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# Aspen, elk, and fire in the Rocky Mountain national parks of North America

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**Abstract** Trembling aspen (*Populus tremuloides*) forests in the Rocky Mountains are an indicator of ecological conditions because they have maintained their presence for thousands of years through vegetative reproduction, and these communities have high biodiversity. Aspen can be tied to ecosystem condition through a 4-level trophic model that links humans, wolves (*Canis lupus*), elk (*Cervus elaphus*), and aspen through the processes of predation, herbivory, burning, and differential wildlife responses to humans. We used a comparative study of research literature and historic photographs to evaluate aspen change over time in 6 Rocky Mountain national parks in Canada and the United States: Jasper, Banff, Yoho, Kootenay, Yellowstone, and Rocky Mountain. Across all parks, aspen has consistent responses to increased browsing by ungulates and decreased frequency of fire. Although aspen was historically vigorous in all parks, today most stands are in decline. Trees are intermediate to mature in age (60-120 years old), and elk browse off new suckers before they reach 2 m in height. Fire, combined with browsing, has hindered regeneration of aspen. The exception to this pattern is northern Jasper National Park where elk densities appear to have been reduced by wolves in the 1970s, and aspen regenerated. We found a gradient of increasing human-caused ecosystem changes in Rocky Mountain national parks: (1) historic conditions with frequent fires and low elk density regulated by humans, wolves, and other predators (i.e., all parks); (2) current conditions of patches of high elk density, where wolves are displaced by human land use, within a matrix of moderate elk density, where wolves and other predators are present (i.e., Banff and Jasper national parks); (3) recent conditions inside parks, where wolves are absent, and very high elk density is regulated by competition for food (i.e., Yellowstone before 1995); and (4) potential future conditions, where increasing human land use around parks displaces carnivores and reduces hunting, and very high elk density occurs throughout landscapes. Aspen stands regenerate well in areas of low elk density and in some areas of moderate elk density; however, in areas of high and very high elk density, aspen does not regenerate to heights >2 m, and burning accelerates clone deterioration. Our recommendations to national park managers are to restore carnivores, use fire in areas of low elk density, and control human uses that displace carnivores.

**Key words** *Cervus elaphus*, ecological integrity, elk, indicator species, national park management, *Populus tremuloides*, trembling aspen

Trembling aspen (*Populus tremuloides*) forests are an important community type in the Rocky Mountain national parks of Canada and the United States. In Banff and Jasper (Alta., Can.) and Yoho and Kootenay (B.C., Can.) 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

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(Wyo., 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 (Colo., U.S.), aspen stands are found throughout the montane ecoregion (Marr 1961, Peet 1981). 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). Frequent (<40-yr return interval), low-intensity fires in low-elevation areas (Houston 1973, Tande 1979, Arno 1980, White 1985) 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; Kay et al. 1994, Romme et al. 1995). Small aspen stands in conifer forests may survive through long fire-free intervals (>100 yr) by periodic release of suckers in forest gaps (Kay 1997*c*).

Because aspen stands occupy moist, nutrient-rich sites at low elevations, they have very high biodiversity, exceeded only by riparian zones in the Rocky Mountains. 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 (*O. virginianus*), moose (*Alces alces*), and a diverse range of small mammal species. Bird diversity is also greater in aspen stands than nearby conifer forests or grasslands (Flack 1976, Turchi et al. 1995).

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

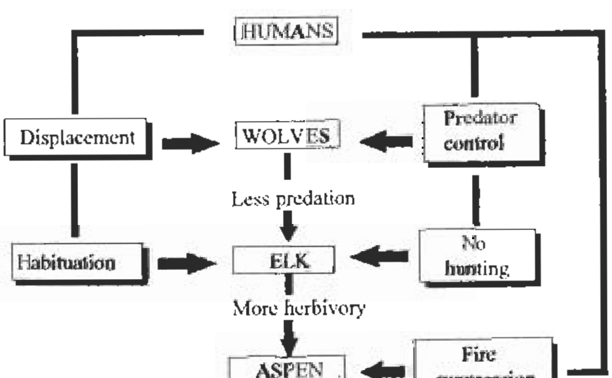


Fig. 1. A simple ecological model linking humans, wolves, elk, and aspen under current conditions in and near Rocky Mountain national parks.

processes have been altered substantially during the last 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. 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). Explanations for an observed decline of aspen and willow (*Salix* spp.) in Rocky Mountain national parks fall into 3 general categories (Keigley 1997): climate change (Singer et al. 1994, Romme et al. 1996), fire suppression (Houston 1982), and human land-use changes that have caused high densities of elk (Cahalane 1941, Kay 1990, Keigley 1997).

Alternative viewpoints on the reasons for aspen and willow decline are based upon a fundamental ecological question: was the Rocky Mountain montane ecosystem generally structured from the "top-down" (i.e., predator-driven), or from the "bottom-up" (i.e., resource-limited)? Current ecological theory (Hunter and Price 1992, Estes 1996) holds that numerous factors may determine whether resources or predators will dominate in the regulation of natural communities. We used a comparative-studies approach to evaluate factors that may be important in determining aspen condition and trend through time in the Rocky Mountain national parks and to determine whether top-down or bottom-up forces predominate.

## Study area and methods

We reviewed the literature to provide a general overview of aspen's value as an ecological indicator. We then conducted a detailed review of published and unpublished literature to compare trembling aspen condition and trend in Jasper, Banff, Kootenay, Yoho, Yellowstone, and Rocky Mountain national parks for 1872–1997. Primary sources of information included analyses of historical photographs, ungulate browsing impacts, wildlife exclosures, and responses of vegetation to prescribed burning. For each park, we attempted to obtain responses of aspen or willow to various states of the trophic model's key indicators and processes, such as density of elk, frequency of fire, and presence of wolves. We then analysed aspen condition over time in each park (1) to test the general hypothesis that Rocky Mountain montane ecosystems were historically maintained by strong, "top-down" predator regulation of herbivores such as elk, and (2) to describe a general pattern of the effects of increasing, modern, human land uses on the montane ecoregion of Rocky Mountain parks.

# Results

## *Aspen as an ecological indictor*

In the montane-ecosystem model (Fig. 1), aspen has high value as an indicator of overall ecosystems and ecosystem processes. Aspen is responsive to major ecological processes such as fire, vegetation succession, and herbivory, and is easily evaluated over space and time.

***Fire and vegetation succession.*** Aspen has consistent, predictable responses to various Rocky Mountain fire regimes (Arno 1980). One of aspen's vital attributes is its capacity to produce suckers from surviving roots after burning. Pure aspen stands in areas otherwise dominated by conifers are indicative of short fire intervals (<20 yr) that reduce the cover of seed-reproducing conifers, but favor aspen sprouting (Noble and Slayter 1980, Kessell and Fischer 1981). Further, aspen is relatively intolerant to the conditions created by increasing conifer cover and has low densities in older forests dominated by conifers.

***Herbivory.*** Aspen is bighly palatable to elk, deer, and moose. Elk use the twigs of aspen <2 m in height, and they strip the bark off taller trees (Fig. 2). We used forage-value ratings for elk provided by Nelson and Leege (1982) to compare aspen to other Rocky Mountain plant species (Table 1). Aspen have similar forage ratings to other high-value shrubs, such as serviceberry (*Amelanchier alnifolia*), willow (*Salix* spp.), and rose (*Rosa* spp.). Optimal-foraging theory (Stephens and Krebs 1986) predicts that elk will eat the most nutritionally profitable portions of these favored species before browsing moderately palatable trees and shrubs, such as Douglas-fir and buffaloberry (*Shepherdia canadensis*), or low-palatability species, such as spruce (*Picea* spp.) and shrubby cinquefoil (*Potentilla fruticosa*). This predictable spectrum of shrub use allows us to relate the condition of aspen browsed by elk to numerous other plants and food chains. For example, Keigley (1997) showed that in areas of northern Yellowstone National Park where aspen is heavily browsed, narrowleaf cottonwood (*Populus angustifolia*) also experiences intense herbivory. If aspen is heavily used, willow will also be heavily browsed, with food-chain impacts on beaver (*Castor canadensis*; Chadde and Kay 1991, Nietvelt and Bayley 1997). Similarly, when aspen is heavily used by elk, berry abundance on shrubs such as buffaloberry and serviceberry, important food sources for grizzly bears (*Ursus arctos*), is sharply reduced (Kay 1990).

In contrast, grass species may not be sensitive indicators of long-term herbivory. Climatic variables (e.g., rainfall, temperature, overwinter snowfall) are primary

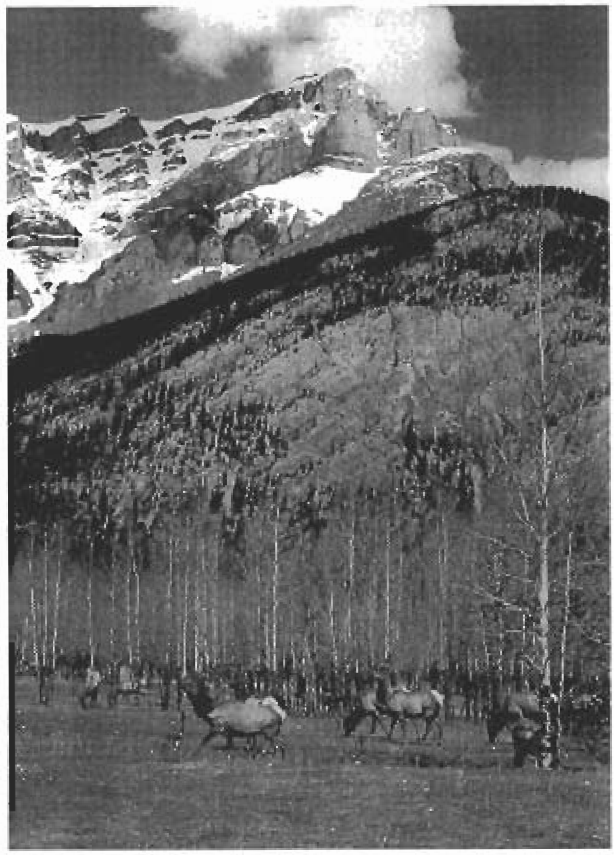

Fig. 2. Human-habituated elk in Banff National Park, Canada foraging in aspen stands with no young age classes of trees and extensive bark scarring on mature trees.

factors driving biomass production in grasslands (Lauenroth 1979). Further, some palatable species, such as timothy grass (*Phleum pratense*), respond to intense herbivory with increased biomass production (Frank and McNaughton 1992, 1993). This enhances the competitive status of these grasses in comparison to other less grazing-adapted species (Wallace and Macko 1993).

***Measurement and evaluation.*** One of aspen's greatest values as an indicator is the ease with wbich it can be monitored over space and time by simple measurement techniques, such as repeat photography, ungulate-proof exclosures, and belt transects (Olmsted 1979, Houston 1982, Gruell 1983, Kay 1990, Kay et al. 1994). For example, aspen stand conditions, such as density, age class, and degree of ungulate browsing, are visible in historic photographs. Herbivory levels can also be evaluated over long time periods because of the visibility of barking scars. Bark stripping occurs on small-diameter (<20 cm) trees at even moderate elk densities, thus giving a long-term record of variable elk populations (Kay and Wagner 1994, Kay 1997*b*).

Table 1. Examples of montane ecoregion plant species grouped by different levels of forage use based upon forage ratings developed by Nelson and Leege (1982).

| Plant species type | Low forage use | Moderate forage use | High forage use | Very high forage use |
|---|---|---|---|---|
| Shrubs and trees | Low use of all species | Moderate use of trembling aspen, serviceberry, willow, rose, red osier dogwood (*Cornus stolonifera*) | High use of all species to left plus moderate use of lodgepole pine, Douglas fir, balsam poplar (*Populus balsamifera*), gooseberry (*Ribes* spp.), snowberry (*Symphiocarpus* spp.), buffaloberry, wolf willow (*Eleagnus commuta*) | High use of all species to left plus moderate use of: spruce, bearberry (*Arctostaphos uvaursi*), birch (*Betula* spp.), shrubby cinquefoil, alder (*Alnus* spp.) |
| Grasses | Low use of all species | Moderate use of most fescues (*Festuca* spp.), bluegrasses (*Poa* spp.), wheatgrasses (*Agropyron* spp.), common timothy | High use of all species to left plus moderate use of most reedgrasses (*Calamagrostis* spp.) | High use of all species to left plus moderate use of muhly (*Muhlenbergia* spp.) |
| Herbs | Low use of all species | Moderate use of fireweed (*Epilobium angustifolium*), cow parsnip (*Heracleum lanatum*), lupine (*Lupinus* spp.), beard tongue (*Penstemon* spp.) | High use of all species to left plus moderate use of fleabanes (*Erigeron* spp.) cinquefoils (*Potentilla* spp.), and groundsels (*Senecio* spp.) | High use of all species to left plus moderate use of buttercups (*Ranunculus* spp.), goldenrods (*Solidago* spp.), horsetails (*Equisetum* spp.) |

## *Aspen condition over time in Rocky Mountain national parks*

Our literature review provided relatively complete summary information for past and present factors related to aspen stand conditions in select Rocky Mountain parks (Table 2). We have also included data on beaver and willow communities in landscapes near aspen stands.

Photographs of aspen taken prior to 1910 (Fig. 3) show a consistent pattern for all Rocky Mountain areas (Gruell 1979, 1980, 1983; Houston 1982; Kay and Wagner 1994; Kay et al. 1994; Baker et al. 1997). In all parks, at the time of establishment, most aspen stands were shrub-like in young age classes. Photographs provide abundant evidence of frequent fires, such as burnt snags and young forest regeneration. No evidence of browsing on aspen or willow twigs is visible. The few mature aspen stands seen in old photographs (Fig. 3) show no sign of elk bark-stripping (Kay 1990, Kay and Wagner 1994, Baker et al. 1997, Kay 1997*b*). This is evidence of low elk densities as early as the 1850s.

Researchers in all parks observed a consistent pattern of declining vigor in aspen stands when elk populations became high (Packard 1942; Cowan 1947; Olmsted 1977, 1978; Kay 1990). Declining aspen stands have low density (<500 stems/ha), trees are intermediate to mature in age (60- to 120-yr-old), and new suckers are browsed off by elk before reaching 2 m in height (Fig. 2). As a result of early observations of habitat degradation, several parks culled elk herds between 1940 and 1970 (Houston 1982, Woods 1991, Hess 1993, Dekker et al. 1996). Elk populations declined to levels permitting aspen regeneration in Rocky Mountain National Park (Olmsted 1979, Baker et al. 1997) and immediately outside Yellowstone National Park, where culling reduced the number of elk migrating across the park boundary (Kay 1990).

Aspen inside wildlife exclosures (Fig. 4) is multi-aged and vigorous in all parks (Olmsted 1977, 1979; Trottier and Fehr 1982; Kay 1990; Kay et al. 1994; Baker et al. 1997). In Banff National Park, the largest area of regenerating aspen is within the recently fenced area along the Trans Canada Highway (Kay et al. 1994). Within this corridor, new aspen stems now exceed heights of 2 m on sites that range from xeric to hydric.

Elk culling ceased in all Rocky Mountain national parks by 1970 (Houston 1982, Woods 1991, Hess 1993). Since then, elk near developed areas increased in numbers. They have become highly habituated to humans and browse intensively on aspen and willow (Kay 1990, Hess 1993, Banff-Bow Valley Study 1996). The greatest impacts on aspen and other vegetation are in northern Yellowstone National Park where the

Table 2. State of trembling aspen-related attributes in the montane ecoregion of selected national parks in the Rocky Mountains of Canada and United States. Due to similar data, we have grouped Banff with Jasper, and Yoho with Kootenay.

| Attribute | Banff and Jasper (Alta., Can.) | Yoho and Kootenay (B.C., Can.) | Yellowstone Ecosystem (Wyo. and Mont., USA) | Rocky Mountain (Colo., USA) |
|---|---|---|---|---|
| Aspen bark stripping before c. 1850 from historic photographs | No bark stripping visible (from photos in Whyte Museum of Canadian Rockies collection) | No bark stripping visible (from photos in Whyte Museum of Canadian Rockies collection) | No bark stripping visible (Kay 1990) | No bark stripping visible (Baker et al. 1997) |
| Aspen sucker condition at park establishment from historic photographs | Prolific suckering, no twig browsing visible (Kay et al.1994) | | Prolific suckering, no browsing visible (Gruell 1979, 1980, 1983; Houston 1982; Kay 1990; Kay and Wagner 1994) | Prolific suckering, no browsing visible (Baker et al. 1997) |
| Aspen condition c. 1930–1970 in areas with high elk density during elk culling period | Suckers browsed off before reaching 2 m in height, stems barked (Cowan 1947) | Stand aging indicates little regeneration during this time period (Kay 1997*c*) | Suckers browsed off before reaching 2 m in height, stems barked (Houston 1982, Kay 1990) | Most suckers browsed off before reaching 2 m in height, stems barked (Packard 1942, Olmsted 1979, Hess 1993) |
| Aspen condition c. 1970–1990 in high visitor use areas with high elk density | Suckers browsed off before reaching 2 m in height, stems barked, no trees less than 80 years old (Kay et al. 1994) | Suckers browsed off before reaching 2 m in height, stems barked, few trees less than 60 years old (Kay 1997*c*) | Suckers browsed off before reaching 2 m in height, stems barked, no trees <80 years old (Kay 1990, Kay and Wagner 1994) | Suckers browsed off before reaching 2 m in height, stems barked, few trees <80 years old (Olmstead 1979, Baker et al. 1997) |
| Aspen condition c. 1970–1990 in wildlife exclosures | Abundant suckers, all-aged stands (Trottier and Fehr 1982, Kay et al. 1994) | No wildlife exclosures | Abundant suckers, all-aged stands (Kay 1990, Kay and Wagner 1994) | Abundant suckers, all-aged stands (Olmsted 1979, Baker et al. 1997) |
| Aspen response to fire c. 1970–1990 | Many trees >2 m killed by fire, prolific post-fire suckers browsed off before reaching >2 m in height (Kay et al. 1994) | Aspen stands burned in 1968 wildfire were at high elevations with low elk use and have produced suckers >2 m (C. E. Kay, unpubl. data) | Many trees >2 m killed by fire, prolific post-fire suckers browsed off before reaching >2 m tall, some clones killed completely (Bartos and Mueggler 1979, 1981; Bartos et al. 1994; Kay and Wagner 1996; Romme et al. 1995; C. E. Kay, unpubl. data) | Aspen stand burned by 1977 prescribed fire did not regenerate any stems >2 m in height, or lasting increases in sucker production (C. E. Olmsted, unpubl. data) |
| Condition of willows and beaver populations c. 1970–1997 | In areas with moderate or greater elk density, heavy willow browsing, beaver populations decreasing (Nietvelt and Bayley 1997) | | Willow browsing by elk heavy, beaver numbers down substantially from historic levels (Kay 1990, 1997*a*; Kay and Wagner 1994; Chadde and Kay 1991; Singer et al. 1994) | Willow browsing by elk heavy, beaver numbers down substantially from historic levels (Hess 1993) |
| Aspen and willow response in areas recolonized by wolves | Abundant suckers, stems near trails reaching >2 m height (Dekker 1985; Dekker et al. 1996; C. A. White, unpubl. data) | | No data available | No areas recolonized by wolves |
| Elk density on winter ranges c. 1970–1990 | 3–10 elk/km$^2$ in low wolf predation areas; 1–2 elk/km$^2$ in wolf predation areas (Dekker et al. 1996, Paquet et al. 1996, Banff-Bow Valley Study 1996) | | 12–25 elk/km$^2$ (Houston 1982, Singer et al. 1994) | 15–25 elk/km$^2$ (calculated from data in Hess 1993: 21–26, Baker et al. 1997) |

Fig. 3. Company D, Minnesota National Guard camp at Little Blacktail on Yellowstone National Park, Wyoming northern winter range in 1893 showing no elk-induced bark injury, multi-sized (aged) aspen, and little or no twig browsing by ungulates. Photo by F. J. Haynes, H-3070, courtesy of Haynes Foundation Collection, Montana Historical Society, Helena.

elk population is food-regulated (Coughenour and Singer 1996). Elk eat all palatability classes of forage, including normally unpalatable species such as spruce (*Picea engelmanii*; Kay 1997*a*).

Prescribed fires conducted between 1974 and 1985 in Banff and Jasper national parks and in Jackson Hole, Wyoming failed to regenerate aspen to heights >2 m (Kay 1990, Bartos et al. 1994, Kay et al. 1994, White et al. 1994, Kay 1997*a*). Fires killed mature trees, and elk browsed off new suckers before they reached tree height. Some burn areas were small and may have concentrated elk use (Bartos and Mueggler 1979, 1981). Subsequent large prescribed fires in Banff and the 1988 wildfires in Yellowstone National Park stimulated abundant aspen suckering (Fig. 5A), but also failed to regenerate aspen to heights >2 m (Kay et al. 1994, White et al. 1994, Romme et al. 1995, Kay and Wagner 1996). In Yellowstone, the 1988 wildfire, followed by intense elk browsing, killed some aspen clones (C. E. Kay, unpubl. data; Fig. 5B).

Researchers in United States and Canadian parks report sharp declines in beaver colonies and surrounding areas of willow habitat. In Banff National Park, the number of beaver lodges in Vermilion Lakes declined >90% since the 1970s because elk herbivory on willows has significantly reduced the amount of food and dam-building material available for beaver (Nietvelt and Bayley 1997). Although beaver and tall-willow communities were once common along northern Yellowstone streams, beaver are now "ecologically extinct," and willow cover is sharply reduced, except in wildlife exclosures (Kay 1990, 1997*a*; Chadde and Kay 1991, Kay and Wagner 1994, Singer et al. 1994). Similarly, beaver and willows are in sharp decline in Rocky Mountain National Park (Hess 1993).

Dekker (1985, Dekker et al. 1996) was the first to record a deviation from the general pattern of aspen and willow decline in the Rocky Mountain parks. In areas of northern Jasper frequented by wolves during the 1970s (Carbyn 1974*a*, 1974*b*), Dekker (1985) noted prolific aspen and willow regrowth. C. A. White (unpubl. data) verified those observations. A collection of 1950s photographs shows intensive elk browsing on aspen with no young age classes visible. Carbyn (1974*a*) documented high kill rates of elk by recolonizing wolves during the 1970s. He calculated that wolves could eliminate elk in the area within a few years if observed predation rates continued. At approximately the same time, tree-ring dates indicate that a new cohort of aspen suckers regenerated in many stands, particularly those close to wolf-frequented trails (C. A. White, unpubl. data). By 1997 many of the new stems had reached 3–5 m tall (Fig. 6), and although elk use of aspen appears to be increasing, many stems will likely survive to mature tree age. Similar conditions may be occurring in areas recently recolonized by wolves in Banff National Park (C. A. White, unpubl. data).

## Discussion

### *Evaluating alternative hypotheses for aspen decline*

We use information on trembling aspen condition and trend in several Rocky Mountain national parks to test hypotheses on the decline of aspen. Alternate explanations for aspen decline are based upon whether, over the long-term, elk population levels were generally high and regulated by competition for food (1 principal hypothesis with 2 variants), or generally low at a predator-regulated equilibrium.

Fig. 4. Ungulate-proof wildlife exclosure in Upper Beaver Meadows, Rocky Mountain National Park, Colorado, in September 1997.

Fig. 5. Aspen burn plot 27A in Yellowstone National Park, Wyoming: (A) August 1989 after the clone was top-killed by the 1988 fire, and abundant new suckers sprouted from the live root system; and (B) August 1996 after several years of heavy elk browsing when no live suckers remained and the root system appeared to be dead.

***Food-regulation ("bottom-up") hypothesis.*** This paradigm predicts that a long-term, stable state of montane areas occurs when aspen is browsed extensively by abundant, food-regulated elk. This is termed "natural regulation" in Yellowstone National Park (Cole 1971, Boyce 1991, Coughenour and Singer 1996). 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 food-regulated 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 do not support this viewpoint in any of the Rocky Mountain parks. Photographs of mature aspen taken at the time of park establishment show no bark-stripping (Table 2), indicating long-term low elk density (Kay and Wagner 1994). Furthermore, archaeological-site data and early explorer journals for the Rocky Mountains in the United States (Kay 1990, 1994, 1997*b*) and Canada (Kay et al. 1994, Kay and White 1995) repeatedly show a pattern of low elk abundance.

***Fire-suppression hypothesis.*** A variant on the food-regulation hypothesis is based upon fire effects. Gruell (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 "swamp" 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). However, monitoring of numerous burn areas in and near Rocky Mountain national parks (Table 2) shows that this has not happened (Bartos et al. 1994, Kay et al. 1994, Kay 1997*b*). Instead, the combination of fire and high-intensity elk browsing actually accelerated the demise of aspen (Kay and Wagner 1996). Given the long-term historical regime of frequent fires (<40-yr fire cycle) in the montane ecoregion (Houston 1973, Tande 1979, Arno 1980, White 1985), the change of the role of fire in these ecosystems—from acting as a stimulant to becoming a deterrent of aspen growth—

Fig. 6. Aspen regeneration at Willow Creek, Jasper National Park, Canada that occurred during a period of intensive wolf use in the area.

has serious ecological implications. Reoccurrence of a short fire regime in areas of high herbivory could rapidly degrade aspen stands.

***Climate-change hypothesis.*** A further elaboration of the food-regulation hypothesis proposes that a warmer and dryer climate since the 1930s has been a significant factor in the failure of aspen to regenerate (Houston 1982, Romme et al. 1995). However, this view appears to be without support because of the consistent regeneration and growth of aspen in numerous wildlife exclosures in parks throughout the Rocky Mountains (Table 2). If climate were a significant factor, aspen condition in exclosures should be the same as outside (Kay 1990, 1997*b*; Baker et al. 1997). Also, if climate were a major factor, aspen outside of park boundaries should also be declining, but this is often not the case (Kay 1990).

***Predator-regulation ("top-down") hypothesis.*** Many 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 and White 1995; Baker et al. 1997). From our analyses of aspen in various Rocky Mountain parks, we hypothesize that the current die-back of aspen clones inside parks is due to recent human-caused changes to the long-term ecological conditions that once favored 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 predator-regulation hypothesis (Kay and White 1995; Kay 1997*b*,*c*; White et al. 1998), 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.

## Predicted patterns of predators, elk, and aspen in Rocky Mountain national parks over space and time

On the basis of the predator-regulation model, we hypothesize that there are 4 general landscape-ecology types that influence human–wolf–elk–aspen interactions in Rocky Mountain national park ecosystems (Fig. 7). We view these as a gradient from long-term ecological conditions to recent situations of increasing impact by modern human land uses. This hypothetical framework simplifies reality and does not account for factors such as highway and culling mortality that also alter park wildlife density and behavior patterns. However it provides a preliminary model to make predictions for ecosystem attributes under a variety of landscape-level "treatments" (Table 3).

***Low elk density: open, shifting mosaic system with human and wolf predation.*** This is our hypothetical long-term condition for the Rocky Mountains (Kay et al. 1994, Kay and White 1995, Kay 1997*b*). Information on ecological conditions for this type of environment comes from dendrochronology (i.e., fire-scars), old photographs, explorer journals, and current areas in the northern Rocky Mountains where wolves, humans, and other predators prey on elk (Kay et al. 1994, White et al. 1998). We predict that elk density was generally low (<1 elk/km$^2$) 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) 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) and low ungulate browsing structured aspen and other montane vegetation types into vigorously regenerating communities. A few older stands occurred, which by chance alone, escaped frequent burning (Johnson et al. 1995).

***Moderate and high elk density in open system with spatially fixed patch-predator and prey-refuge zones.*** The pattern of wolf recolonization and effects on elk population observed by Dekker et al. (1996) in Jasper is now being studied in Banff National Park (Huggard 1993, Paquet et al. 1996, Banff-Bow Valley Study 1996, Hurd et al. 1997). Current human land use has fixed montane landscapes into patterns of park and nonpark areas, developed and nondeveloped zones, hunted and nonhunted areas, and large areas with low fire occurrence (Fig. 7B). Compared to long-term ecosystem states and processes, landscape pattern is unique in space and time (Kay 1990, Kay et al 1994, White et al. 1994, Kay and White 1995). Heavy human use on elk winter ranges with no hunting results in human habituation of elk inside parks (Shultz and Bailey 1978, Casserier et al. 1992, Banff-Bow Valley Study 1996), whereas hunted elk outside parks often avoid humans (Lyon 1979). Wolves, which are more wide-ranging than elk, remain wary of humans due to hunting or other sources of human-caused mortality in or near parks (Paquet et al. 1996).

The result of differential behavior of elk and wolves is a predation zone in park areas with low human use. Our prediction (Table 3) is that elk density here is moderate (e.g., 1–3 elk/km$^2$). Aspen regeneration >2 m tall is sporadic, occurring mainly

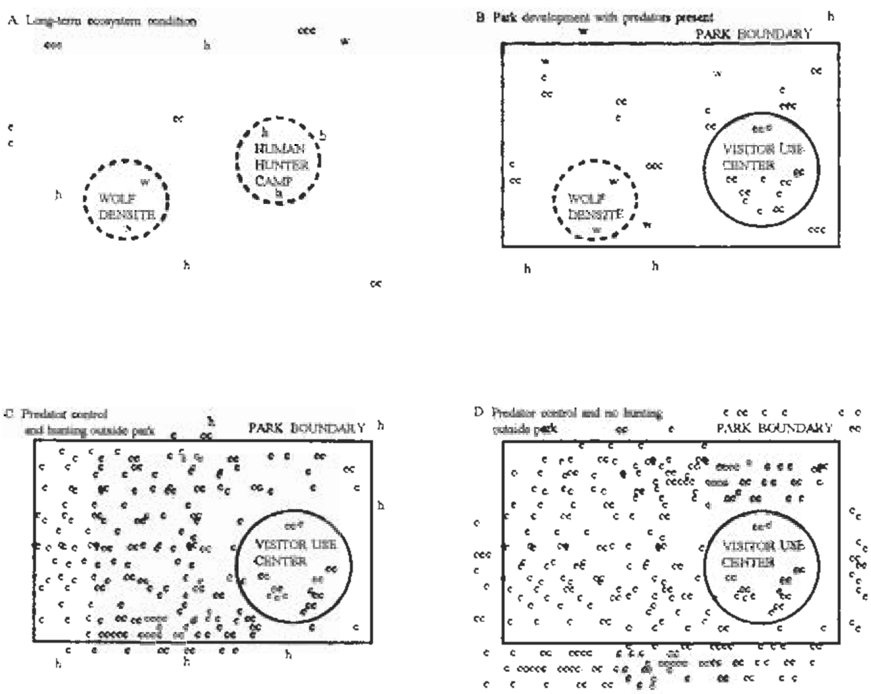


Fig. 7. Past and current patterns of human land use in and around Rocky Mountain national parks with human hunters (h), wolves (w), elk (e), shifting activity centers (dashed lines), and permanent land-use boundaries (solid lines).

near trails frequented by wolves but avoided by elk (C. A. White, unpubl. data). In the absence of some human predation on elk, wolves and other carnivores do not appear capable of reducing elk to the low density (Kay 1994, 1997*b*; Boyce 1996) necessary to propagate all aspen clones. The predation-zone matix surrounds prey-refuge patches near visitor service centers or busy roads avoided by carnivores (Dekker et al. 1996, Paquet et al. 1996). In prey-refuge patches we predict high density (e.g., 4–10 elk/km²) of human-habituated elk (Banff-Bow Valley Study 1996, Nietvelt and Bayley 1997). Many refuge-patch elk are nonmigratory (Woods 1991) but may partially self-regulate their population density by temporary movement, or dispersal, out of the refuge before they starve. They do not generally use very low palatability species such as spruce, but may exert high impacts on numerous species of palatable plants, such as aspen and willow, and moderately palatable species, such as buffaloberry (Woods 1991).

***Very high elk populations in closed, spatially fixed systems with low predation.*** An extreme manifestation of intensifying modern human land uses in and near parks occurs in areas where few elk are hunted by humans and other wildlife predators may be eliminated (Fig. 7C). Elk do not disperse to lower density areas because of developments, blocked movement routes, or unfamiliarity with alternative habitats. Competition for food resources regulates elk at densities of >10 elk/km² (Coughenour and Singer 1996). In this situation elk severely impact high and moderately palatable montane plant species (Kay 1990, 1997*b*). Starving elk will consume even low palatability species such as spruce (Kay 1997*a*).

***Very high elk density throughout ecosystems.*** Further intensification of human occupation often includes "gateway" communities and recreational developments around park boundaries. If these land uses reduce hunting mortality, displace carnivores, and cause ungulates to habituate to humans, ungulate populations may increase throughout the landscape, as in the case of white-tailed deer in the eastern United States (Donahue 1997). Though food-driven migration and dispersal may occur across park boundaries, eventually, populations will increase towards a food-regulated density throughout the landscape (Fig. 7D).

## *Future research needs and interim management recommendations*

Comparative analysis of trembling aspen in Rocky Mountain national parks under various elk population and human land-use conditions can be used to test general models that predict herbivory effects and montane ecosystem conditions over space and time. Aspen is a key indicator in these models because it responds relatively consistently to various treatments of human impacts, herbivory, and fire in all parks. The existing data provide strong evidence to support the role of top-down processes (e.g., predation and human-caused fires) in the long-term structuring of montane trembling aspen communities. This 4-level model may be like the key role human harvesting of sea otters (*Enhydra lutris*) plays in structuring kelp forests along the North American west coast (Estes and Duggins 1995, Estes 1996).

In the montane aspen case, there are substantial needs to test the generality of the model over broader temporal and spatial scales. We need to know effects

Table 3. Predictions made for ecological conditions in human–wolf–elk–aspen–willow communities in valley bottom, montane ecoregion at 4 levels of elk densities.

| Predicted attribute | Low elk density (<1 elk/km$^2$) | Moderate elk density (1–3 elk/km$^2$) | High elk density (4–10 elk/km$^2$) | Very high density (>10 elk/km$^2$) |
|---|---|---|---|---|
| Description | Human and wolf predation, shifting mosaic | Predator zone | Prey refugia zone | Closed system, low predation |
| Type areas | Long-term pre-Columbian ecosystem, some current areas with human hunting, wolves, and other predators | Most areas in Banff, Jasper national parks away from towns | Near Banff and Jasper, high visitor-use areas | Northern Yellowstone Winter Range (1975–1995) |
| Wolf density | Low due to lack of prey | Moderate to high | Low | No wolves |
| Wolf habituation level to humans | Unhabituated | Moderate habituation | A few wolves become highly habituated, but have high human-caused mortality rates | No wolves |
| Summer elk migration to higher elevation areas | Yes, predator-driven | Yes, predator-driven | No, predator-driven | Yes, food-driven |
| Elk population regulatory mechanisms | Predator-regulated | Predator-regulated | Regulated by competition for food causing dispersal into surrounding low-density areas | Competition for food causes high overwinter mortality and low birth rates |
| Elk habituation level to humans | Extremely wary of humans | Moderately to highly wary depending on human hunting outside refugia | Highly habituated, may attack humans | Moderately to highly habituated |
| Elk utilization of aspen, willow, and other shrubs | Low, no browsing evident | Moderate use of highly palatable species such as aspen, willow, saskatoon | Highly palatable species heavily utilized | Very high with all vegetation utilized |
| Beaver and willow condition | Abundant beaver and willow | Abundant beaver and willow | Low abundance of willow and beaver | Very low abundance of willow and beaver |
| Conifer utilization by elk | No browsing | No browsing | Douglas-fir browsed, spruce increases in abundance | All conifers browsed, reduced abundance |
| Fire effects | Maintenance of long-term willow and aspen abundance | Potential reduction of long-term willow and aspen abundance | Reduction of long-term willow and aspen abundance | Major reduction of long-term willow and aspen abundance |
| Ecological integrity and biodiversity | High | Moderate | Low | Very low |

of herbivory, fire, and forest succession on montane plant assemblages, and the interactive effects of these factors (Romme et al. 1995). As Schmitz and Sinclair (1997) proposed for understanding interactions between white-tailed deer and shrubs, a complex relationship may exist between plant condition and elk density, only discernible by analyzing a range of conditions, not just inside–outside exclosure comparisons, in areas of high elk density. Researchers must quantify herbivore density, distribution and behavior patterns, and fire regimes that assist managers in achieving various objectives. We recommend holistic ecosystem analysis similar to approaches of research on white-tailed deer habitats in eastern North America (de Calesta and Stout 1997, Waller and Alverson 1997).

Further, we need much better information on the long-term factors that regulated montane elk populations. Predictions made by Fryxell et al. (1988), based on African ungulates may apply to these elk populations: it appears that even migratory elk in mountain environments were regulated by predators to low population densities (Kay et al. 1994). How did these long-term patterns differ from the refuges from predators that have developed in Rocky Mountain parks today (Banff-Bow Valley Study 1996)? In western national parks, public pressures and perceptions will continue to limit human predation on elk (e.g., elk culls). Therefore, it is important to explore whether non-human predation (i.e., wolves and other carnivores) can regulate elk populations to levels that allow aspen stand regeneration. If recolonizing wolves in parks dramatically reduce elk populations, this will trigger needs for further research on maintaining wolf populations in low-density herbivore systems. Current research in Banff and Yellowstone national parks focuses on wolves in landscapes with high elk density (Boyce 1996, Paquet et al. 1996).

Finally, demonstrating and quantifying the significance of aspen's ecological relationships has implications for definitions of ecological integrity required by many national park management plans (Woodley and Theberge 1992, Canadian Heritage 1994). Maintenance of aspen and related communities is confounded by almost contradictory policies in Rocky Mountain national parks that stipulate (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 (Boyce 1991). However, we make 4 specific interim recommendations that have application in many Rocky Mountain parks: restore carnivores, bison (*Bison bison*), and fire, and carefully manage human use. These recommendations are derived from the Banff-Bow Valley Study (1996), a 3-year independent commission, that reported to Canada's minister responsible for national parks on the state of Canada's first national park. This direction forms the basis for a recently approved management plan for Banff National Park (Parks Canada 1997, Zinkan and Syme 1997).

***1. Restore carnivores***. The weight of evidence clearly demonstrates the role of carnivores in the long-term structuring of Rocky Mountain ecosystems. In the past, keystone species (Mills et al. 1993) in these landscapes were humans and wolves. Their combined effects on ungulates structured much of the ecosystem (Kay 1994, 1997*b*; Kay et al. 1994). In national parks, where human hunting is now largely prohibited, we must, wherever possible, maintain populations of predators such as wolves. Where predators cannot be restored, the Banff-Bow Valley Study (1996:179) recommends that elk culling or relocation and fencing may be necessary. Where predators are restored and herbivore populations decline, managers must anticipate how large carnivores can be sustained in park ecosystems with much lower prey density.

***2. Restore bison***. In Banff and Jasper national parks, bison were once the dominant large herbivore in low-elevation areas. They have since been extirpated and elk are now predominant (Kay et al. 1994). This is significant because bison are mainly grazers, but elk browse extensively. Bison restoration may help maintain long-term ecological conditions (Kay et al. 1994).

***3. Restore fire, but with caution.*** Managers often view fire as a panacea to maintain "natural" ecological conditions in Rocky Mountain national parks. Clearly, frequent fires, often started by Native peoples, structured low-elevation ecosystems. However, to simply add fire back into landscapes with high elk density is ecological malpractice that will damage, possibly permanently, numerous plant and animal populations (Olmsted 1979). We can successfully restore fire only while maintaining herbivore density at levels where palatable species assemblages regenerate. Further research is required to identify these herbivore population thresholds over a range of fire regimes (e.g., size, intensity, frequency) and site conditions.

***4. Manage human use.*** The Rocky Mountains are one of the world's scenic treasures. They are a regional, national, and international attraction driving a massive tourist, recreation, and real-estate industry 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). Furthermore, in developed areas, complete control of fire and human hunting changes ecosystems from long-term ecological conditions. 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).

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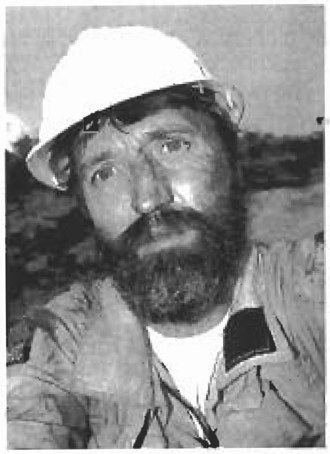

***Clifford A. White*** (photo) is a conservation biologist for Banff National Park. His interest in wildlife and vegetation interaction was stimulated by over 20 years of work with wildland fire, including stints as a fire-crew member, a park warden, and the National Fire Management Coordinator at Parks Canada headquarters in Ottawa, Ontario. During the 1980s, Cliff conducted prototype large-area, high-intensity prescribed burns in the Rockies, burning many stands of trembling aspen. From 1990 to 1996 he managed Banff's team of wildlife and plant ecologists, conducting research and adaptive management in Canada's first national park. He has a B.S. from the University of Montana and an M.S. from Colorado State University (both in forest science). Cliff's ongoing doctoral research at the University of British Columbia in Vancouver focuses on elk herbivory under various conditions of predation and landscape disturbance. He has served on advisory committees and boards of directors for environmental and cultural resource organizations including the Alpine Club of Canada, the Whyte Museum of the Canadian Rockies, and the Biosphere Institute of the Bow Valley. ***Charles E. Olmsted*** is a professor of environmental studies and the Coordinator of the Environmental Studies Program at the University of Northern Colorado. He received a Bachelor's degree from Earlham College, a Master's degree from the University of Oklahoma, and a doctorate from the University of Colorado in Boulder. Dr. Olmsted is a second generation professional ecologist. He has worked in a broad variety of Rocky Mountain ecosystems. His pure research efforts have focused on allelopathic influences and plant succession, and plant herbivore interactions as they influence larger ecosystem processes. His applied research has included contract and consulting work with the National Parks Service and the Nature Conservancy. He has served on the board of directors of the Defenders of Wildlife, the Colorado Wildlife Federation, the Colorado Native Plant Society, and the Colorado Alliance for Environmental Education. ***Charles E. Kay*** has a B.S. in wildlife biology and an M.S. in environmental studies, both from the University of Montana, and a Ph.D. in wildlife ecology from Utah State University. He is an adjunct assistant professor in the Department of Political Science and a senior environmental scholar at Utah State University's Institute of Political Economy. Charles takes a "consilience" approach to science, integrating wildlife and vegetation ecology with archaeological and historical research. In 1990 he completed a detailed, independently funded evaluation of Yellowstone National Park's "natural regulation" management program. He continues to study Rocky Mountain ecosystems through contracts with Parks Canada, the U.S. Agricultural Research Service, the U.S. Forest Service, and large ranch owners. Charles is currently writing a book for Oxford University Press on Native Americans' role in structuring western North American ecosystems, and compiling ecological observations from the original Lewis and Clark journals. As a long-time researcher, hunter, wildlife photographer, and natural history writer, Charles is familiar with the Rocky Mountains from Utah to the Yukon.

*Associate Editor: Krausman*