RESTORING ASPEN RIPARIAN STANDS WITH BEAVER ON THE

NORTHERN YELLOWSTONE WINTER RANGE

by

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Samuel David McColley

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ABSTRACT

Aspen (*Populus tremuloides*) on the Gardiner Ranger District, Gallatin National Forest, have declined over the last half-century. In an attempt to reverse this trend, beaver (*Castor canadensis*) were reintroduced in Eagle Creek in 1991. Beaver promote aspen suckering through their dam and lodge building activities. In 2005, I assessed the long-term effects of beaver on aspen stands and the associated riparian area in the Eagle Creek Drainage.

Aerial photographs taken in 1990 and 2005 were used to compare changes in riparian area vegetation where beaver were reintroduced. Aspen canopy cover decreased (P<0.05) from 43% to 25% on Eagle Creek (29 ha) between 1990 and 2005. Willow (*Salix* spp.) cover increased (P<0.05) from 10% to 14% and alder (*Alnus incana*) cover and water surface area doubled during the same period.

Aspen recovery was estimated by comparing vegetative changes among control sites with <10% beaver use (n = 5), active beaver sites (n = 6), sites abandoned for 1-3 years (n = 7), sites abandoned for 4-6 years (n = 4), and sites abandoned for 7-11 years (n = 5). Thirty, 1-m^2 plots were used to determine aspen density and one 60-m^2 belt transect was used to calculate size-class distributions at each site.

Aspen stem densities in active sites and sites abandoned by beaver for 1-3 years were similar (2.6/m^2) and increased (P=0.01) compared to all other sites (1/m^2). In addition, sprout and sapling densities were greater (P=0.01) in these sampling areas. However, aspen suckers were not able to grow taller than 2m on sites absent of beaver for 4-11 years, which prevented aspen recovery.

Ungulate herbivory on aspen was assessed by comparing differences in 14 fenced (3 x 3m) and unfenced (3 x 3m) areas over 2 growing seasons. Growth rate of aspen suckers was greater (P=0.001) in fenced areas (32cm/year) compared to unfenced areas (0.25cm/year) due to ungulate herbivory. Total ungulate density for Eagle Creek was equivalent to 17.6 elk/km^2 in the winter of 2005-06. Beaver activity stimulated the growth of aspen sprouts and saplings, but ungulate herbivory prevented successful aspen recovery in Eagle Creek.

INTRODUCTION

The canopy cover of aspen (*Populus tremuloides*), willow (*Salix* spp.), and other woody plants have declined over the last century on the northern Yellowstone winter range (NYWR) (Houston 1982, Kay 1990, Beschta 2003). Elk (*Cervus elaphus*) herbivory has reputedly been the most significant contributor to this decline (Kay 1990, St. John 1995, NRC 2002a, Wagner 2006). One-third of the NYWR is located on the Gardiner Ranger District, Gallatin National Forest (GNF). The GNF is directed in the Forest Plan to provide wildlife habitat by maintaining and enhancing aspen and willow stands (GNF 1987). In an effort to comply with this mandate, beaver (*Castor canadensis*) were reintroduced into Eagle Creek, Gardiner Range District, in 1991(D. Tyers pers. comm. 2005).

Beaver create disturbances in aspen and willow stands by cutting down the overstory. These species usually respond by increasing the production of vegetative stems, or ramets. Beaver utilize aspen and willow as a food source and as construction material for dams and lodges. Dams impound water which promotes the growth of woody plants, including aspen and willow. Beaver often deplete their food resources and consequently disperse to a different segment of the stream. In the absence of beaver, ramets may be able to grow into mature stems.

Recent surveys (Smith 2005 unpub) indicate beaver are virtually nonexistent in aspen riparian communities across the NYWR, although historically they were abundant (Warren 1926, Smith 2005 unpub). Currently, Eagle Creek is the only area on the NYWR that has the once common ecological assemblage of beaver, aspen, willow and elk. This unique area presents an opportunity to study how aspen and willow stands respond to beaver disturbance in riparian areas with high ungulate densities.

Warren (1926) and Jonas (1955) speculated that aspen stands may recover 20-30 years after beaver disturbance on the NYWR. Although aspen stands have only been free of beaver activities for no more than 11 years in Eagle Creek, findings from this project will help managers predict the long-term effects of beaver on aspen under current condition on the NYWR. These insights, in turn, may help explain the overarching ecological processes at work on this important ungulate winter range.

Wolves (*Canis lupus*) were reintroduced in Yellowstone National Park (YNP) in 1995. Reestablishing an apex predator on the NYWR may have a trophic cascade effect (Ripple et al. 2001, White et al. 2003). Schmitz et al. (2000) describe a trophic cascade as the direct and indirect influences of predators on herbivores resulting in reduced herbivory pressure on plant communities. A 50% decline in the elk population on the NYWR since 1995 and changes in ungulate movements and foraging habits support these claims (Fortin et al. 2005, White 2007). Ripple and Beschta (2005a, 2006) have reported the

recovery of woody plants in localized riparian areas on the NYWR, which they believe is in response to reduced elk herbivory. Reduced herbivory may enable aspen suckers to escape the browse zone (<2m). If woody plants are able to escape ungulate herbivory, then beaver cutting could stimulate the growth of more ramets and help restore aspen and willow riparian stands.

In this study I evaluated the condition of aspen and willow riparian stands in Eagle Creek 15 years following beaver reintroduction. I investigated if beaver were able to stimulate vegetative growth in these stands through overstory cutting and the creation of water impoundments. In addition, I investigated if new sprouts could progressively increase in height and eventually grow into the overstory given current ungulate densities.   My objectives were to determine if (1) beaver disturbance since 1991 had altered aspen and willow cover or water surface area for the entire Eagle Creek riparian area, (2) aspen and other woody plant were able to produce enough recruitment stems to sustain the stand after disturbance, and (3) ungulate herbivory was influencing aspen recovery after beaver disturbance.

LITERATURE REVIEW

Aspen

Aspen is one of the few deciduous tree species in the northern Rocky Mountains and has occupied this area for thousands of years (Jones and DeByle 1985). In the western U.S., aspen are more commonly found at sites with enhanced soil moisture, such as seeps, riparian areas, and swales. Aspen communities are a small portion of the vegetative cover, but sustain abundant and diverse wildlife species (DeByle 1985a). For example, they provide a critical forage source for ungulates within coniferous forests and the single source of tree canopy cover in grassland habitats (DeByle 1985a). Other plants found within aspen stands, such as forbs, grasses, and shrubs, are also important for wild ungulates. Aspen stands can produce 3 to 4 times more forage than adjacent uplands. As deciduous riparian species, they also maintain healthy watersheds by decreasing erosion and increasing groundwater levels and water quality (DeByle 1985c).

Aspen reproduce via seeds and vegetative processes. However, establishment of aspen by seeds is rare (Kay 1993). Vegetative reproduction is stimulated by disturbances sustained to the overstory. Aspen is a clonal species that is apical dominate. The apical meristem tissue produces auxin, a growth suppressor hormone, that prevents vegetative growth (Hicks 1972). Once the apical meristem is removed, the growth stimulator hormone cytokinin builds up in

the root mass. This initiates the growth of ramets, an asexual reproductive stem,

which emerges from meristematic tissue on the root mass (Schier et al. 1985).

Vegetative reproduction stimulated by disturbances decrease auxin levels

permitting ramet growth. Ramets emerge as small stems and may eventually

grow to be mature trees as succession progresses.

Ramets may be categorized into different size-classes based on height

and diameter measurements. By evaluating the distribution of ramets among

size-classes, land managers are able to assess if stands are self-perpetuating.

One way to determine this is by calculating recruitment. Recruitment stems are

>2m in height and have a diameter at breast height (DBH) <5cm (Kay 1985).

Stems that have achieved this size-class have escaped most effects of herbvory

and are likely to grow into the overstory (Kay 1985). If recruitment stems are

greater than, or equal to, the number of overstory stems (>2m in height and

>5cm in DBH), then that stand is considered self-replacing (Kay 1990).

If aspen clones are not replacing themselves, disturbances can initiate

ramet growth. Theoretically, ramets take ≈20-30 years in YNP to reach the

overstory after disturbance, but in areas with high ungulate densities this may

take as many as 75-150 years (Warren 1926, Jonas 1955, Smith 1980). In

riparian areas wind, flooding, and beaver are some of the natural disturbances

that can initiate aspen ramet growth.

Willow

Willows are an abundant shrub species in riparian areas in the Rocky Mountains. There are numerous species and most are confined to moist sites. Willow species distribution changes with elevation and geomorphology (YNP 1997). For example, Bebb willows (*Salix bebbiana*) are common along high elevation steams with gravely substrates. Similar to aspen, willows provide forage and a source of cover for wildlife (YNP 1997). They also play a role in maintaining healthy watersheds. Willows preserve riparian systems by reducing erosion and stream corridor channelization and by protecting water quality (Brooks 1997).

Willows reproduce asexually by advantageous rooting by truncated or buried stems, and sexually through seed production. Numerous wind-dispersed seeds are often produced in early summer (Wolf 2004). Willows reproduce asexually in riparian areas via disturbances, such as beaver cutting and flood events. Unlike aspen, willows recover more quickly from disturbances. For example, willows recovered in two years after simulated beaver cutting when protected from ungulate herbivory in Rocky Mountain National Park (RMNP) (Baker et al. 2005). This capacity for rapid recovery enables willow to be successful in highly disturbed riparian areas.

Beaver

Beaver have been used as a management tool to enhance and maintain streams and riparian areas (Scheffer 1938, Smith 1983, Kay 1994, Olson and Hubert 1994). Their impacts on a stream system can create and sustain new riparian areas (YNP 1997). Beaver create impoundments that increase water surface area, increase the water table, and provide a catchment for nutrients (Naiman et al. 1986, 1988, Lowry and Beschta 1994). Munther (1983) calculated that, on average, streams that are absent of beaver have a riparian area of 2-4 acres/mile in the Rocky Mountains, whereas streams with beaver have a riparian area of 24 acres/mile. An increase in riparian area can equate to an increase in forage production for ungulate species. However, over-browsed riparian areas can reduce suitable beaver habitat (Olson and Hubert 1994).

Beaver use aspen and willow for food and building material for structures such as dams and lodges. Beaver cutting creates a disturbance in aspen and willow riparian stands which initiates an asexual growth response. Moreover, willow stems not eaten by beaver can develop asexually. In many cases, beaver deplete the woody riparian plants in an area and disperse to more suitable habitat. Abandoned beaver sites provide ideal conditions for sexual and asexual woody plant establishment (Wolf 2004).

In northern Ontario, aspen did not show signs of recovery on 15 abandoned (7 sites <12 years since abandonment and 8 sites > 12 years since

abandonment) beaver sites (Barnes and Mallik 2001). However, willow and alder (*Alnus incana*) were able to recover to original levels 5 years after beaver abandonment. Three reasons were provided for the lack of aspen recovery: (1) a function of their sampling methods; (2) re-cutting of aspen suckers by beaver; and (3) herbivory by white-tailed deer.

Ungulates

Elk, mule deer (Odocoileus hemionus), white-tail deer (Odocoileus virginianus), bison (*Bison bison*), and moose (Alces alces) utilize aspen, willow and other woody plants as a food source year-round (DeByle 1985a, YNP 1997). Ungulates often prefer the new growth of woody plants. Elk also strip the bark off mature aspen for food (DeByle 1985b). Heavy, continuous browsing by ungulates can prevent the growth of aspen and willow stems into mature-sized trees or shrubs (Kay 1994, Romme et al. 1995, Ripple and Larsen 2000). Ramets continually suppressed by ungulates through browsing are unable to replace mature stems. Mature stems eventually die of senescence, fungal infections, or other causes (Kay 1994). Without the replacement of mature stems, aspen and willow stands can decline.

Beaver and Ungulates

Research indicates that beaver and ungulates individually alter woody plants (Barnes and Dibble 1988, Naiman et al. 1988, Kay 1990, Baker et al.

1997, Donkor and Fryxell 1999, Barnes and Mallik 2001). However, less is known about the compounding affects of these herbivores on aspen and willow stands on ungulate winter range, including the NYWR.

In Allegany State Park, New York researches suggested that white-tail deer had a negative effect on the recovery of aspen after beaver disturbance (Gese and Shadle 1943). This and other studies caution that continuous herbivory by ungulates and beaver may preclude aspen from recovering (Barnes and Mallik 2001).

Moreover, the compounding effects of multiple herbivores may change aspen communities' composition (Jonas 1955). If aspen are not able to recover after beaver disturbance, the vegetative type may change to willow and alder communities (Barnes and Mallik 2001). Since aspen recover 20-30 years after beaver disturbance (Warren 1926, Jonas 1955) and willows take 2-3 years to recover, willows might gain a competitive edge over aspen in areas with high ungulate densities.

As with aspen, the cumulative effects of beaver and ungulates on willow have been reported. In RMNP, 90% of willow stems were browsed by ungulates after simulated beaver cutting (Baker et al. 2005). Additionally, willow stems recovered 148% when fenced from ungulate browsing compared to 78% when unfenced after cutting (Baker et al. 2005). This suggests that cutting promotes willow growth, but ungulate browsing prolongs recovery rates.

The Northern Yellowstone Winter Range

The NYWR boundary is commonly defined as the winter range of Rocky Mountain elk (Houston 1982). It is 1500km² in size (YNP 1997). Approximately two-thirds of the NYWR lies in the north central portion of YNP and the remainder is located north of the park on federal, state and private lands. Elevation varies from 1500m to about 2500m, but the majority of the landscape is approximately 2000m (Despain et al. 1986). The NYWR has long, cold winters and short, cool summers. The average precipitation ranges from 25-30cm (Despain 1990). Climate varies considerably, but is highly correlated with elevation. Higher elevations receive larger amounts of precipitation (usually in the form of snow) and have greater fluxes in temperature (YNP 1997). The dominant vegetation type is sagebrush (*Artemisia tridentata*) steppe intermixed with Douglas fir (*Pseudotsuga menziesii*). Aspen and willows stands are comparatively uncommon, but are wide-spread. The NYWR is home to the largest elk herd (6,738) in the Greater Yellowstone Ecosystem (GYE) (White 2007). Sympatric cervids include: mule deer, white-tail deer, bison, pronghorn antelope (*Antilocapra americana*), and moose.

Over the last century aspen and willow have declined on the YNP portion of the NYWR. Houston (1982) estimated that aspen occurred on 4% to 6% of the range when the park was established in 1872, but it is likely now about 1% (Wagner 2006). Similarly, willow canopy cover was 0.8% of the range prior to

1872 and is currently estimated at 0.4% (Houston 1982). Researchers have

hypothesized that climate changes (Despain et al. 1986, Romme et al. 1995),

lack of fire (Romme et al. 1995 and Singer et al. 1998), ungulate herbivory (Kay

1990, Baker et al. 1997, and Ripple and Larsen 2000), and fewer predators

(Despain et al. 1986) have contributed to the decline of these woody species.

<u>History of the Northern Yellowstone Winter Range</u>

In order to understand the current state of aspen, willow and ungulates on

the NYWR we must look to the past. In this next section I will discuss four

different time frames: (1) before 1872 and the advent of YNP, (2) from the

establishment of YNP in 1872 to 1967, a period of invasive management

practices, (3) from 1968, when management implemented the "Natural

Regulation" paradigm, to 1994, and (4) from 1995, when wolves were

reintroduced into YNP, to the present.

<u>Before 1872</u>

Pond sediment and core samples from aspen trees give us some

understanding of the ecological conditions during this time frame. The analysis

of Warren's (1926) aspen core samples provides evidence that aspen

recruitment was successful prior to 1871 (Ripple and Larsen 2000). More recent

core samples of aspen trees also substantiate recruitment success prior to 1871

(Romme et al. 1995, Ripple and Larsen 2000). Pollen records of small ponds on

the NYWR indicate the presence and reproductive abilities of aspen and willow during this period (Engstrom et al. 1991).

Archeological records also indicate that elk, bison, beaver and unknown canid species were present in the area (Wright 1982, Cannon 1992). The abundance of these populations is unknown. Although a controversial premise, it has been hypothesized that the NYWR was only summer range for ungulate populations before the establishment of YNP (Tyers 1981, Houston 1982). Ungulates are thought to have migrated out of this region during the winters, suggesting that ungulate populations were at levels that allowed aspen and willow reproduction.

Houston (1973) postulated that the fire interval on the NYWR was 25-30 years prior to 1872. This included 8-10 extensive fires during the 300 years before the establishment of YNP. Fire is a natural disturbance that can be a restorative process for aspen and willow stands. Fire not only removes the overstory and stimulates ramet growth, but also removes competing vegetation such as conifers. The frequency of fires on the NYWR may have aided in maintaining aspen and willow stands in this ecosystem prior to the establishment of YNP.

<u>1872-1967</u>

Historical photographs from the late 1800's indicate that aspen stands during this period were characterized by multiple tree size-classes. In addition,

an ungulate browse-line was not evident (Kay 1990). Aspen core samples reveal that recruitment was moderate from 1872-1920 with 17% of the trees originating from this time period (Romme et al. 1995, Ripple and Larsen 2000). Range managers first mentioned a decline in aspen in the late 1920's and the discussion persisted in the annual reports until the 1960's (Barmore 1981). The decline in aspen was attributed to ungulate herbivory. Ripple and Larsen (2000) concluded that less than 1% of aspen stems reached the overstory during this time period.

Historical photographs demonstrate that tall willow stands existed along most of the streams prior to 1900 (Houston 1982). Personal accounts from the US army corroborate that there were dense thickets of willow on the NYWR prior to 1900 (Kay 1994). However, using cores of pond sediment Engstrom et al. (1991) found a substantial decrease in willow pollen production after 1900. Heavy ungulate herbivory on willow may have reduced its sexual reproduction, which could have reduced pollen production. Consequently, the decrease in willow pollen in pond sediments could have reflected an increase in ungulate use (Engstrom et al. 1991).

Elk numbers fluctuated during this time period (Tyers 1981). Market and subsistence hunting was allowed throughout the park for the first decade. Few records are available for harvest rates during this time, but one record indicates that in 1875, 8,000 elk were killed on the NYWR (Schullery and Wittlesey 1992). In 1883, subsistence and market hunting became illegal. From 1886-1918 the

U.S. Cavalry was called in to enforce this mandate (YNP 1997). During this period, management practices included efforts to eradicate predators such as wolves, mountain lions, and coyotes (Skinner 1926). Furthermore, elk and other ungulates were fed in the winter (Tyers 1981, Kay 2001). With few predators, no hunting pressures and supplemental winter feeding, elk numbers increased to 15,000 - 40,000 (YNP 1997). There is much speculation on the highest elk population during this time (Houston 1982).

Early-day park managers speculated that rangeland development, fencing and settlement on and around the NYWR in the early 1900's truncated winter migratory routes (Skinner 1925). This resulted in high and artificial concentration of elk and other ungulates on marginal wintering habitat. Woody plants on the NYWR are one of the main sources of nutrients for ungulates in the winter and are available above the snow pack for browsing. For these reasons, park managers were convinced that high ungulate use had suppressed woody plants and their reproductive capabilities (Tyers 1981).

In response to the concern of deteriorating range conditions, from the 1920's to the 1960's the National Park Services (NPS) trapped and shot elk in the park. Hence, this era is referred to as the "reduction period". As a result of the direct reduction, the elk population was reduced to 3,172 by 1967 (Houston 1982). However, aspen were still unable to grow into the overstory within the park portion of the NYWR after elk numbers were decreased (Kay 1990). The portion of the NYWR on the GNF was a notable exception and successful aspen

recruitment did occur on this part of the range (Kay 1990). This was most likely in response to the decrease in the number of migrating ungulates out of the park (Kay 1990). In 1967, active elk reduction in YNP was curtailed because of public pressures and a reinterpretation of ecological processes on the NYWR (Tyers 1981).

During this management era, high elk densities were not only implicated in the decline of aspen and willow communities, but other native species were thought to be affected as well. One species of concern was beaver. Historically, beaver were ubiquitous on the NYWR.

In the summers of 1921 and 1923, YNP conducted its first beaver survey in the Tower Falls-Yancey region (Warren 1926). This area is located in the north central portion of the park and is within the NYWR. An estimated 240 beaver inhabited this region in 1923 (Warren 1926). Although this is a small area of the NYWR it is indicative of the former abundance of beaver. Additionally, it was reported that other regions of the NYWR showed a historical presence of beaver (Sawyer 1925, 1926, Demmink 1926, and Smith 1931).

In 1953 and 1954 a beaver survey was completed for all of the NYWR (Jonas 1955). The results indicated that beaver were extinct from the Tower Falls-Yancey region. Furthermore, beaver were absent throughout the NYWR, except Slide Creek. Jonas (1955) concluded that over-browsing by elk on aspen and willow riparian stands reduced suitable habitat for beaver. The ungulate impact on the riparian area was so severe in the Slide Creek area; it forced

beaver to sustain themselves on sagebrush (Jonas 1955). Additionally, Jonas

(1955) reexamined aspen stands that had been disturbed by beaver (Warren

1926) and found that in some areas they were being replaced by alder and

chokecherry (*Prunus virginiana*).

Fires were infrequent during this time frame, perhaps because the land

management agencies suppressed fires across the GYE (NRC 2002b).

However, some suggest that this era coincided with a lull in the natural fire cycle

(Romme 1982). Regardless, it has been theorized that the lack of fire

disturbance contributed to a decline of woody plants (Singer et al. 1998).

<u>1968-1994</u>

The natural regulation policy was implemented in 1968 by the NPS. A

primary tenet involved minimizing human effects in deference to a reliance on

natural processes to establish an ecological equilibrium (NRC 2002c). In

practical terms, this meant the cessation of actively reducing ungulate

populations and a more relaxed policy on suppressing naturally caused wildfires.

The rationale was that ungulate numbers would be naturally regulated through

limiting environmental factors such as winter severity and forage availability. Elk

numbers increased in this time frame from 4,305 in 1968 to 19,045 in 1994

(Houston 1982, Lemke 2003).

Researchers reported that high elk densities continued to affect aspen and

willow communities on the NYWR during this time period (Kay 1990, St. John

1995). A survey of aspen stands on the NYWR illustrated that stems available to ungulates were unable to grow taller than 2m (Kay 1990). Many aspen clones still existed in shrub form, but were unable to escape ungulate browsing and reach tree size (YNP 1997). Ungulate herbivory also affected aspen recruitment on the Gardiner Ranger District, GNF. In a survey of aspen stands in the Gardiner Basin, only 22% of aspen stems available to ungulates reached the overystory, whereas in scree fields where ungulates are not able to access aspen stands 78% of the stems reached the overstory (St. John 1995).

Continued change in willow stands was also documented (Kay 1990). A photographic comparison of 44 sites on the NYWR revealed that on 41 sites, tall willow had disappeared over the time period of 1893-1988. At the remaining 3 sites, only 5 -10% of the original willow still existed (Kay 1990).

In an effort to understand the effects of ungulate herbivory on aspen and willow communities the NPS established a series of exclosures between the 1930's and the 1960's. By comparing vegetation inside and outside of enclosures the influence of ungulate herbivory could be assessed. Willow and aspen communities inside the exclosures had greater mean height and canopy cover compared to outside (Kay 1994). Additionally, aspen stands inside exclosures had multiple size-classes indicating that they were able to regenerate successfully (Kay 2001). Most aspen stands on the NYWR accessible to ungulates only have mature trees and stems <2m (Kay 1990). This suggests that ungulate herbivory prevented the maturation of ramets into overstory stems.

Kay (1994) concluded that aspen and willow were able to successfully regenerate under current climate changes and fire regimes in the exclosures, but when exposed to heavy ungulate browsing outside the exclosure they were unable to do so.

The beaver population on the NYWR remained low from the late 1960's until the mid 1980's (YNP 1997). By the late 1980's, beaver were allegedly absent on the NYWR (Kay 1990). Kay (1994) concluded that, by preventing the maturation of aspen and willow ramets, elk and other ungulates had eliminated beaver foods. Kay also observed that ungulate herbivory had also limited the abundance of tree-size stems, which are needed to construct dams and lodges. This has ultimately reduced suitable beaver habitat on the NYWR.

Under the natural regulation management policy, natural wildfires were allowed to burn. The wildfires of 1988 enabled managers to evaluate the effects of disturbance on aspen and other woody vegetation. The 1988 fires burned 22% of the NYWR, including many aspen stands (Romme et al. 1995). Sucker density was greater in burned areas compared to unburned areas for the first 2 years after the fires (Romme et al. 1995). However, 3 years after the fires browsing pressure had returned sucker density in the burned stands to pre-fire levels and had precluded aspen suckers from growing >2m (Romme et al. 1995). This demonstrates that fire disturbances were able to induce aspen suckering, but ungulate herbivory prevented aspen recovery. Moreover, fire disturbance in areas with high ungulate densities may have accelerated the decline of aspen

stands by killing the existing mature trees and making suckers available for herbivory (Bartos et al. 1994).

<u>1995-Present</u>

Wolves were reintroduced into YNP as an experimental population in 1995. Before wolves were extirpated from this ecosystem they were the main predator for ungulates. Currently, there are 7 packs of wolves with an estimated 64 individuals that use the NYWR (Smith 2006). In YNP, elk comprised 92% of wolf kills examined from 1995-2001(Smith et al. 2003). Since wolves were reintroduced, the elk population has declined from 17,290 in 1995 to 6,738 in 2007 (White 2007). Wolf predation is not solely responsible for this decline. For example, a large number of elk died due to winter severity in1996-97. Moreover, large numbers of elk were harvested during the hunting season of 1995-2002 north of YNP on the GNF (White 2007).

The reestablishment of wolves on the NYWR has also changed summer and winter elk habitat selection (Mao et al. 2005, Fortin et al. 2005). Elk have chosen more open habitat in the presence of wolves (Mao et al. 2005). This strategy enables elk to have a high probability of predator detection. Additionally, elk selection for aspen stands in the winter has decreased as wolf use increased on the NYWR (Fortin et al. 2005). One area of high wolf use is along riparian corridors (Ripple and Larsen 2000). Therefore, aspen riparian stands are areas of high risk for elk. Consequently, elk use in aspen riparian stands on the NYWR

has decreased in localized areas. Aspen suckers stem heights were greater in riparian stands compared to aspen upland stands (Ripple et al. 2001). Moreover, willows and cottonwood (*Populus spp.*) have been able to escape ungulate browsing in localized riparian areas since wolves were reintroduced (Ripple and Beschta 2005a, 2006). Nevertheless, it has been stated that it is too early to attribute these changes to wolves (Smith et al. 2003).

Although wolves have been able to effect elk habitat selection and herbivory patterns, they have been unable to alter selection for aspen stands in the winter (Mao et al. 2005). Mao et al. (2005) reported that elk highly preferred aspen stands in the winter even were wolf use is high.   White and Feller (2001) proposed that browsing pressures on aspen would not decrease until elk densities have been reduced to 3-5 elk/km^2. Current elk densities on the NYWR are 4.5 elk/km^2. Thus, elk density may be low enough to observe a measurable response in aspen stand vigor.

In addition to the recent changes in woody vegetation, there has been an increase in the beaver population (Smith et al. 2003). An aerial survey of YNP completed in 1996 revealed that beaver were extinct from the NYWR (Smith et al. 1997). However, the most recent beaver survey showed that 9 colonies exist in willow riparian stands on the park portion of the NYWR (Smith 2005 unpub). The newly established colonies are most likely individuals that have dispersed from populations north of YNP on the GNF (D. Tyers pers. comm. 2005). Regardless, this could lead to changes in willow stands on the NYWR. Beaver

may be able to positively affect aspen and willow stands with the decline in elk densities. Yellowstone National Park has recommended that more research is needed to elucidate the relationships between beaver, ungulates, wolves and riparian woody vegetation on the NYWR (YNP 1997).

METHODS

Study Area

Eagle Creek is located 4 km northeast of Gardiner, Mt. It is a second order stream, with a 7% overall slope. The Rosgen classification for this stream is an A4 and represents the dominate slope, moderate sinuosity, and gravely substrate (Rosgen and Silvey 1996). Davis Creek flows into Eagle Creek at the northern end of the drainage and beaver activity on this tributary was included in this study. The stream reach elevation ranges from 2150m to 1800m in the 5km study area on Eagle Creek. Aspen, willow, sedges and grasses are the main vegetative components with inter-dispersed Engelman spruce (*Picea engelmannii*) within the riparian area. The dominant willow species in the order of abundance are, Bebb willow (*Salix bebbiana*), Geyer's willow (*Salix geyeriana*), and sandbar willow (*Salix exigua*). Other common woody species include: mountain alder, chokecherry, and serviceberry (*Amelanchier alnifolia*). Upland-sagebrush grasslands surround the perimeter of the riparian area and are dominated by bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*Artemisia tridentata* spp*. vaseyana*). The Eagle Creek drainage is managed by the Gardiner Ranger District, GNF.

Historical Data

Beaver have been monitored on this stream reach since they were reintroduced in 1991. Currently, there are 2 active colonies on Eagle Creek, but numbers have ranged from 1 to 5. Active and inactive beaver structures, including dams, lodges, and caches, have been observed and documented annually by the GNF (D. Tyers pers. comm. 2005).

Vegetative and Abiotic Cover

The first objective of this study was to determine if beaver disturbance since 1991 had altered aspen and willow canopy cover or water surface area for the entire Eagle Creek riparian area. A comparison of aerial photographs taken in 1990 and 2005 was used to determine changes in riparian cover on Eagle Creek. The 1990 photoset was taken one year before beaver were reintroduced. This component of the study gives us a perspective of overall change in riparian cover. The scale of the photographs was 1:15000. The aerial photos were acquired from the USDA Aerial Photography Field Office in Salt Lake City, Utah. Aerial photos were digitized (600 dots/in) and orthocorrected by the Remote Sensing Application Center (RSAC). In addition, orthomosaics were created for each photoset (1990, 2005).

Stereo Analyst (extention of ArcGIS v9.0) and Digital Mylar Image Sampler (RSAC software) was used to sample and determine the percentage of

canopy cover for all riparian vegetation for each aerial photoset. First, I delineated a digitized polygon (29 ha) that included all the riparian vegetation in the study area. Then, a random 300 point sample grid was laid over the polygon. All 300 points (3m diameter) were assigned a vegetative type or aboitic feature. The vegetative types were: mature aspen (>2m in height), immature aspen (<2m in height), sagebrush-grasslands, riparian herbaceous plants, conifer, alder, and willow. The aboitic feature was surface water. Each point was a circular plot divided into four equal parts. The vegetative type representing the majority of the circular plot was assigned. An overall percentage for each type was rendered after all points were assigned.

To test the accuracy of my aerial photo analysis I visited one-third of the points on the ground from one of the samples in the 2005 aerial photoset (R. Lawrence per. comm. 2006). Each point generated in a sample had corresponding UTM coordinates. One hundred points and their UTM coordinates were randomly chosen from one of the 2005 samples. The 100 points proportionately represented the percentage of vegetative types and the abiotic feature. For example, the total canopy cover for mature aspen in 2005 was 15%, therefore 15 mature aspen points were chosen. I visited each of the 100 UTM coordinates and categorized them into one of the types used in the aerial photo analysis. By comparing the points visited on the ground to the points attributed in the aerial photo analysis, I was able to determine a percentage of accuracy.

Each photoset was sampled 6 times using another 300 points: 1990 (n =

6), and 2005 (n = 6). The number of points and number of samples used in this

study were deduced from a sub-sample plot that provided a standard error <10%

(K. Megown pers. comm. 2006). The sub-sample plot was 0.29 hectares, and 30

points were used following the same procedures as described above. After 6

samples were completed the standard error was <10%.

<u>Aspen and Woody Plants</u>

The second objective of this study was to determine if aspen and other

woody plants were able to produce enough recruitment stems to sustain the

stand after disturbance. Beaver activity throughout Eagle Creek for the last 15

years was identified by using the USFS historical inventory. In an attempt to

determine how long it takes aspen and other woody plants to recover from

beaver disturbance, I grouped sites by the number of years it has been since

beaver were present. Five control sites were identified throughout this stream

reach. Control sites were defined as areas that have received <10% beaver use

on woody plants. I identified an additional 22 sites of past and present beaver

activity. Sites were classified as active or inactive. Active sites had beaver

present within the last 2 years. Inactive sites were identified as having past

beaver activity, but the sites have been abandoned for more than 2 years.   Six

active and 16 inactive sites were identified. I further classified the inactive sites

into 3 categories: 1-3 (n = 7), 4-6 (n = 4) and 7-11 (n = 5) years since

abandonment. The division into 3 year increments was based on a previous study that reported major changes in woody plants 3 years after beaver abandoned (Donkor and Fryell 1999). Comparisons were made for a number of variables between each of these categories or "treatments" to determine if plant responses differed due to the length of time it had been since beaver disturbance.

Beaver use was recorded at each site to validate the treatments. Beaver use was defined as the number of cut stems. Beaver cuts were classified as old or new. Old and new cuts were determined by examining the color of aspen stumps. Aspen stumps that have been exposed to winter conditions turn black. New cuts have a light colored wood appearance. These data were used to confirm that the assigned treatments were valid.

Woody vegetation was sampled at each site by establishing 30-1m^2 plots on multiple line transects within aspen stands and were distributed so they proportionately represented each stand. The line transects were completed in the summer of 2005. Line transects were placed perpendicular to the stream and extended from the stream bank to the edge of the riparian area. A tape measure was placed on the transect line to measure the riparian zone. The length of the riparian zone varied at each site, therefore the number of line transects varied.   A 1m^2 frame was then placed on the line transect at every other meter on the tape until all 30 plots were read to prevent sampling biases. All woody vegetation was identified to the species level for each frame. Aspen

stems were classified into different basal diameter classes based on their

diameter at 30cm (Johnson and Naiman 1990a). The majority of aspen stems in

disturbed sites were ramets. This method was used because the standard for

measuring the diameter of trees is DBH or 1.37m and most aspen ramets in

Eagle Creek were <2m. The basal diameter classes were: sprout 0-1cm, sapling

1-2cm, pole 2-12.5cm, and mature >12.5 (Hann and Jensen 1987). Each basal

diameter class represents a different age class of aspen stems. The composition

of basal diameter class at each site gave a distribution of age classes. Aspen

stem density and stem density for each basal diameter class was derived at each

site from this information.

In the summer of 2006, multiple belt transects were established at each

site equaling 60m^2 and were laid out similarly to the line transects (Kay 1990). I

assessed the height of aspen stems to determine if ramets were recovering and

growing into the overstory after beaver disturbance. For ramets to grow into the

overstory they must first escape the effects of ungulate browsing. Elk are able to

browse above 2m (Keigley et al. 2002). However, the browsing zone of most

ungulates is <2m in height and if the terminal leader exceeds this height, the

stem may escaped most effects of browsing (Kay 1990). The basal diameter

classification method did not take into consideration the height of aspen stems,

therefore this method was added. I categorized all aspen stems on the belt

transects into height/DBH size-classes. Height/DBH size-classes were based on

height for stems < 2m tall and height and DBH for stems >2m tall. The

height/DBH size-class categories were sprouts, saplings, recruitment poles, non-recruitment poles and mature trees. Sprouts were identified as stem <1m in height whereas saplings are between 1 and 2m in height (Hann and Jensen 1987). Recruitment poles were identified as aspen stems >2m in height and have a DBH less than 5cm (Kay 1990, Bartos et al. 1991). Non-recruitment poles were identified as aspen stems >2m in height with a DBH between 6-9cm. If a stem has reached the non-recruitment pole criteria it is likely that it is in the overstory and is not consider a recruitment stem. Mature trees were >2m in height with a DBH >9cm. Recruitment refers to the process of younger stems replacing mature stems. I examined aspen height/DBH size-classes to determine if stems were able to recover after beaver disturbance.   If aspen stems reached the recruitment pole criteria (>2m in height and <5cm DBH) then we determined that recruitment was occurring.   Stegeman's (1954) analysis of aspen stem growth suggests that it would take <6 years to achieve the recruitment pole criteria.

Dead aspen stems were also counted in the 30-1m^2 plots at each site. Aspen mortality can be induced by many factors including: ungulate browsing, beaver cutting, fungal infection and standing water. Total amount of dead stems were counted for each site. The amount of dead stems at each site was counted to determine the rate of mortality after beaver disturbance. I compared number of dead aspen stems/m^2 among the treatments.

Species richness and diversity for woody plants was calculated at each site and were based on the 30-1m^2 plots. The ecological indices will determine if beaver disturbance influences the make up of woody species in the riparian community associated with Eagle Creek. Species richness identifies the number of species at a given location and was calculated by counting the total number of species at each site. Species diversity determines the number of species and their relative abundance (Smith and Smith 2000). There are many species diversity indices, but the Shannon index is the most widely used (Smith and Smith 2000). The Shannon index measures the degree of uncertainty when picking a species at random. If an area has high species diversity, then it is difficult to predict the identity of a randomly picked species.

$$\text{Shannon Index} = -\sum_{i=1}^{s} (P_i)\,(\log_2 P_i)$$

In the equation above, s is the number of species, and P_i is the proportion of individuals in a total sample belonging to the ith species. Species richness and diversity may suggest the stability of these sites. Control sites represented a baseline for comparison. Higher species richness and diversity may indicate high stability in a community (Elton 1958).

Herbivory

My third objective was to determine if ungulate herbivory was influencing aspen recovery after beaver disturbance. Exclosures were erected to assess

aspen recovery in the absence and presence of ungulate and beaver herbivory.

They were constructed between the winter of 2004 and the summer of 2005.

The sites were distributed throughout the stream reach and classified as active,

inactive and control sites by using the USFS beaver inventory. Fourteen sites

were identified: 5 sites without beaver activity, 4 sites with beaver activity, and 5

inactive sites (abandoned from 1-9 years). Twelve of the sites were established

in the winter of 2004-2005 and 2 additional control sites were established in the

summer of 2005.

A 3 x 3m fenced area at each site was enclosed using 1.5m welded wire

(5 x 10cm mesh) and t-posts. Adjacent to the fenced area a 3 x 3m unfenced

area was established. The fenced and unfenced areas were divided into 6 - 1 x

1½m plots. Aspen height and basal diameter were measured in each plot for the

fenced and unfenced areas. I measured these variables at the time each site

was established in 2004-05 and again in the fall of 2006. These measurements

were used to determine the average stem height and stem density (stems/m^2) of

aspen in fenced and unfenced areas. Average stem height was determined for

the first sampling period by calculating the total number of stems in the fenced

and unfenced area and then dividing it by the total number of stems in each area.

Average stem height was determined for the second sampling period by

calculating total stem height and dividing it by the original stem density since

stems were removed in some areas. Stems removed were assigned a 0 growth

rate. Differences in the average aspen stem height and densities (stems/m^2)

were calculated at each site between the 2 sampling periods. An average growth rate/aspen stem for the fenced and unfenced area over the 2 sampling periods was then determined.   Average growth rate/aspen stem and aspen stem densities were compared between the fenced and unfenced areas for all sites. Differences in density and height among the fenced and unfenced areas were used to quantify the influence of ungulate and beaver herbivory on aspen.

Ungulate use was also recorded for aspen suckers in each 30 x 1m^2. Ungulates browse the new growth of aspen stems, whereas beaver cut aspen at the trunk of the stem. Ungulate use was defined as the percentage of branches on a ramet removed by ungulates within the current year. Sprouts and saplings are most available to ungulates therefore; the percentage of ungulate use for each of these basal diameter classes was recorded. This data will identify ungulate use of aspen suckers for each treatment.

To understand the amount of browsing pressure in Eagle Creek, winter ungulate density was measured.   Multiple ungulates browse aspen in Eagle Creek and incorporating their densities represents an indirect estimate of the browsing pressure in this area. In addition to elk, bison and mule deer also browse available aspen stems (DeByle 1985a, Blyth and Hudson 1987). Ungulate density was determined by performing ground surveys. This area was surveyed from December of 2005 until the end of March 2006. Twice a month I walked the length of Eagle Creek two times (total distance was 5km) and counted elk, mule deer, bison, and white-tailed deer. The same transect was

walked each time; the area was approximately 3.75km^2. Ungulate density per km^2 was calculated for each species by dividing the average number of animals from the 8 observations by the area. I then converted the densities of all ungulates species to an elk equivalent density. Elk equivalency was used because elk/km^2 is a common wild ungulate standard in other aspen use studies (White and Feller 2001, White et al. 2003, Mao et al. 2005, Fortin et al. 2005). The following weights (kg) were used for this conversion: elk ≈ 225, bison ≈ 450, mule deer ≈ 50, and white-tailed deer ≈ 50. An example of calculating elk equivalence is 1 bison (450 kg) ≈ 2 elk (225 kg).

<u>Statistical Analysis</u>

I used a one-way analysis of variance (ANOVA) to detect differences in the percentages of riparian vegetative and aboitic types between the 1990 and 2005 photosets (Devore and Peck 2001, SAS 9.1). The null hypothesis tested was:

H$_o$: Percentage of riparian cover did not changed from 1990 to 2005 within the study area.

I used ANOVA for unequal sample sizes to test for differences in aspen density, basal diameter class density and height/DBH size-class density among control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years (Devore and Peck 2001, SAS 9.1). In addition, I compared the percentage of ungulate use for the sprout and sapling basal

diameter classes, aspen mortality, species richness and species diversity among the different treatments. A Duncan multiple comparison procedure was completed for each variable to assess how each treatment differed from one another. The null hypotheses tested were as follows:

H_o: There are no differences in aspen stem densities, basal diameter class densities, and height/DBH size-class densities among control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years.

H_o: Ungulate use of sprouts and saplings did not differ among control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years.

H_o: Aspen mortality, woody species richness, and woody species diversity did not differ among control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years.

I used ANOVA to detect differences in fenced and unfenced areas for average aspen stem growth rate and change in densities between the two different sample periods (Devore and Peck 2001, SAS 9.1). The null hypothesis tested was as follows:

H_o: There are no differences in average stem height and the density of aspen in the fenced and unfenced areas between sampling periods.

Each variable was tested for normality using the Shapiro-Wilk procedure (D'Agostino et al. 1990). One hundred and four out of one hundred and twelve

tests met the Shapiro-Wilk criteria for normality. Since the other 8 data sets were

based on an n = 27, the central limit theorem (n = 30) would suggest that these

data could be analyzed using ANOVA.   All results were considered significant at

a 0.05 α level.

RESULTS

Vegetative and Aboitic Cover

Ninety-six percent of the 100 random points visited during ground truthing matched the categories assigned in the aerial photo analysis (Table 1). Accuracy for individual vegetative types is listed in Table 1. An average accuracy of 96% indicates cover type assignments were correct.

Table 1. Ground truthing data to assess the accuracy of assigned cover types from aerial photographs taken in 2005 of Eagle Creek, Montana.

	Number of Points	Number of Points Correct	Accuracy (%)
Mature aspen	15	13	86
Immature aspen	10	10	100
Willow	14	13	93
Alder	3	3	100
Conifer	11	11	100
Riparian Herbaceous Plants	12	12	100
Sagebrush Grasslands	33	32	97
Surface Water	2	2	100
Total	100	96	96

Canopy cover was different between 1990 and 2005 ($P<0.05$) for all riparian vegetative types, but did not differ for sagebrush grasslands and conifers (Table 2). Canopy cover of mature aspen decreased from 39% in 1990 to 15% in 2005. However, canopy cover of immature aspen, riparian herbaceous plants, willows, and alder all increased from 1990 to 2005.

Table 2. A comparison of vegetative and abiotic cover types from aerial photographs in 1990 to 2005 in Eagle Creek, Montana. The 1990 photographs were taken prior to beaver reintroduction and the 2005 photographs were the most recent available.

	1990 (n=6)	2005 (n=6)
Mature Aspen	39^a	15^b
Immature Aspen	3^a	10^b
Willow	10^a	14^b
Alder	0^a	3^b
Conifer	12	11
Riparian Herbaceous Plants	5^a	12^b
Sagebrush Grasslands	31	33
Surface Water	0^a	2^b

[a] Different superscripts within each row represent significant differences ($P<0.05$). The riparian area sampled was 29 ha.

Beaver Use

The results of beaver use in Table 3 list the degree of use associated with each treatment. The control sites had no beaver cutting and fit the criteria of <10% use. Only active sites had new beaver cuts. All sites inactive for 1-11 years had old beaver cuts and no recent cuts. Therefore, I concluded the assigned treatments were valid and our initial assessment of beaver activity from the USFS annual beaver inventory was correct.

Table 3. Beaver use of aspen stems (old and new cut stems/m^2) in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Old Cuts	0	0.43	1.4	0.39	0.28
New Cuts	0	0.61	0	0	0

Densities calculated from 30-1m^2 plots per site.

Aspen and Woody Plants

Active sites and sites inactive for 1-3 years had the highest aspen stem densities when compared to all other sites, with 2.7 and 2.6 stems/m^2 respectively (Table 4).

Table 4. A comparison of aspen density in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Stems/m^2	0.95^a	2.7^b	2.6^b	1.09^a	1.01^a

[a] Different superscripts within each row represent significant differences ($P<0.05$).
Densities calculated from 30-1m^2 plots per site.

The basal diameter class densities differed between the treatments in the sprout, sapling and mature categories (Table 5). Sprout densities were the greatest for active sites and sites inactive for 1-3 years. Similarly, the sapling densities were greatest for the active sites and sites inactive for 1-3 years. The basal diameter class densities did not differ for the pole category across all sites. Mature stem density was the lowest for the sites inactive for 4-6 years (Table 5).

Table 5. A comparison of basal diameter class densities in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

Basal Diameter class (stems/m^2)	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Sprout	0.32^a	1.35^b	1.29^b	0.26^a	0.23^a
Sapling	0.33^a	0.93^b	0.9^b	0.46^a	0.34^a
Pole	0.13	0.36	0.4	0.36	0.37
Mature	0.17^a	0.04^a	0.07^a	0.01^b	0.07^a

[a] Different superscripts within each row represent significant differences ($P<0.05$).
Densities calculated from 30-1m^2 plots per site.

Aspen height/DBH size-class densities were not different among the treatments for all size-classes except for the sprout category (Table 6). The sprout density was the greatest for sites inactive for 1-3 years and was different than all of the treatments except the active sites. The sprout densities were not different for active sites, sites inactive for 4-6 years, sites inactive for 7-11years, and control sites.

Table 6. A comparison of aspen height/DBH size-class densities in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

Height/DBH Size-class (stems/m^2)	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Sprout	0.31^a	1.31^{ab}	1.75^b	0.29^a	0.14^a
Sapling	0.17	0.45	0.72	0.15	0.15
Recruitment Pole	0.14	0.18	0.04	0.14	0.15
Non-recruitment Pole	0.01	0.01	0	0	0
Mature	0.09	0.01	0	0	0.05

[a] Different superscripts within each row represent significant differences ($P<0.05$).
Densities calculated from 60m^2 belt transect per site.

Dead aspen stem densities differed among the control sites and the sites inactive for 1-3 years and were similar for all other sites (Table 7).

Table 7. A comparison of dead aspen stems in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Stems/m^2	0.37^a	0.54^{ab}	0.69^b	0.60^{ab}	0.60^{ab}

[a] Different superscripts represent significant differences ($P<0.05$).
Densities calculated from 30-1m^2 plots per site.

Sites inactive for 4-6 years had the highest woody plant species richness and differed from the control and active sites. However, species diversity was similar among all treatments (Table 8).

Table 8. A comparison of woody plant species diversity and richness in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Species Richness	4.8[a]	4.7[a]	5.8[ab]	7.3[b]	6.2[ab]
Shannon Index	1.3	1.0	1.1	1.3	1.3

[a] Different superscripts within each row represent significant differences (*P*<0.05). Indices calculated from 30-1m^2 plots per site.

Herbivory

Fenced areas had the highest average annual growth rate/aspen stem with 32cm/year compared to unfenced aspen stems (Table 9).   Change in aspen stem density (stems/m^2) did not differ (P=0.07) in the fenced and unfenced areas (Table 9).

Table 9. A comparison of average annual growth rate and annual change in aspen stem density in 3x3m fenced and unfenced areas in Eagle Creek, Montana.

	Unfenced (n=14)	Fenced (n=14)
Average Annual Growth Rate (cm)	0.26[a]	32.11[b]
Change in Aspen Stem Density (stems/m^2)	-1.13[a]	-0.19[a]

[a] Different superscripts within each row represent significant differences (*P*<0.05).

Ungulate use for sprouts was the greatest in the control sites (Table 10). Percentage of ungulate use for saplings was the greatest in the control sites and sites inactive for 7-11 years compared to all other treatments. The active sites and sites inactive for 4-6 years had the lowest sapling ungulate use and were not different, but differed from the control sites and sites inactive for 7-11 years.

Table 10. A comparison of ungulate use for saplings and sprouts in control sites, active sites, sites inactive for 1-3 years, sites inactive for 4-6 years, and sites inactive for 7-11 years in Eagle Creek, Montana.

	Control (n=5)	Active (n=6)	Inactive 1-3 Years (n=7)	Inactive 4-6 Years (n=4)	Inactive 7-11 Years (n=5)
Sprout	61[a]	19[b]	43[ab]	20[b]	32[ab]
Sapling	69[a]	16[b]	37[ab]	18[b]	54[a]

[ab] Different superscripts within each row represent significant differences ($P<0.05$).
Ungulate use calculated from 30-1m^2 plots per site.

Elk winter density in Eagle Creek was 8.3 elk/km^2 (Table 11). The elk equivalent density was 17.6 elk/km^2 for the study area.

Table 11. Average ungulate densities (animals/km^2) and elk equivalent density (elk/km^2) for the winter of 2005-06 in Eagle Creek, Montana.

Type of Ungulate	Ungulate Density/km^2 (n = 8)	Elk Equivalent Density/km^2 (n = 8)
Elk	8.3	8.3
Mule Deer	7.3	1.5
White-tailed Deer	0.1	0.02
Bison	3.9	7.8
Total	19.6	17.6

Densities are based on a 3.75km^2 area.
1 bison = 2 elk, 5 mule deer = 1 elk.

DISCUSSION

Beaver Impact on Vegetative and Abiotic Cover

The canopy cover of mature aspen decreased by 60% in the Eagle Creek riparian corridor between 1990 and 2005. Cutting from beaver is the most likely cause of the decline. In 1990, immature aspen comprised only 3% of the total riparian cover in Eagle Creek, but has more than tripled in area since beaver reintroduction. However, this increase was not sufficient enough to offset the net loss of mature aspen. Therefore, the total net loss of aspen canopy cover, inclusive of changes in mature and immature aspen, was 40% over this 15 year period.

Prior to beaver reintroduction, willow was limited to the banks along Eagle Creek. However, willow has responded favorably to beaver-created disturbance and cover increase by 40%. Most of the increase was probably because of enhanced water tables and new establishment sites created by beaver dams, ponds, and side channels. Most of the willows appeared to have established asexually. Propagules cut by beaver from existing plants took root at disturbed sites, especially along dams. Barnes and Mallik (2001) reported a similar willow response to beaver activity in northern Ontario. Willow stem density at disturbed sites in their study area was equal to non-disturbed sites 5 years after beaver cutting.

Alder stands also increased along Eagle Creek following beaver reintroduction. In 1990, this species was a minor understory component in aspen stands, as indicated by a lack of detection on aerial photographs. Fifteen years later, alder comprised 3% of the total riparian cover. This increase appeared to be directly linked to the effects of beaver. Alder establishment was primarily associated with abandoned dams and side channels. Beaver can use alder for construction purposes, but it is a nominal component of their diet (Hall 1960). Moreover, alder is not a preferred browse species; little use by ungulates was documented in this study. For these reasons, alder may have a competitive edge over highly palatable browse species, such as aspen and willow.

Like alder, surface water was not measurable on the 1990 aerial photographs of the Eagle Creek study area. Ponds created by beaver had increased surface water 2-fold by 2005. Consequently, this has elevated the water table providing more habitat for hydrophilic plants, which had increased cover of riparian herbaceous plants almost 2½-fold during this same time period. Similarly, Johnson and Naiman (1990b) reported that beaver activity at various locations in North America increased surface water and therefore the over-all biomass of water-tolerant grasses and sedges.

Before beaver were reintroduced, Eagle creek was a very small second order stream with low annual flow. My field observations suggest that beaver may have increased year-around flow, providing enhanced habitat conditions for fish and waterfowl. Beaver ponds have also reduced the sediment load in the

stream, which can improve water quality (Lowry and Beschta 1994). This is evident in Eagle Creek by the retained sediment in drained beaver ponds. The bare areas of sediment emerge as water recedes from abandoned beaver ponds. The organic material in the sediment provides a good growth medium, which has been colonized by willow and other woody plants.

<div align="center">Aspen and Woody Plants</div>

Aspen stands in Eagle Creek produced large amounts of suckers after beaver disturbance, but restricted sucker growth and decreased sucker density over time suggests some limiting factor is preventing recovery. High densities of aspen sprouts and saplings were observed in active sites and in sites inactive for 1-3 years (Table 5). However, by the fourth year after beaver abandonment, sprout and sapling densities had decreased and were similar to non-disturbed sites. Additionally, aspen cohorts stimulated by beaver cutting did not graduate into larger size-classes.

On average, aspen stems grew about 32cm per year within exclosures (Table 9). The inference is that aspen suckers need about 6-7 years to grow above 2m to escape ungulate browsing effects. This is not occurring along Eagle Creek; the recruitment pole densities did not differ in the sites that were inactive for 7-11years compared with non-disturbed sites. In addition, there was no increase in non-recruitment poles or mature stem densities at any of the abandoned sites.

I examined species richness and diversity to evaluate if beaver disturbances increased or decreased the number and abundance of woody plant species. High species diversity can be correlated with stable systems (Elton 1958). A flux in species composition could indicate a change in the stability of a system (McCann 2000). I found that woody species richness increased at sites abandoned for 4-6 years compared to non-disturbed sites. Beaver disturbance may have provided opportunities for the establishment of new species. Willow, alder, chokecherry, and serviceberry were some of the newly colonized species in sites abandoned for 4-6 years.

While species richness increased at the sites abandoned for 4-6 years, the abundance of these species was restricted. When examining species diversity using the Shannon index there were no differences among the treatments. This indicates that most of the disturbed areas were reestablished by existing woody species in Eagle Creek and that beaver disturbance did not change the stability of these stands. However, beaver were able to influence successional trends in disturbed sites. Beaver disturbance created gaps in the canopy of riparian aspen stands by removing most mature stems. Secondary succession occurred when the sites were re-colonized by aspen suckers. Barnes and Mallik (2001) also reported no change in woody species diversity 12 years after beaver disturbance in a study area in northern Ontario.

Herbivory

Aspen suckers were unable to increase in height when exposed to ungulate herbivory in Eagle Creek. Aspen suckers in unfenced areas grew 0.5cm over 2 years, whereas aspen suckers in fenced areas grew 64cm over 2 years. Therefore, ungulate herbivory has inhibited sucker growth and the recovery of aspen stands after beaver disturbance. Few beaver cuts were reported in the unfenced areas of the active sites. This suggests that repeat cutting by beaver had little influence on the decrease in aspen densities. Ungulates had similar effects on aspen stems in 6 historical exclosures on the NYWR (Kay 2001). Aspen stems outside these YNP exclosures were unable to grow taller than 2m and had few size-classes. Aspen inside the exclosures had multiple size-classes and were able to regenerate successfully. If similar ungulate use of aspen stems exists across the NYWR, then disturbances, like beaver cutting, will not aid in restoring aspen stands.

Natural barriers created by cut aspen stems may have prevented ungulate use initially. Active beaver sites had numerous downed aspen stems that made access difficult for ungulates. This provided a refugia for sucker establishment. The highest density of aspen sprouts and saplings were recorded in the active sites. Ungulate use was also the lowest for sprouts and saplings at the active sites. However, continual cutting and eating of standing and downed aspen stems by beaver made the sites more accessible to ungulates. Thus, after

beaver abandonment, there was an increase in ungulate use on aspen sprouts and saplings, which may have caused the decrease in their density.

Repeated ungulate browsing has reduced the high densities of aspen suckers (sprouts and saplings) that were stimulated after beaver disturbance. The average number of branches browsed by ungulates for each aspen sprout and sapling was ≈40% along Eagle Creek. This amount of use has prevented most aspen suckers from escaping the browse zone (>2m) and growing into the overstory. Furthermore, the decline of riparian aspen stands in Eagle Creek has been accelerated by the compounding effect of beaver and ungulate use. Beaver removed most of the existing mature stems in the disturbed sites and the suckers stimulated by this disturbance have not been able to replace them under current ungulate use.

In 2006, elk density was 4.5 elk/km^2 on the NYWR and when factoring in mule deer and bison densities on a weight basis the elk equivalent density was 9.6 elk/km^2 (White 2007). By contrast, the elk density in the Eagle Creek drainage was 8.3 elk/km^2 and the total equivalent elk density was 17.6 elk/km^2 for the winter of 2005-06. This suggests that elk density is higher in and around riparian areas compared with the overall density of elk on the NYWR. It also illustrates the general attraction of ungulates to riparian aspen stands.

Trophic Cascades

The return of wolves has caused a trophic cascade in localized areas on the NYWR, as expressed by the escape of aspen, willow and cottonwood from ungulate browsing effects (Ripple et al. 2001, Ripple and Beschta 2005a, 2006). Ripple and Beschta (2005a) hypothesized that restoring wolves in this ecosystem may offset the long-term impacts of ungulates on aspen stands in this area. In 1994, before wolves were reintroduced, the elk population was estimated at 16,791 on the NYWR (Lemke 2003). The elk population has declined by over 10,000 animals since then and the 2006 estimate was 6,738 (White 2007). The decline of elk may not solely be in response to the return of wolves. This trend may be the cumulative effect of numerous factors, including: other predators, such as grizzly bears and mountain lions, hunter harvests north of the park, prolonged drought, and harsh winter conditions (Smith et al. 2003).

Since wolf reintroduction, elk foraging behavior has changed on the NYWR (Laundré et al. 2001 Fortin et al. 2005, Mao et al. 2005). Cow elk vigilance has increased in areas with wolves (Laundré et al. 2001). The presence of wolves has increased the risk of predation and consequently decreased their foraging efforts by 30%. Additionally, wolves have altered winter habitat selection by elk (Fortin et al. 2005, Mao et al. 2005). Elk select more open habitat since wolves have been reintroduced (Mao et al. 2005). Elk now select more open habitat, which increases their ability to detect predators and

may increase survival (Mao et al. 2005). This change in elk behavior and habitat selection has indirectly influenced browsing pressure on woody plants.

Aspen stands were highly preferred by elk before wolves were reintroduced in YNP, a behavior that has not changed (Mao et al. 2005). However, Fortin et al. (2005) reported that elk used aspen riparian areas less where wolf use is high. Wolves frequently use aspen riparian areas as a corridor to travel and hunt (Ripple et al. 2001). Therefore, if a wolf-elk-herbivory-aspen trophic cascade is taking place on the NYWR the first indications of aspen recruitment should occur in these areas. Ripple et al. (2001) reported increases in mean aspen sucker height in riparian areas on the NYWR where wolf use was high compared to areas where wolf use was low. However, the aspen recruitment stage had not been reached within these stands.

Eagle Creek is part of the home ranges for 2 wolf packs, the Casey Lake and Swan Lake packs, which each consist of 3 individuals (US Fish and Wildlife Service 2007). Wolf predation on elk did occur in Eagle Creek during this study. A bull elk carcass, appeared to be killed by wolves, was located within the riparian area during my winter field observations. This suggests that wolves are having some effect on elk in Eagle Creek. Nevertheless, elk density still remains high in this area at 8.3 elk/km^2, which is almost 2-fold more than the overall NYWR density. Ungulates often congregate in riparian areas due to the high productivity and abundant available forage. Although elk density has been

reduced on the NYWR, riparian areas may still have ungulate densities that prevent aspen stand recovery.

White and Feller (2001) postulated that browsing pressure on aspen stems should decrease when elk densities are reduced between 3-5 elk/km^2, which corresponds with current NYWR elk densities. However, browsing pressure is still high enough to preclude aspen recovery following beaver disturbance in Eagle Creek. In this context, it is significant that the elk density and elk equivalent density were much higher in Eagle Creek compared to the entire NYWR, which would result in comparatively greater browsing impacts. White et al. (1998) propose that elk densities may have to be reduced to <1 elk/km^2 if aspen stands are to produce sufficient amounts of suckers to replace the overstory. As stated earlier, ungulates are drawn to riparian communities with woody browse. Therefore, to achieve elk densities on Eagle Creek that allow aspen stand recovery it may require reducing the overall NYWR elk density below <1 elk/km^2. Moreover, bison and especially mule deer populations may also have to be greatly reduced.

A wolf-elk-herbivory-aspen trophic cascade may be occurring across the NYWR. To date, this effect has only been reported in localized areas (Ripple et al. 2001). Wolves have had some impact on elk in Eagle Creek, which could have reduced the herbivory pressure on riparian aspen stands. The extent of wolf influence on herbivory levels is unknown and the time frame may be too short to detect any changes in aspen stands. However, current herbivory

pressure is still the main factor limiting the growth and recovery of aspen stands after beaver disturbance in Eagle Creek.

Management Implications

Aspen stands can be stimulated to produce additional suckers through the disturbances caused by beaver. Increased asexual reproduction can provide the necessary stem recruitment to ensure stand longevity. However, this process obviously requires the presence of beaver, habitat to sustain their activities, and sufficient aspen stand vigor to produce new sprouts. Given these caveats, the role of beaver in aspen stand restoration on the NYWR is currently limited and the future is uncertain.

The NYWR is accessible to beaver from existing colonies, which provides the potential to repopulate the area. If future climatic conditions and ungulate herbivory levels provide a favorable circumstance for willow and aspen recovery, beaver should be able to disperse from existing population sources and reestablish across the NYWR.

Beaver are persistent residents of the Yellowstone River north and down-river from YNP. In addition, as the result of a GNF reintroduction effort, beaver are well established in the upper reaches of Hellroaring, Buffalo Fork, and Slough Creek; all of which are drainages that flow from high mountain regions into YNP's portion of the NYWR (D. Tyers pers. comm.).

However, the beaver population on the NYWR is currently well below historical levels (Sawyer 1925, 1926, Demmink 1926, Warren 1926, and Smith 1931, Smith 2005 unpub.). Most beaver colonies on the NYWR, excluding Eagle Creek, exist on lower Slough Creek (Smith 2005 unpub.). This area is on the periphery of the NYWR and is adequate beaver habitat because of the presence of tall willow stands that are protected from extensive browsing by deeper snow. Regardless, these beaver colonies are on a waterway that is connected to the central portion of the NYWR. The long-term viability of beaver colonies on Eagle Creek is questionable because deciduous vegetation is limited along the narrow riparian corridor. Consequently, food supplies may ultimately be exhausted, therefore reducing or eliminating this population as a source to repopulate the NYWR.

In the late 1980s, the GNF proposed an aspen restoration project in the Eagle Creek drainage utilizing a combination of disturbances, including prescribed fire and felling mature trees with a chain saw. However, mesic conditions and lack of understory fuels prevented ignition of the riparian aspen stands. Consequently, the original proposal was abandoned and beaver were reintroduced as an alternative method to provide a disturbance. If the prescribed burn and mechanical treatment had been carried out, I propose that the resulting aspen suckers would not have been able to recover in the disturbed areas. Romme et al (1995) reported that numbers of suckers increased in aspen stands burned in the 1988 fires, but ungulate herbivory returned sucker density to pre-

fire levels. In this context, they suggested that fire hastened the reduction of mature trees in some aspen stands on the NYWR without a desired accompanying increase in recruitment stems. Therefore, I predict that disturbances that remove the overstory, such as those originally proposed for Eagle Creek, in areas with high ungulate densities will not promote aspen stand recovery.

Fencing aspen stands after disturbance may protect suckers from herbivory, thus enabling recovery. Aspen suckers fenced in Eagle Creek study plot exclosures prior to this project had a substantial annual growth rate. Suckers were able to grow out of the browse zone in 5-6 years. However, fencing is very costly to install and maintain and therefore, may not be a viable solution. Additionally, fencing may cause habitat fragmentation with its associated negative environmental affects. These disadvantages would limit the fencing option to localized areas and prevent a landscape level application.

Natural barriers may be a more applicable solution. Following the 1988 fires, fallen conifers provided a natural barrier from ungulate access to aspen suckers (Ripple and Larsen 2001). Ripple and Larsen (2001) reported that aspen suckers surrounded by fallen conifers at a NYWR study site had greater mean heights compared to suckers outside these areas. Kay (1990) stated that 21% of aspen stands on the NYWR had > 10% conifer canopy cover. Felling these conifers could create natural barriers that prevent ungulates from browsing aspen suckers.   This method could also reduce further conifer encroachment,

providing additional benefits to aspen stands. Felling conifers would also be more cost efficient as an ungulate barrier by eliminating most of the material and maintenance costs associated with fencing.

Disturbances may not be necessary for aspen recovery on the NYWR. Kay (1990) suggested that 50-65% of aspen stands on the NYWR are climax stands. If ungulate herbivory, in concert with favorable climatic conditions, is at a level that allows recruitment, then most aspen stands would produce ample amounts of suckers. However, the level of ungulate density required for this to occur is unknown. Currently, the combined effects of predators, weather conditions, climate, and hunting on NYWR ungulates have not reduced browsing pressure enough to allow aspen recovery at a landscape level. If aspen restoration is a priority, as defined by the presence of stands with multiple age classes, then land and game managers may have to implement alternative solutions, recognizing that options are limited under current environmental and political conditions.

The reestablishment of beaver provided many benefits to the riparian area associated with Eagle Creek. Identifying and quantifying all the advantages of returning this native keystone species to the drainage is beyond the scope of this project. In brief, beaver were able to increase surface water by creating impoundments. This indirectly increased willow and alder cover. Reestablishing beaver may not aid in increasing aspen stands on the NYWR under current

ungulate densities and climatic conditions, but, in Eagle Creek, many effects were positive for other species in the riparian community.

The restorative effects of beaver on aspen stands in areas with high ungulate densities are limited. The disturbances created by beaver in Eagle Creek were able to increase aspen suckering. However, suckers were unable to grow out of the browse zone and reach the overstory. Ungulate densities in this area were too high to enable aspen stand recovery. Beaver cutting in tandem with heavy ungulate herbivory accelerated the decline of the aspen canopy cover in Eagle Creek.

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APPENDIX A

VEGETATION AND MAP OF EAGLE CREEK

Scientific and Common Names of Woody Species in Eagle Creek

Scientific Name	Common Name
Populus tremuloides	Quaking aspen
Salix bebbiana	Bebb willow
Salix geyeriana	Geyer's willow
Salix exigua	Sandbar willow
Salix lasiandra	Pacific willow
Salix pseudomonticola	Mountain willow
Salix scouleriana	Scouler's willow
Salix boothii	Booth's willow
Salix plantifolia	Flat-leaved willow
Alnus incana	Mountain alder
Prunus virginiana	Chokecherry
Betula occidentalis	Water birch
Rosa woodsi	Wood's rose
Symphoricarpos albus	Snowberry
Cornus stolonifera	Red-osier dogwood
Ribes setosum	Northern gooseberry
Ribes lacustre	Prickly currant
Ribes hudsonianum	Northern black currant
Rubus idaeus	American red raspberry
Amelanchier alnifolia	Saskatoon serviceberry
Rhus trilobata	Skunkbush
Artemisia tridentata ssp. *wyomingensis*	Wyoming big sagebrush
Artemisia tridentata spp. *vaseyana*	Mountain big sagebrush
Picea engelmannii	Engelmann spruce

Scientific and Common Name of Forbs and Grasses in Eagle Creek

Scientific Name   Common Name

Forbs

Epilobium angustifolium   Fireweed
Cirsium arvense   Canada thistle
Mentha arvensis   Mint
Solidago canadensis   Golden rod
Maianthemum stellatum   False soloman's-seal
Glycyrrhiza lepidota   Wild licorice
Achillea millefolium   Yarrow
Geranium viscosissimum   Sticky purple geranium
Heracleum maximum   Cow parsnip
Cynoglossum officinale   Hound's tongue
Iris missouriensis   Iris
Thalictrum spp.   Meadow rue
Aster conspicuous   Showy aster
Aster foliaceus   Leafy aster
Equisetum spp.   Horse tail
Helianthella uniflora   Sunflower
Fragaria virginiana   Strawberry

Grasses

Poa pratensis   Kentucky bluegrass
Bromus inermis   Smooth brome
Elymus glaucus   Smooth wildrye
Phleum pratense   Timothy
Calamagrostis canadensis   Blue joint grass
Agrostis stolonifera   Red top

Map of the Eagle Creek Drainage including Davis Creek.