figure 3a). 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 4, Figure 3b).

In historic photographs, young forest regeneration combined with burned but still standing, saplings and trees (Figure 4a, 5a, 6a) show that aspen stands had, in most cases, been recently burned. The historic estimated mean time-since-fire ranged from 24 years in Waterton Lakes to 32 years in Bow-Kananaskis (Table 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 7). 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 high. Conifers were widely spaced in historic views for most watersheds, but were taller and more closely spaced in current views (Table 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 4a) indicate that most aspen stands in the 1874 to 1885 period were dominated by a young age class of very densely spaced stems (Table 5). Single sample *t*-tests on the $\log_{10}$ of stem spacing confirm predictions (Table 1) of spacing means <2 m for tall suckers, and <4 m for saplings ($P < 0.005$). Stems also had no evidence of barking or browsing by ungulates. Larger-sized aspen were widely spaced, and where they occurred, were of low height and narrow diameter at breast height, indicative of young ages. Aspen saplings and tall suckers were also relatively closely spaced in the complete set of historic images (e.g., Figures 3a, 5a and 6a) with arithmetic mean spacing <18 m (Table 3), and the geometric mean spacing of <3 m (Figure 8) 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 3b, 5b) and had mean spacing of >50 m (Table 4, Figure 8). Saplings remained abundant in other study areas (e.g., Figures 4b, 6b). There was a significant difference between historic and current sapling and tall sucker spacing in Banff and Jasper (Table 6), but no significant difference between current and historic stem spacing in the other five study areas ($P < 0.005$). Historically, aspen saplings showed little evidence of stem barking in all study areas. Currently sapling stems in the Banff and Jasper areas have high black bark cover, but stems in other areas have low black bark cover (Table 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 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 favored sites for trails, roads, camping, hunting, or horse grazing (Byrne 1968).

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 7). 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 four-step mechanism. First, we 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 perhaps logged. All these activities could favor 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 deter-

Table 3. Total number of historic images and sectors (in parentheses) that clearly show aspen stands on the Eastern Slopes, Alberta, repeat-photographed from 1996 to 1999. Photographs are classed by study area and decade of original photograph.

	Study area[a]							
Decade	AJ	BB	EN	BK	ES	OM	WL	Total
1870–1879							11 (11)	11 (11)
1880–1889		5 (5)		5 (9)		2 (3)	1 (2)	13 (19)
1890–1899		1 (2)						1 (2)
1900–1909	1 (1)	11 (12)	4 (4)	2 (3)		6 (8)	1 (2)	25 (30)
1910–1919	14 (15)	5 (5)	13 (14)	4 (4)	3 (4)	8 (11)	2 (2)	49 (55)
1920–1929	4 (4)	8 (12)	4 (5)	11 (14)	9 (12)	4 (5)	5 (7)	45 (59)
1930–1939		3 (3)		1 (3)	6 (11)			10 (17)
1940–1949					1 (1)		1 (1)	2 (2)
Total	19 (20)	33 (39)	21 (23)	23 (33)	19 (28)	20 (27)	21 (25)	156 (195)

[a] Study area codes: AJ = Athabasca-Jasper, BB = Bow-Banff, BK = Bow-Kananaskis, EN = Eastslopes-North, ES = Eastslopes-South, OM = Oldman, WL = Waterton Lakes.

Table 4. Sample sizes per study area, means, and standard errors on means (in parentheses) for repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Attributes estimated in aspen stands are classed by study area and historic (H) and current (C) view.

		Study area[a]													
		AJ		BB		EN		BK		ES		OM		WL	
Attribute	*n*	H	C	H	C	H	C	H	C	H	C	H	C	H	C
Stand age (yr)	15	26 (3)	109 (2)	31 (4)	120 (5)	27 (3)	81 (8)	32 (7)	79 (8)	28 (6)	85 (7)	27 (5)	84 (6)	24 (5)	117 (7)
Conifer (>2 m) spacing (m)	15	39 (9)	13 (6)	31 (6)	6 (1)	99 (24)	70 (26)	59 (10)	30 (8)	77 (11)	45 (11)	72 (18)	25 (8)	124 (43)	69 (33)
Conifer width (m)	15	3.6 (0.8)	3.6 (0.3)	2.6 (0.4)	3.5 (0.3)	1.0 (0.3)	3.0 (0.5)	1.8 (0.4)	2.8 (0.3)	1.5 (0.4)	3.0 (0.4)	4.8 (0.7)	4.2 (0.5)	2.2 (0.3)	4.8 (0.3)
Aspen (>4 m) spacing (m)	15	36 (12)	6 (1)	22 (8)	25 (9)	30 (12)	3 (1)	38 (12)	9 (6)	50 (13)	9 (7)	61 (20)	10 (5)	54 (11)	6 (2)
Aspen (>4 m) height	15	7 (2)	12 (1)	5 (1)	11 (1)	7 (1)	9 (1)	6 (1)	9 (1)	5 (1)	8 (1)	5 (1)	8 (1)	5 (1)	7 (1)
Aspen (>4 m) dbh (cm)	15	10 (2)	18 (2)	9 (1)	18 (2)	11 (1)	16 (2)	11 (1)	17 (2)	11 (2)	14 (2)	9 (1)	14 (1)	9 (1)	12 (1)
Stem (>4 m) barking (%)	10	15 (7)	50 (8)	5 (4)	68 (6)	12 (8)	12 (4)	4 (2)	12 (4)	2 (2)	4 (2)	2 (1)	6 (3)	3 (2)	3 (1)
Aspen (2–4 m) spacing (m)	15	18 (9)	78 (10)	3 (1)	72 (9)	2 (1)	8 (7)	11 (7)	2 (1)	6 (4)	4 (2)	8 (7)	6 (3)	3 (1)	3 (1)
Stem (2–4 m) barking (%)	10	1 (1)	74 (8)	4 (4)	71 (11)	1 (1)	4 (3)	0 (0)	6 (4)	0 (0)	0 (0)	1 (1)	9 (5)	2 (2)	1 (1)
Aspen (1–2 m) spacing (m)	15	3.9 (3.3)	61.7 (10.3)	0.6 (0.1)	77.3 (9.1)	1.2 (0.2)	1.6 (0.6)	2.3 (1.6)	1.8 (0.6)	1.2 (0.6)	1.6 (0.6)	7.5 (6.6)	11.8 (7.1)	0.8 (0.1)	1.7 (0.4)
Stem (1–2 m) browse class	15	1	4	1	4	1	2	1	2	1	1	1	1	1	1

[a] Study area codes: AJ = Athabasca-Jasper, BB = Bow-Banff, BK = Bow-Kananaskis, EN = Eastslopes-North, ES = Eastslopes-South, OM = Oldman, WL = Waterton Lakes.

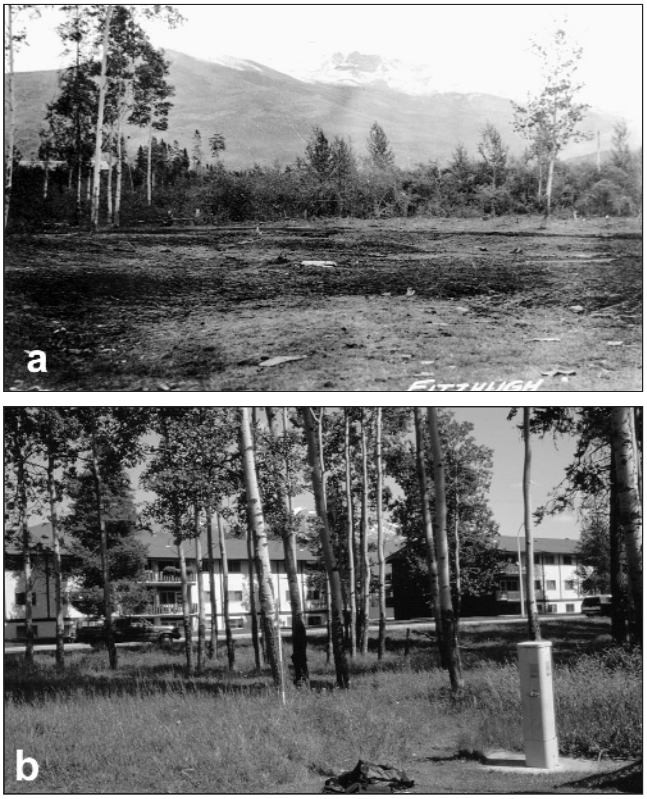

Figure 3. Jasper, Alberta, townsite (foreground) looking east towards Signal Mountain in ca. 1915 (a) and 1999 (b). UTM coordinates: 0426325–5858625. (a) An open overstory of large-diameter aspen trees with an understory of dense sapling and tall sucker regeneration. The large trees likely originated 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 (±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 (approximately 2 m high) indicative of past stripping by elk. All suckers in the foreground of the photograph were recently browsed down to a height of <0.5 m, and several elk pellets groups were found in the stand. Photograph by C.A. White (99-07c-34).

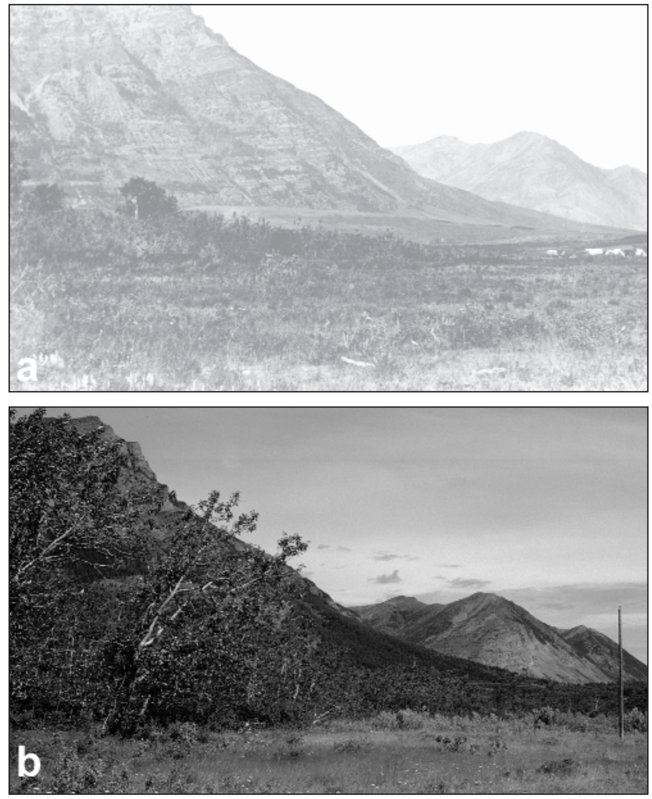

Figure 4. From aspen stands near the northwest shore of Middle Waterton Lake, Alberta, looking northward towards Mt. Crandell (left background) and Bellevue Hill (right background) in 1874 (a) and 1998 (b). UTM coordinates: 0288874–5438586. (a) Dense aspen sucker and sapling regeneration (<4 m high) 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 eastward 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 >300 elk utilize a large grassland area immediately east of the area during the winter. 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 C.A. White (99-08c-27).

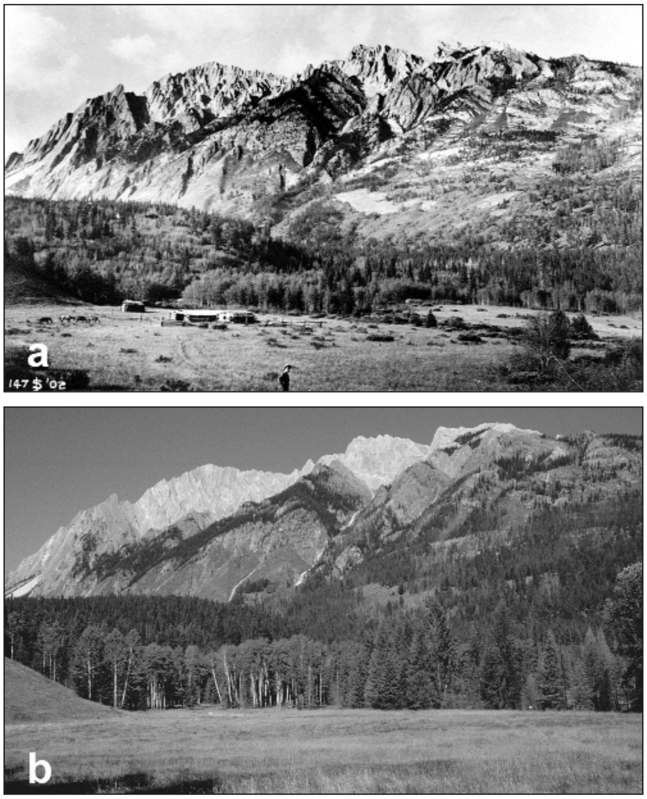

Figure 5. Hillsdale Meadows in Banff National Park, Alberta, looking north towards Mt. Ishbel in 1902 (a) and 1999 (b). UTM coordinates: 0584825–5675683. (a) Dense, multi-aged aspen surround the meadow with aspen saplings and willows along intermittent stream in the center of the photograph. There is 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 ca. 1853 (White 2001, White et al. 2002), 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 <0.5 m. Mature aspen (left and center middle ground) all have extensive bark-scarring to 2 m high. This resulted from extensive elk bark stripping that began in ca. 1940 (Cowan 1947). Portions of the view were burned by wildfires in 1905, 1931, 1945, and most recently by prescribed burns in 1993 and 1998 (White 2001, White et al. 2002). However, these fires appear to have been patchy, and large white spruce and mature aspen and balsam poplar (*Populus balsamifera*) continued to occupy the center-view stream course. Much denser conifer cover occurred in middle ground and background areas. Photograph by C.A. White (99-09c-26).

Figure 6. Site of old Red Deer Ranger Station, Alberta, looking southeast towards upper Panther and Red Deer river valleys in ca. 1915 (a) and 1999 (b). UTM coordinates: 0623279–5724372. (a) Closely spaced, young aspen saplings in draws in right middle ground 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 middle ground and background). Photograph by Dominion Forest Service, courtesy of Glenbow Museum (NA-1943-30). (b) The repeat photopoint, taken approximately 85 years later, was moved about 20 m east of the original location due to aspen regeneration obscuring the view. The ranger station had been moved 2 km up the valley, 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 C.A. White (99-09a-9).

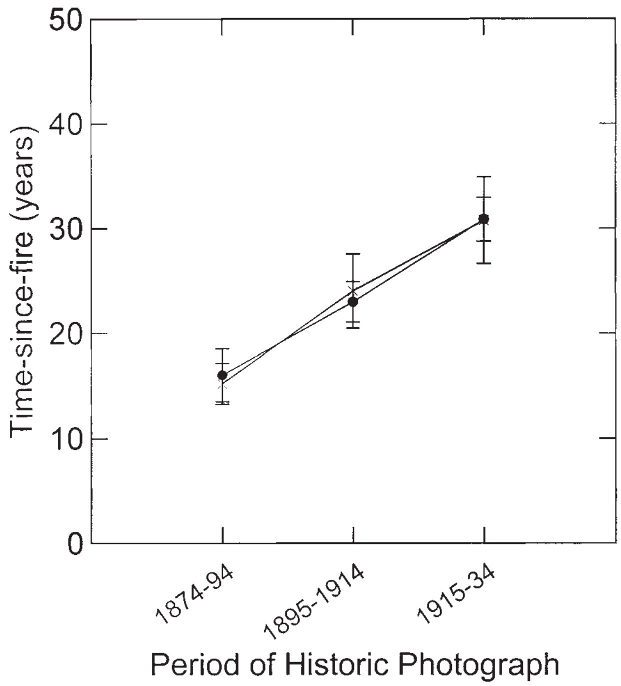

Figure 7. Means ± SEM for time-since-fire (years) as estimated from vegetation conditions visible in historic pictures taken during three periods for two regions in a repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. North region (•) is the combined BB, BK, and ES study areas. South region (×) is the combined OM and WL study areas. See Table 1 for sample sizes.

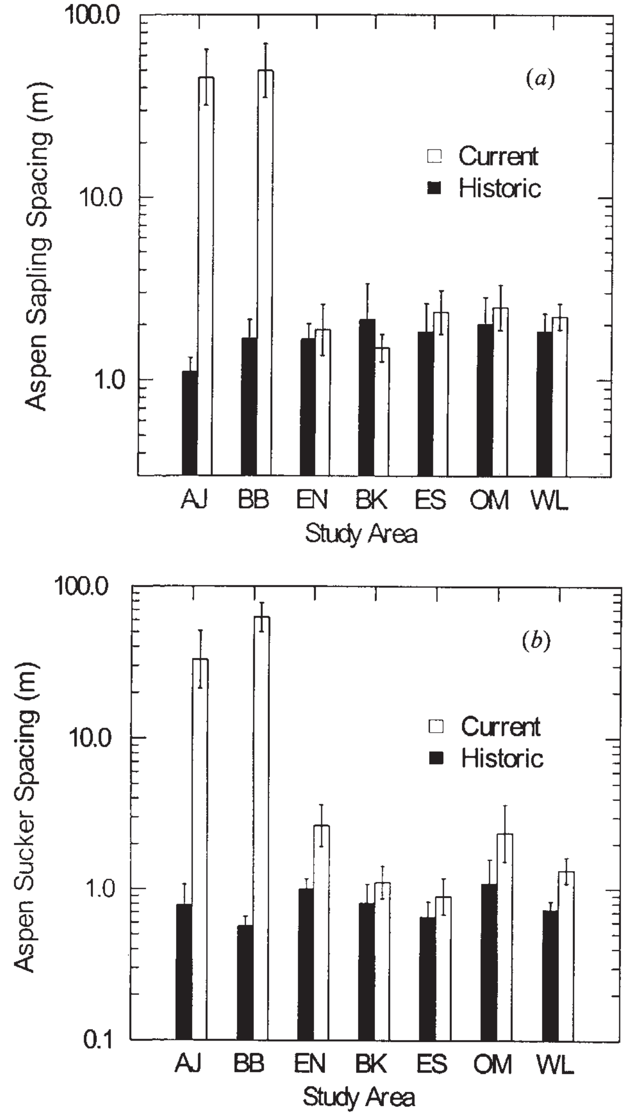

Figure 8. Geometric means ± SEM for (a) spacing (m) of sapling (2 to 4 m), and (b) tall suckers (1 to 2 m) height classes in historic and current photographs of study areas in a repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. The Athabasca-Jasper (AJ) 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 for study area codes and elk density estimations.

mined by general elk density and use patterns (Figure 8). Finally, elk use patterns are, in turn, likely influenced by level and type of human use, as well as by predator travel routes (White and Feller 2001). 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 areas heavily used by people that are avoided by more wary predators such as wolves (Dekker et al. 1995, Paquet et al. 1996, White et al. 1998*b*). This combination of factors, which 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 areas where hunting occurs.

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) 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

Table 5. Sample sizes, means, and standard error on means (SE) for selected attributes of aspen stands in historic photographs taken 1874 to 1885 for repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Sample sizes are uneven because some attributes are not visible in historic photographs.

Attribute	Sample size	Mean	SE
Aspen (>4 m) spacing (m)	25	77	27
Aspen (>4 m) height (m)	18	5	1
Aspen (>4 m) diameter at breast height (cm)	13	9	1
Aspen (2–4 m) spacing (m)	25	2	0
Aspen (2–4 m) barking (%)	10	3	2
Aspen (1–2 m) spacing (m)	16	0.7	0.1
Aspen (1–2 m) browse class (4 levels)	17	1	—

Rhemtulla (1999) to compare historic and current aspen stand conditions due to the small scale of the photographs.

In this study, we 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. However, 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 a 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 4, Figure 8), and can be compared in relative magnitude to other studies.

Elk Populations Before 1870

Although few historic photographs show aspen of sufficient diameter to have regenerated before the 1870s (Figure 3a), 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^2) during this period (Prediction 1). The low level of historic bark-scarring corroborates other sources of evidence that support the low elk density hypothesis for this period (Kay 1990, 1994; 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 traveling 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

Table 6. Mean differences and standard error on mean (SE) differences between current and historic spacing (m) of aspen saplings (2–4 m high) and suckers (1–2 m high) for study areas in repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Different letters in a column denote significant differences between areas ($P < 0.05$). See Table 2 for description of the study areas.

	Saplings		Suckers	
Study area	Mean	SE	Mean	SE
Athabasca-Jasper	70 A	11	57.8 A	11.0
Bow-Banff	69 A	10	76.7 A	9.1
Eastslopes North	6 B	6	0.4 B	0.7
Bow-Kananaskis	–9 B	7	–0.5 B	1.8
Eastslope South	–2 B	4	0.4 B	0.9
Oldman	–3 B	7	4.4 B	10.2
Waterton Lakes	0 B	1	0.9 B	0.4

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. However, Keigley and Wagner (1998) reanalysed those data and concluded that elk were not as abundant as proposed for this area. Further, Martin and Szuter (1999) concluded that wildlife may not have been abundant ca. 1800 throughout the much of the northern Rocky Mountains due to the regional distribution patterns of Native American tribal groups.

Decreasing Fire Frequency

Evidence of frequent, recent fires in historical photographs (Figures 3a, 4a, 5a, 6a) corroborates dendrochronological findings of short fire return intervals (<40 years) in the Rocky Mountain montane ecoregion prior ca. 1930 (Houston 1973; Tande 1979; Arno 1980; White 1985*a*,*b*; White 2001). Current photographs clearly illustrate the success of recent government fire exclusion policies (Murphy 1985, White 1985*a*), which have lengthened the estimated time-since-fire in all Alberta east slope areas by at least 50 years since the historical photographs were taken (Table 4).

Government-organized fire fighting (Murphy 1985) or climate change (Masters 1990) are two possible hypotheses for reduced fire activity. However, these effects are not proposed to have occurred until after 1910 contrary to the data provided here. Alternatively, the cultural burning hypothesis (Prediction 2) is that fire activity would have declined as early as the 1890s due to changing human-use patterns (Kay et al. 1999). Numerous sources (e.g., Lewis 1980, 1982; Barrett and Arno 1982; White 1985*a*; 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 (Barrett 1980, Lewis 1980, Kay et al. 1999). Leafed-out aspen stands are relatively fireproof in midsummer (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 anthropogenic fires that began as early as the 1880s (Murphy 1985, White 1985a). The increase in time-since-fire (years), estimated for photographs from both south and north regions over consecutive 20-year periods after 1874 (Figure 7), 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 midsummer by lightning (Masters 1990, Johnson et al. 1995, Weir 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 anthropogenic 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. Declining fire occurrence at this time may have been particularly pronounced in areas such as Waterton Lakes which likely had less frequent use by native peoples and was not occupied by early settlers (Barrett 1996).

Therefore, reduced cultural burning during dormant seasons appears to be a more robust explanation for the observed decline in fire occurrence over time in montane aspen communities than is climate change (Johnson and Larsen 1991) or other factors. However, more definitive conclusions for this heterogeneous fire regime will require finer-scale contrasts of human use and fire history across study areas and through time, and should include a combination of dendrochronological and anthropological techniques (e.g., Lertzman et al. 1998, White et al. 2002).

Aspen Condition in Historic Photographs (1874 to 1940)

The available evidence supports the hypothesis that herbivory levels were low, and fire frequency was 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 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 (Millar 1915). 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 after 1940 (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 relatively closely spaced saplings and suckers with few larger stems in all areas (Table 4, Figure 8). 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. 1998*b*), and to aspen conditions outside of parks where elk densities are lower (Kay 1990).

We also compared our findings to analyses of historical United States photographs of Rocky Mountain aspen from the Bridger-Teton National Forest (Gruell 1980), 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 U.S. photos show abundant aspen saplings and suckers, but the spacing appears wider in some U.S. views, especially those after about 1910 when elk populations were increasing in Yellowstone and Jackson Hole, Wyoming. However, the older (before 1890) U.S. 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 U.S. 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. 1998*a*). 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). Variants of the bottom-up hypothesis (climate change and fire suppression) predict a general decline of aspen throughout the east slopes. Comparisons of recent photographs (Figures 3b, 5b), however, provide convincing evidence that high levels of herbivory alone dramatically changed aspen stand conditions in Banff and Jasper areas (Table 6, Figure 8), which have the highest ungulate densities of the 7 study areas (Table 1). Aspen stems in Banff and Jasper were heavily barked and browsed by ungulates in comparison to other areas (Table 4)

In the remaining study areas with lower elk densities, aspen regeneration visible in recent photographs is similar to historical pictures (Figures 4b, 6b, 8). 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). As a result, in contrast to efforts 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 fire frequency and long-term elk herbivory patterns created a major difference in aspen stand-age distributions between high and low elk-density areas. Stand-age distributions (Figure 9) from a concurrent study (White 2001) were used to quantify and contrast the conditions visible historically and currently in Banff National Park's Bow-Banff (Figure 5) and the Eastslopes-South study areas. In Banff, few stems have reached tree size (>4 m high) 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 curve" stand-age distribution characteristic of multi-aged forests. In both areas, stem ages >120 years are uncommon due to the historically frequent fires prior to 1900 that maintained almost all aspen stands in young age classes (Table 4).

This stand-age pattern allows a reinterpretation of research conclusions on aspen age-class structure in Yellowstone National Park (Houston 1982, Romme et al. 1995, Meagher and Houston 1998). These studies proposed that the bell-shaped age-class distribution, centered on the period 1870 to 1890, occurred as a result of complex, interacting climatic, disturbance, and herbivory conditions. However, we argue 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) usually prevented Yellowstone aspen 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 centers on the period 1890 to 1930 (Figure 9). 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 1985*a*), and later (ca. 1940) high elk densities (Holroyd and Van Tighem 1983). In contrast, in the nearby Eastslopes South study area with low elk herbivory, aspen continues to regenerate (Figure 9). Thus, we concur with other researchers (e.g., Olmsted 1979, Baker et al. 1997, Kay et al. 1999, Ripple and Larsen 2000) in concluding 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.

However, it is possible that interaction between top-down predation and burning processes could partially explain aspen stand conditions at low and moderate elk density (e.g., mean annual densities of about 2 to 4 elk/km^2). In the Waterton Lakes area, for example, a herd of >300 elk use approximately 30 km^2 of relatively snow-free grasslands for 3 to 6 months each winter (K.J. Van Tighem, Parks Canada, personal communication). These elk have not heavily browsed inclusions of dense thickets of aspen saplings and suckers (Figures 4b, 8; Table 4), and are relatively wary of humans due to periodic hunting seasons on nearby lands. Besides humans, the most common predator in the region is the cougar (*Puma concolor*) (K.J. Van Tighem, Parks Canada, personal communication), which kills by ambushing prey, often near areas of dense cover (Kunkel et al. 1999).

These observations suggest an anthropogenic hypothesis for long-term elk and aspen coexistence in the Rocky Mountains, and aspen's recent decline. Historically, frequent fires, often of human origin, maintained large areas of open habitats interspersed with thickets of recently burned, dense-stemmed aspen. Predator-sensitive elk (Laundré et al. 2001), held at low densities by humans and other carnivores (White et al. 1998*b*), preferentially foraged in the grassland habitats (Ripple and Larsen 2000, Ripple et al. 2001, White and Feller 2001). Forage was abundant here, snow depths were lowest, and predators were most visible. Elk would not frequently forage in or near areas of thick cover, such as dense, young aspen stands, where predation risk may be higher (White and Feller 2001). Thus, the anthropogenic hypothesis holds that long-term, traditional human use (hunting and burning) was critical to the development of montane ecosystems. Those conditions changed, though, with reduced burning by First Nation cultures before 1875 and were accelerated in national parks where, in addition to fire, hunting and predators were also aggressively controlled (Kay et al. 1999).

MANAGEMENT IMPLICATIONS

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. 1998*b*). Where ecosystem objectives require maintenance of ecological integrity or biodiversity (Woodley 1993, Parks Canada Agency 2000), the decline of aspen must be closely monitored and restoration activities carefully considered. One of the most useful paradigms for restoring 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).

If the anthropogenic hypothesis for aspen decline is correct, management of aspen through the long-term 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 land uses. However, managers of Banff National Park have recently implemented conservation strategies based upon long-term range of variability concept that may have application to maintain aspen in many Rocky Mountain parks (Banff-Bow Valley Study 1996; Zinkan and Syme 1997; White et al. 1998*b*; Parks Canada 1997, 1999, 2001). These actions include 1) restoring carnivore populations and movement patterns; 2) managing human use that displaces wary carnivores; 3) translocating or culling elk in

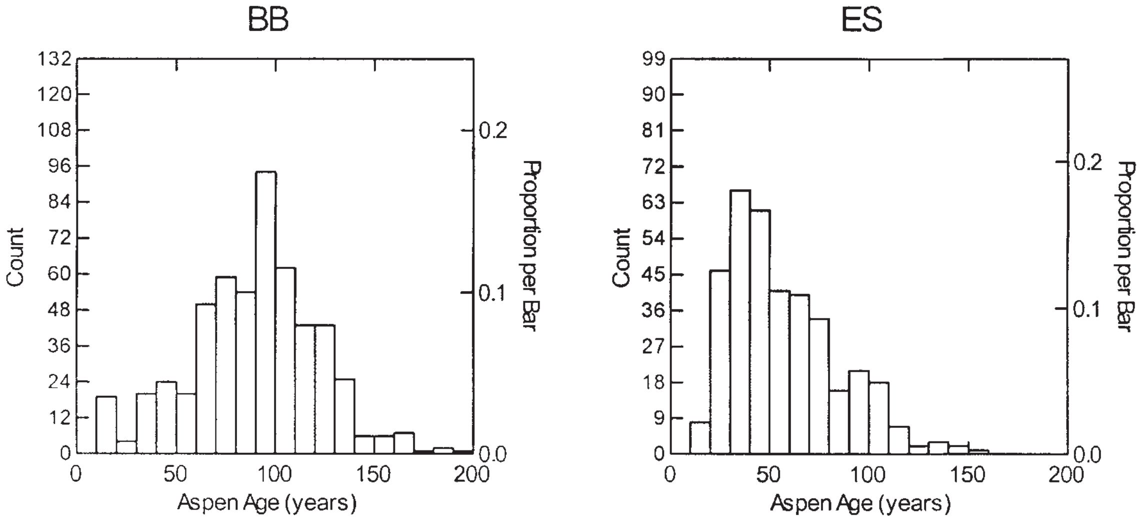

Figure 9. Age distributions (counts and proportion of total sample) for aspen trees (>4 m high) in a repeat-photography analysis of trembling aspen stand conditions in the Rocky Mountains, Alberta. Age distributions in the Bow-Banff (BB) and Eastslope-South (ES) study areas based on a diameter-at-breast-height and tree-age relationship from data in White (2001). Although trees aged <20 years were very abundant in the ES study area, they had not reached tree height and were not included.

areas that have low predation due to high human use; 4) evaluating the restoration of bison, primarily a grazer species, which were an important component of the historic and prehistoric large herbivore assemblage in the area (Kay et al. 1999); and 5) using relatively large prescribed burns in areas of low herbivore density. Implementation of this restoration program recognizes that minimal human ecosystem manipulation is necessary to maintain national parks as ecological baselines (Arcese and Sinclair 1997).

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