EFFECTS OF BEAVER REINTRODUCTION AND UNGULATE BROWSING ON

ASPEN RECOVERY IN THE EAGLE CREEK DRAINAGE OF THE NORTHERN

YELLOWSTONE WINTER RANGE

by

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ABSTRACT

Ungulate browsing and lack of overstory disturbance have historically prevented aspen regeneration on the Northern Yellowstone Winter Range (NYWR). Aspen clones regenerate if sprouts are produced that grow into recruitment stems (>2 m tall) and replace the mature overstory. Beaver were reintroduced to the Eagle Creek drainage on the NYWR in 1991 in an attempt to facilitate recovery of riparian aspen communities by removing aspen overstory and increasing sprouting. However, intense ungulate browsing, primarily from the Northern Yellowstone elk herd, was preventing aspen recruitment in Eagle Creek in 2005. Wolf predation has contributed to a 56% decrease in this elk herd from 2005 to 2012. I investigated the effects of beaver reintroduction and ungulate herbivory on aspen recovery in the Eagle Creek drainage in 2012.

Aerial photos taken of Eagle Creek in 1990, 2005, and 2011 showed that although beaver activity stimulated aspen sprouting, the mature overstory of many aspen stands has not been replaced 21 years after beaver reintroduction (p>0.05). Sprouting and recruitment were investigated using 4-m radius circular vegetation plots (n=31) established in aspen stands throughout Eagle Creek in 1997 and monitored annually until 2012. Beaver activity stimulated increased sprouting in 71% of these plots, and 77% of the plots had ≥1 recruitment stem in 2012. Prolonged flooding and high browsing levels contributed to lack of recruitment in 23% of the plots (p<0.05). In 2012, 75% of the paired plots associated with aspen exclosures had unfenced aspen stems with an average stem height ≥2 m. Recent increases in aspen recruitment in Eagle Creek indicate that aspen communities are regenerating. This is likely the result of decreased browsing pressure on aspen saplings from 2005 to 2012. These findings are consistent with the predictions of a density-mediated trophic cascade following wolf reintroduction.

LITERATURE REVIEW

Aspen Ecology

Quaking aspen (*Populus tremuloides*) is the most widely distributed tree species in North America (Jones 1985). In western North America, aspen communities can grow in most vegetational zones, including upland and riparian environments (Mueggler 1985). Aspen trees can exist as pure stands or dispersed among conifer forests, and are found on the edges of many different cover types (Jones 1985). Aspen is often considered an early successional community because it is a shade intolerant pioneer species, but aspen can also exist as a climax community (Kay 1985; Mueggler 1985). Kay (1997) hypothesized that roughly one-third of western aspen stands are climax communities. Aspen forests often support diverse undergrowth, providing forage and habitat for many wildlife species such as cavity-nesting birds (Hollenbeck and Ripple 2008) and ruffed grouse (DeByle 1985*a*).

Aspen is a clonal species that often reproduces asexually by root propogation, producing suckers that are genetically identical (ramets; Farmer 1962). Aspen are dioescious and can reproduce via seeds, but sexual reproduction is not common in the western United States (Kay 1993). This is likely because seedlings require more specific moisture and light conditions for germination and survival than do root suckers (Jones et al. 1985). Suckers form new aspen trees and perpetuate the life of the clone. Individual ramets in western states commonly live to 100-150 years (Jones and Schier 1985), and aspen clones may persist on the landscape for thousands of years. Forest managers and

silviculturalists are interested in understanding the factors affecting aspen suckering and survival in order to increase the health and productivity of aspen forests.

Several factors influence the suckering patterns of an aspen clone. Suckers most often originate from primordia (composed of meristematic cells) in the cambium of roots (Schier 1973*b*). Strong and LaRoi (1983) found that most aspen suckers originated on lateral roots in mineral soil near ground level (3-15 cm of surface). Most ramets sprouted from a depth of 5-30 cm in aspen clones of northern Utah (Gifford 1966). Though deeper roots are able to produce suckers, lower temperatures deeper in the soil profile and greater distances for new shoots to reach the soil surface probably retard the growth of suckers on deep roots (Fraser et al. 2002).

Plant growth regulators have a significant impact on suckering in aspen clones. Auxin is a hormone produced in aboveground plant tissues of aspen trees (twigs, buds, and leaves), and transported to root meristems (Farmer 1962). High auxin levels produced in older aspen stems can inhibit sucker bud growth in root meristem, stifling shoot development and preventing suckering (Eliasson 1971; Farmer 1962; Wan et al. 2006). By limiting the outgrowth of lateral root buds, water and nutrients are more available to support the growth of older trees (Cline 1991). This plant growth strategy is called 'apical dominance.' When the apical dominance of an aspen clone is weakened (i.e. auxin production is prevented or auxin flow interrupted), new ramets are able to grow from the root system, reach recruitment height (>2m), and replace the mature overstory (Schier et al.1985*a*). However, low auxin production in early spring and late fall can allow suckering to occur even when the apical dominance of the mature overstory

is not weakened (Eliasson 1971), and undisturbed aspen stands are often able to produce substantial numbers of suckers (Durham and Marlow 2010). Fire (Durham and Marlow 2010) and clear-cutting (Mueggler and Bartos 1977) can remove overstory stems, release suckers from apical dominance, increase sucker densities, and stimulate regeneration in aspen stands.

The hormone cytokinin counteracts the activity of auxin. Cytokinin is produced in growing root tips and transported toward aspen stems, stimulating shoot development in root primordia (Cline 1991). High cytokinin-to-auxin ratios aid shoot regeneration by promoting bud outgrowth and radial cambium growth (Nieminen et al. 2008). When apical dominance is weakened, abscisic acid (ABA) inhibits sucker development (Schier et al. 1985*b*) to ensure that sucker buds do not begin to grow until the spring after overstory disturbances. This enhances sucker survival because spring provides better growing conditions for suckers. Another growth regulator, giberellic acid, promotes bud flush and sucker elongation after root primordia are developed (Schier 1973*a*). Levels of these growth regulators and the interactions between them influence the development of aspen root suckers, though the specific mechanisms by which they operate are still debated (Cline 1991, Schmulling 2002).

Nutrients such as calcium and nitrogen increase in availability after stand-replacing disturbances (i.e. fire or clear-cut harvesting; Ahlgren and Ahlgren 1960), which may be one reason such disturbances result in prolific suckering. Fraser et al. (2002) found that fertilizing root sections with $CaSO_4$ and NH_4NO_3 did not increase the number of suckers produced on root sections. However, roots that were fertilized had 2.5

times greater dry mass than unfertilized roots. These results suggest that the added nutrients stimulated sucker growth. Aspen seedlings have fairly low solution and tissue calcium requirements (61 µM in solution and 0.17% leaf concentrations), and increased solution calcium can increase shoot and root elongation in aspen seedlings (Lu and Sucoff 2001).

Soil temperature is an important driver for sucker growth in an aspen clone. In a study by Fraser et al. (2002), aspen roots grown at maximum soil temperatures of 20°C began sucker initiation 12 days earlier than roots grown at 12°C. Earlier initiation times can provide suckers with a longer growing season, improving growth and survival of young ramets. Soil temperatures between 12 and 20°C were sufficiently high for roots to produce numerous suckers (Fraser et al. 2002), but at soil temperatures of 10°C or colder, water uptake by roots is limited (Wan et al. 1999). Reduced water flow in roots and plant tissues can prevent cell elongation and growth of aspen suckers. Cold soil temperatures (6°C) can also result in smaller leaf area and lower photosynthetic rates for aspen seedlings, but do not delay bud flush (Landhausser and Lieffers 1998). Soil temperatures above 10-12 °C and nutrient availability are critical interacting factors for successful sucker initiation and growth.

Carbohydrate reserves in the root system are necessary for sucker growth early in the spring because leaves have not developed yet, photosynthesis is not occurring, and carbohydrates are not being transported to the root system (Frey et al. 2003). Higher amounts of total nonstructural carbohydrates (TNC) do not increase the number of suckers produced, but do contribute to increased sucker dry weights (Schier and Zasada

1973). Suckers originating from the roots of fall-cut saplings (which have more TNC stored in the root system in preparation for winter) have greater height growth, biomass production, and leaf area development than spring-cut saplings (Landhausser and Lieffers 2002). Dense sucker growth after stand-replacing disturbances is important for replenishment of carbohydrate reserves in the clonal root system, and ensures persistence of the clone on the landscape (Landhausser and Lieffers 2002).

Soil moisture has a significant effect on the initiation and growth of aspen suckers. Aspens require 40-100+ cm of annual precipitation, and can thrive in areas with a high water table ($\geq$ 60 cm from the surface; Jones and DeByle 1985*b*). However, flooded soil conditions (even for flooding periods as short as 6-10 days) can reduce or inhibit aspen suckering following disturbances, especially when the suckers are flooded at warmer temperatures typical of the spring growing season (Bates et al. 1998). Flooding can create hypoxic soil conditions that result in root death/decay on low-lying or poorly drained areas, which reduces the ability of root primordia to produce suckers (Bates et al. 1998). Dry soil conditions usually do not have a significant effect on aspen suckering because water is transported to the suckers from a parent root system that can access moisture deeper in the soil profile (Gifford 1966).

Light conditions are also extremely important for early growth of new aspen ramets. The highest rates of sucker growth occur when the entire overstory of an aspen clone is removed, because that provides the maximum light intensity on the forest floor for sucker growth and reduces auxin production (Huffman et al. 1999). As the number of

residual trees (unharvested) decline, sucker densities increase because overstory stems that remain intact after a disturbance shade suckers (Huffman et al. 1999).

Competition with other pioneer species can inhibit sucker growth and survival because of nutrient, water, and sunlight limitations. Competition with Marsh reedgrass (*Calamagrostis canadensis*) reduced height growth of aspen suckers, especially with low nutrient availability (Landhausser and Lieffers 1998). Root competition and/or allelopathic effects of this invasive, densely growing grass species likely contributed to decreased aspen growth. Leaf and stem litter in patches of Marsh reedgrass insulates the soil, resulting in low soil temperatures that can inhibit sucker initiation. Romme et al. (2005) found that removing lodgepole pine competitors in aspen stands in YNP did not increase height growth of aspen seedlings. The effect of competition depends on limiting resource factors that vary between each aspen stand.

The density of sucker regrowth after a disturbance may affect the survival of suckers. Higher sucker densities have a higher collective leaf area, which results in higher growth rates and biomass production (Landhausser and Lieffers 2002). High leaf area should limit the encroachment of competing vegetation also (Landhausser and Lieffers 1998). High sucker density also provides insurance against losses to browsing, pathogens, and insects. However, high sucker densities are associated with decreased dry weight of individual suckers, indicating that suckers compete for resources from parent roots (Schier and Zasada 1973).

Sucker densities increase dramatically directly after overstory disturbance and can reach >43,000 stems/ha (Huffman et al. 1999). Suckers densities begin to gradually

decline 3-4 years after fire disturbance, sometimes down to 15,000-20,000 stems/ha (Bartos and Mueggler 1981). Durham and Marlow (2010) reported average sucker densities of 24,500 stems/ha three years after prescribed fire in aspen stands in Southwest Montana. Mueggler (1989) hypothesized that sucker densities ≥ 2,500/ha are sufficient to replace the mature overstory. Natural thinning of aspen suckers ensures that aspen clones retain enough suckers to replace the mature overstory but that sucker numbers do not remain high enough to decrease the vigor and health of individual suckers (Bartos and Mueggler 1981).

Aspen suckers that survive and grow taller than 2 meters are considered recruitment stems that will eventually replace the mature overstory (Kay 1985). Stems >2m in height and <5 cm in diameter at breast height represent recent recruitment (Kay 1985). Aspen recruitment can be inhibited when saplings are overtopped by larger trees and do not receive enough sunlight to continue height growth into the overstory (Jones and DeByle 1985*a*). Severe wind can blow aspen trees over, and heavy snow and ice can break sapling boles and branches (Jones and DeByle 1985*a*). Cryptospora canker, wood boring insects (such as poplar borers), and aspen bark beetles can compromise the health and vigor of larger aspen stems, and may contribute to rapid mortality of aspen overstory (Worrall et al. 2008). Ungulate herbivory can prevent aspen recruitment (Kay 1985; Kimble et al. 2011) and ungulate rubbing and gnawing can remove the bark of recruitment stems, causing stem mortality (Keigley and Frisina 2008). Conifer establishment in upland aspen stands can also reduce recruitment of aspen saplings (Kimble et al. 2011).

Mueggler (1989) suggested that recruitment stem densities ≥ 1,235/ha are sufficient to replace aspen overstory. Kay (1985) defined an aspen stand as "reproducing" if the number of recruitment stems was equal to the number of mature aspen overstory stems. However, Durham and Marlow (2010) suggest that this criterion may not be adequate for stands in poor condition that only have a few mature and recruitment stems. Aspen stands exposed to intense ungulate herbivory may only replace the overstory if they contain large numbers of recruitment stems (Durham and Marlow 2010). Areas with low ungulate densities may only require a 1:1 ratio of recruitment stems to overstory stems in order to remain sustainable. Other studies use the number of ramets >2 meters tall to represent recruitment in aspen stands (Kaye et al. 2003; Winnie 2012; Halofsky and Ripple 2008*a*). Generally, aspen stands that contain multiple size classes of trees, including sprouts and saplings growing > 2 meters tall, can be considered successfully regenerating. The density of mature overstory stems will only be maintained if suckers are produced and survive to reach recruitment height.

<u>Beaver Herbivory</u>

Beaver activity can benefit riparian ecosystems by elevating the riparian water table, providing suitable growing conditions for diverse wetland plant species, retaining sediment, reducing flooding from high spring runoff, and augmenting low stream flow in dry months (Naiman et al. 1988). The association between beaver and healthy riparian areas in western states has prompted land managers to augment or reintroduce beaver populations to public lands for many years (Ruedermann and Schoonmaker 1938; Heter

1950). Beaver management has been an objective for public lands such as Yellowstone National Park (Smith and Tyers 2008), the Absaroka-Beartooth Wilderness Area (Smith and Tyers 2012), the Elkhorn Mountains in Montana (Vore 1993), and the Bighorn National Forest in Wyoming (Emme and Jellison 2004).

Beavers heavily utilize aspen resources (Smith and Tyers 2008), but their characteristic foraging strategy can actually stimulate growth of aspen suckers because they often harvest mature overstory trees, disturbing the apical dominance of the stand and allowing increased sprouting under low auxin production (Schier et al. 1985*b*; Wan et al. 2006; McColley et al. 2012). Beaver herbivory can result in significant decreases in aspen basal area and mature stem density (Johnston and Naiman 1990). Shorter durations of beaver herbivory and greater species diversity in the riparian vegetation community can mitigate the extent of beaver-caused changes in aspen communities (Johnston and Naiman 1990). Loss of mature aspen overstory increases the light intensity and nutrient and water availability at the forest floor, which can stimulate dense sucker regeneration.

The effects of beaver herbivory on aspen are not limited to increases in sucker stem density. Preferential beaver herbivory of aspens can decrease the density of mature aspen trees, allowing the establishment of less-preferred riparian species like alder (*Alnus spp.;* Johnston and Naiman 1990; Naiman et al. 1988) and conifers (Kaye et al. 2003, Kimble et al. 2011). Because beaver activity can elevate the riparian water table, conditions can become more favorable for the growth of willow and alder (McColley et al. 2012). Woody competition for light, water, and nutrients can exclude aspen growth (Johnson and Naiman 1990), thereby exacerbating aspen decline. Though beaver

disturbance can benefit aspen stands by increasing sprouting, if these sprouts are outcompeted by other woody vegetation, they may be unable to grow and replace the aspen overstory. Stand-replacing disturbances such as beaver cutting may hasten succession to upland vegetation or conifers in seral aspen stands (White et al. 1998). Sprouts near the active stream channel may be exposed to prolonged flooding if beaver build dams in the area, causing reduced sprouting and a lack of recruitment in those areas. Low gradient stream sections, in which most of the aspen clones are located in the floodplain or near the active channel, may experience prolonged flooding over a large area (Westbrook et al. 2011) that reduces sprouting due to beaver activity. The sprouting response of an aspen clone after beaver disturbance, and the fate of those sprouts, directly affects the potential of that clone to produce recruitment stems and sustain regeneration within the clone.

<u>Ungulate Browsing</u>

The buds and twigs of aspen trees provide nutritious and palatable forage for ungulates such as Rocky Mountain elk (*Cervus elaphus;* Baker et al. 1997), moose (*Alces alces*; Beetle 1974), mule and white-tailed deer (*Odocoileus hemionus* and *O. virginianus;* Mueggler and Bartos 1977), and American bison (*Bos bison*; Campbell et al. 1994). Aspen trees may be more heavily utilized by ungulate species in the winter as they migrate to find suitable forage (Romme et al. 1995; White et al. 2010). Ungulate browsing can prevent aspen recruitment in areas of high ungulate density (St. John 1995; McColley et al. 2012; Kimble et al. 2011), and increases in elk populations are associated

with greater damage to aspen stands due to increases in browsing, rubbing, and bark gnawing (Keigley and Frisina 2008). Most ungulate browsing is concentrated on aspen sprouts and saplings less than 2 meters in height (DeByle 1985*b*), but elk and moose can "ride down" and browse trees as tall as 7 meters (Beetle 1974). Lower browsing pressure due to lower ungulate densities in National Forests around Yellowstone National Park may have contributed to higher proportions of recruitment stems in these areas (Larsen and Ripple 2005).

In addition to temporal variation in the browsing level due to fluctuations in ungulate populations, aspen recruitment may also be affected by spatial variation in ungulate distribution. Romme et al. (2005) found that aspen seedlings in Yellowstone National Park (YNP) grew taller at lower elevations (6700 feet) than at higher elevations, but that seedlings were more likely to survive at higher elevations because deep snow limits ungulate browsing. However, Forester et al. (2007) found taller aspen saplings at higher elevations on the Yellowstone Plateau, and suggested that ungulate herbivory of aspen in the spring may be less intense at higher elevations because ungulates avoid browsing in deep snow at higher elevations. However, other studies have found that elevation does not influence aspen recruitment (Kimble et al. 2011; Kaye et al. 2003; Larsen and Ripple 2005). High ungulate densities that prevent aspen recruitment can inhibit aspen clones from regenerating and exacerbate aspen decline.

Ungulate and Beaver Herbivory

Competition between beaver and ungulates for aspen resources could lead to the exclusion of one herbivore from the community or overutilization of aspen. Hood and Bayley (2008) examined the effects of resource competition between beaver and ungulates in Elk Island National Park (EINP; Alberta, Canada) by comparing beaver foraging choices at high ungulate densities inside the park (~13 ungulates/km2) and low ungulate densities outside the park. Though the density of ungulates outside EINP is unknown, predation and hunting pressure outside the park have resulted in lower ungulate densities than inside the park. Beaver inside EINP modified their foraging strategy to cope with high ungulate densities in the park by harvesting larger-diameter *Populus* trees to maximize their energy intake. Many woody plants, including *Populus* species, had lower stem densities, smaller stem diameters, and hedged appearances compared with these species outside of the park. These impacts of ungulate browsing on the vegetation in EINP demonstrate that high ungulate densities, when combined with beaver herbivory, may result in reduced growth and vigor of *Populus* species. This may result in slower regeneration of aspen stands. Though aspen is the dominant tree species in EINP (covering 70% of park), there were several other palatable shrub species that beavers and ungulates used as forage. In a simpler ecosystem with fewer woody browse species, the negative impacts of beaver and ungulate herbivory on aspen communities may be more pronounced (Wagner 2006).

White et al. 1998 suggest that introducing intense fire into ecosystems with high ungulate densities could severely damage aspen communities if suckers are unable to

reach recruitment height and replace the mature overstory. Durham and Marlow (2010) found that burned aspen stands in the Whitetail Basin of southwest Montana (just north of the GYE) were regenerating due to high post-fire sucker densities and low browsing intensity (0.36 elk/km^2), but even this low level of herbivory decreased aspen sucker height in their study area. Similarly, McColley et al. (2012) found that even though beaver disturbance stimulated increased aspen sprouting the Eagle Creek drainage on the NYWR, ungulate herbivory prevented sprouts from reaching recruitment height. They concluded that in areas with high levels of ungulate herbivory (8.3 elk/km^2 in Eagle Creek), beaver disturbance will not aid aspen regeneration.

Clearly, intense disturbances that remove aspen overstory, such as fire and beaver herbivory, do not necessarily result in aspen recovery. Beaver cutting, fire, and intense ungulate herbivory are all factors that can hasten the loss of aspen clones (Wagner 2006). Regeneration of aspen clones depends on factors that influence sprouting, such as fire and beaver disturbance, as well as factors such as browsing that may limit aspen recruitment.

INTRODUCTION

The decline of Quaking aspen (*Populus tremuloides*) cover on the Northern Yellowstone Winter Range (NYWR; Map 1, Appendix A) is potentially of great consequence to wildlife species. Aspen cover probably occupied~ 4-10% of the NYWR landscape from 1872 to the 1930's, but has since declined to occupation of 1% of the NYWR in 2004 (Wagner 2006). Factors hypothesized to have contributed to this aspen decline include overbrowsing by elk, climate change, fire suppression, senescence, conifer encroachment, and disease (Tyers 1981; Houston 1982; Wagner 2006). Aspen stands are successfully regenerating if they produce suckers that grow into recruitment stems (> 2m tall) and replace senescent mature overstory stems (Kay 1985; Wagner 2006). Though aspen clones can naturally produce enough suckers to replace the mature overstory (Eliasson 1971; Durham and Marlow 2010; Kay 1985), disturbances that remove mature overstory stems can stimulate sucker production and aid in clone regeneration (Schier et al. 1985*a*). Management actions aimed at increasing suckering and recruitment of aspen stands have attempted to counteract aspen decline on the NYWR.

Aspen on the NYWR are browsed by Rocky Mountain elk (*Cervus elaphus;* Baker et al. 1997), moose (*Alces alces*; Beetle 1974), mule deer (*Odocoileus hemionus;* Mueggler and Bartos 1977), and white-tailed deer (*Odocoileus virginiana;* Mueggler and Bartos 1977). Bison (*Bison bison*) are generalist grazers, but consume woody browse species such as aspen sprouts in areas of the NYWR where these species are abundant (Ripple et al. 2010). In addition, bison rubbing and wallowing can damage young aspen

stems (personal observation). Studies in 1991 (St. John 1995), 2005 (McColley et al. 2012), 2006 (Kimble et al. 2011), and 2004-07 (Kauffman et al. 2010) have repeatedly shown that ungulate browsing, specifically from the Northern Yellowstone elk herd, is the most important factor preventing aspen recruitment on the NYWR, despite a 50% reduction in the population size of the Northern Yellowstone elk herd from 1995 to 2005 (Northern Yellowstone Cooperative Wildlife Working Group [NYCWWG] 2005). These studies suggest that increasing the recruitment of aspen suckers into the overstory of aspen communities could improve the sustainability of aspen clones and lead to the recovery of aspen in the NYWR.

Historical records indicate that many landscapes of the northern Rocky Mountains supported regenerating aspen stands in an environment where elk density was < 1 elk/km^2 (White et al. 1998). This elk density may have been maintained through intense predation from humans (Kay 1995), wolves, and other carnivores (White et al. 1998). After the extirpation of wolves from Yellowstone National Park in the 1920's, the Yellowstone elk were intensively managed through relocation and direct reductions, and the elk population was at a low of 4,000 animals in 1968 (Huff and Varley 1999). The National Park Service adopted the "natural process management policy," (a.k.a. natural regulation) in 1969, and the Northern Yellowstone elk population grew to around 16,000 animals by 1995 (Eberhardt et al. 2007). Heavy browsing from this large elk herd may have prevented successful aspen regeneration inside the park and on the NYWR beginning in the early 20th century (Ripple and Larsen 2000; Kauffman et al. 2010).

Wolves were reintroduced to YNP in 1995, and the Northern Yellowstone elk population declined by 62% from the decade before wolf reintroduction to the winter of 2007-08 (White et al. 2010) This decrease was mostly due to increased predation and human harvest (White et al. 2010; Montana FWP 2004). Population estimates of the Northern Yellowstone elk herd indicate that the population remained stable from 2006 until 2009 (Lemke et al. 2008). White et al. (2010) reported an average elk density of 6.9 elk/km^2 for the Montana portion of the NYWR for the winters of 2000-02, 2007 and 2008. This estimate is still much higher than the elk density of < 1elk/km^2 proposed by White et al. (1998) as a sustainable level for aspen regeneration despite a significant population decline in the Northern Yellowstone elk herd.

Wolf reintroduction may produce a trophic cascade effect on the woody browse species of the northern range through two mechanisms. Wolves may alter prey behavior, causing elk on the northern range to avoid areas of high predation risk and allowing aspen in these areas to recover: a behaviorally-mediated trophic cascade (Ripple and Beschta 2004). Researchers debate which habitats represent areas of high predation risk. Halofsky and Ripple (2008*b*) and Garrott et al. (2009) suggest that riparian areas, ravines, burned forest edges, conifer forest edges, and meadow edges are areas of higher predation risk. In contrast, Kauffman et al. (2007) suggest that open, flat grasslands near streams and roads are riskier. Creel et al. (2005) found that elk moved from open areas to coniferous forest in the presence of wolves. Christianson and Creel (2008) found that elk diets contained more woody browse when wolves were present in the area than when wolves were absent, indicating that they spent more time foraging in forests when wolves

were present. These results indicate that elk spend more time in forested habitats and may consume more aspen and other woody species in response to predation risk.

Alternatively, wolves may decrease the population size of their elk prey base, resulting in lower elk densities and allowing aspen recovery due to lower browsing pressure: a density-mediated trophic cascade (Kauffman et al. 2010). Declines in ungulate density may be more pronounced in areas of high predation risk because there are fewer elk on the landscape and they avoid risky areas (Ripple and Beschta 2012). Behavioral and density mechanisms may also operate at the same time to allow recovery of woody browse species on the NYWR (Ripple and Beschta 2007; Creel et al. 2005).

Ripple and Beschta (2012) claim that the reintroduction of wolves to Yellowstone in 1995 has altered elk foraging behavior, allowing aspen stems to escape herbivory in areas of high wolf predation risk and replace the mature aspen overstory. In 2003, Halofsky and Ripple (2008*a*) reported that some aspen clones in high-risk areas (defined as riparian areas) of the Gallatin elk winter range of Yellowstone contained stems that had recently reached recruitment height. However, Winnie (2012) found that elk browsing was still preventing aspen recruitment in these same high-risk areas in 2010, and postulated that further declines in ungulate populations would be necessary to reduce the browsing pressure on aspen. Kimble et al. (2011) and Kauffman et al. (2010) found that ungulate population declines had not resulted in a landscape-scale aspen recovery on the NYWR as of 2006. However, recent declines in elk and mule deer populations on the northern range from 2005 to 2012 may indicate a decrease in the exposure of aspen stems to heavy browsing, which may have allowed aspen sprouts on the NYWR to reach

recruitment height, thereby becoming part of the overstory of aspen stands and increasing the sustainability of clones.

In January of 2005, the population of the northern Yellowstone elk herd was estimated to be around 9,545 animals (Lemke et al. 2008). The Northern Yellowstone elk herd recently declined to around 4,635 elk during the winter of 2010-11 (Loveless et al. 2011), and declined further to 4,174 elk in the winter of 2011-12 (NYCWWG 2012). The 56% decrease in the Northern Yellowstone elk herd from 2005 to 2012 may indicate a lower density of elk on the NYWR during the past seven years. In addition, surveys of mule deer on the northern range in May 2011 estimated a population of 1800 animals, a decrease of 15% since 2009 and the lowest population estimate of mule deer on the northern range in 10 years (K. Loveless, Montana Fish, Wildlife, and Parks, personal communication 2011).

Kay (1985) observed that aspen in the Eagle Creek drainage north of Yellowstone, located on the Gallatin National Forest (GNF) portion of the NYWR, were exposed to intense ungulate browsing as the Northern Yellowstone elk herd grew from 1969 to 1983. Age samples of aspen trees in Eagle Creek indicated a lack of recent recruitment during this period. The 1987 Gallatin Forest Plan directed that aspen and willow communities should be restored (Gallatin National Forest 1987). Prescribed fire has been used as a management tool in attempts to stimulate regeneration of aspen communities (Durham and Marlow 2010; Kay 1993), but aspen stands often lack flammable fuels and do not burn very easily (Jones and DeByle 1985*c*). Attempts to burn aspen stands in the Eagle Creek drainage failed because the aspen would not burn, so

forest managers reintroduced two family groups of beavers (8-16 individual beavers) to Eagle Creek in the autumn of 1991 as a means to restore aspen communities (D. Tyers, U.S. Forest Service, personal communication 2011).

Beavers heavily utilize aspen resources (Smith and Tyers 2008), but their characteristic foraging strategy can actually stimulate growth of aspen suckers and seedling establishment because they remove mature overstory trees that produce auxins to inhibit sucker growth (Schier et al. 1985*b*; Wan et al. 2006). When the "apical dominance" of an aspen clone is disturbed, new ramets are able to grow from the root system, reach recruitment height (>2m), and replace the mature overstory (Schier et al. 1985*b*). This unique ecological relationship between beaver and aspen provides an opportunity to restore aspen communities by stimulating regeneration of aspen clones. However, the effects of beaver herbivory on aspen are not limited to increases in sprout stem density. Preferential beaver herbivory of aspens can decrease the density of mature aspen trees, thereby allowing the establishment of less-preferred riparian species like mountain alder and conifers (Johnson and Naiman 1990, Kaye et al. 2003, Kimble et al. 2011).

Ungulate population declines in Yellowstone National Park since wolf reintroductions in 1995 have facilitated an increase in willow since the late 1990's (Ripple and Beschta 2006). Willow recovery, along with beaver reintroduction efforts north of Yellowstone, has triggered an increase in the Yellowstone beaver population (Smith and Tyers 2012). These findings indicate that beaver populations can flourish when willow and aspen resources are not suppressed by ungulate herbivory.

Though beaver were historically common in aspen riparian communities on the NYWR (Warren 1926), they were likely extirpated from Eagle Creek long before the 1970s due to trapping (McColley et al. 2012). In order to aid in the establishment of the beaver population in Eagle Creek and other reintroduced beaver populations in the Absaroka-Beartooth Wilderness Area, a moratorium was placed on beaver trapping in these areas (Smith and Tyers 2008), which is still in place today (Montana FWP 2012). The reintroduction of beaver to Eagle Creek re-established a unique ecosystem, and this drainage is now the only site in the NYWR where aspen, willow, beaver, and elk are all present. Eagle Creek provides the only opportunity to study the ecological relationships among this particular community of species on the NYWR and evaluate the effects of beaver reintroduction on aspen recovery in this drainage with high ungulate density. The reintroduction of beaver to Eagle Creek provided an opportunity to help managers better understand the role of beaver and ungulates in the ecology of aspen on the northern range. If beaver reintroduction has stimulated aspen regeneration in Eagle Creek, other riparian aspen clones in the NYWR with similar ungulate densities may also benefit from beaver reintroduction or beaver recolonization from surrounding drainages on the northern range.

Research conducted in 2005-07 (14 years after beaver reintroduction) by McColley et al. (2012) found that beaver activity in Eagle Creek decreased the mature canopy cover of aspens by 62% from 1990 to 2005, but immature aspen cover more than tripled during this same time period. However, the cover occupied by various riparian

herbaceous plants, willows (*Salix* spp.), and mountain alder (*Alnus incana*) also increased from 1990 to 2005.

The stem density of aspen ramets in Eagle Creek increased due to beaver activity, but ungulate browsing prevented aspen stems from growing to recruitment height, preventing recovery of aspen stands in Eagle Creek (McColley et al. 2012). The majority of ungulate browsing in Eagle Creek can be attributed to elk and deer because moose are not common in Eagle Creek. Bison do migrate out of YNP during the winter, but they are much less numerous than elk. McColley et al. (2012) determined that the elk density in the Eagle Creek drainage for the winter of 2005-2006 was 8.3 elk/km^2, indicating that aspen in Eagle Creek were still exposed to high levels of elk herbivory. Declines in northern range elk and deer populations indicate that woody browse species in Eagle Creek may be exposed to less browsing pressure since 2005. Since the Eagle Creek riparian corridor may be an area of higher predation risk than the surrounding landscape, these ungulate population declines may be even more pronounced than in other, less risky areas (Garrott et al. 2009). Lower ungulate browsing intensity since 2005, due to density or behavioral changes in elk herds, may have allowed immature aspens to replace the mature overstory and aid in recovery of aspen stands in this drainage.

The primary objective of this study was to determine if the aspen stands in Eagle Creek are now successfully regenerating since 2005, following the significant ungulate population declines on the northern range. First, we hypothesized that immature aspen would be starting to replace the mature aspen overstory, causing an increase in the canopy cover of mature aspen since 2005. We tested this hypothesis by assessing the

canopy cover of riparian vegetation in Eagle Creek. Next, we hypothesized that habitat

factors varying between aspen stands would influence the sprouting and recruitment

trends of aspen in Eagle Creek since beaver reintroduction. We tested this hypothesis by

examining sprouting and recruitment trends and evaluating the factors that may have

influenced these trends. Finally, we hypothesized that ungulate browsing is no longer

preventing aspen recruitment in Eagle Creek. We tested this hypothesis by investigating

the influence of ungulate browsing on aspen recovery throughout the Eagle Creek

drainage.

METHODS

<u>Study Area</u>

Eagle Creek is a second-order stream located on the Gallatin National Forest in southwest Montana, about 4 km northeast of Gardiner, MT (Map 2, Appendix A). The study area includes 5 km of the Eagle Creek stream reach, and the Davis Creek tributary at the north end of Eagle Creek. Mean annual precipitation is 50-90 cm, mean annual air temperature is 2-6°C, and elevation of the study area ranges from 1800 to 2100 meters with a 7% overall slope. Aspen communities typically occur on south-facing slopes in Eagle Creek. The Rosgen stream classification for Eagle Creek is A4, indicating moderate slope and sinuosity and a gravelly streambed (Rosgen and Silvey 1996). In addition to aspen, common vegetation in the riparian zone includes Engelmann spruce (*Picea engelmanii*), Bebb's willow (*Salix bebbiana*), Geyer's willow (*S. geyeriana*), sandbar willow (*S. exigua*), mountain alder (*Alnus incana*), and serviceberry (*Amelanchier alnifolia*). Other common vegetation includes snowberry (*Symphoricarpos albus*), basin wildrye (*Elymus cinereus*), smooth brome (*Bromus inermis*), and wild rose (*Rosa woodsii)*. Upland-sagebrush grasslands surround the riparian area, and common species include Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* spp*. Vaseyana*), bluebunch wheatgrass (*Agropyron spicata*), and Idaho fescue (*Festuca idahoensis*).

Historical Beaver Structure Inventory

From the time of beaver reintroduction in 1991, U.S. Forest Service managers monitored the beaver population in Eagle Creek by taking an inventory of beaver structures each fall from 1991 through 2012. Managers recorded locations of active and inactive beaver structures, including dams, lodges, and caches. This inventory provides information about hotspots of beaver activity and approximate beaver numbers in the drainage. Because there are usually 4-8 individual beavers associated with each lodge (Jenkins and Busher 1979), managers can estimate the size of the beaver population each year.

Vegetation Cover Changes

Changes in the percent canopy cover of mature and immature aspen in Eagle Creek indicate whether aspen stands are regenerating. The canopy cover of other riparian vegetation types indicates how beaver herbivory may have changed the plant community in Eagle Creek. Specifically, comparing the canopy cover of mature aspen in 2005 and 2011 indicates whether or not immature aspen are released from ungulate browsing pressure and are beginning to replace the mature aspen overstory. Changes from 1990 to 2005 and from 2005 to 2011 in the composition of cover types in Eagle Creek were investigated by comparing aerial photos taken in 1990, 2005 and 2011. The images used were NAIP (National Agriculture Imagery Program) photographs obtained from the U.S. Department of Agriculture. These images had a 1 meter resolution and 5 meter accuracy. The digital polygon (29 ha in area) used in McColley et al.'s study in 2005 was used to

delineate the riparian corridor of Eagle Creek in 1990, 2005 and 2011 photos (Map 3, Appendix A). Three hundred random points were generated within the polygon for each photo and visually classified into a cover type category according to the dominant cover type at each point. Cover types were determined from the color and texture of the point on the photograph, as well as knowledge of the vegetation on the ground. Each photo was sampled six times, resulting in 1800 random points per photo.

Accuracy of cover type classification was checked by visiting100 points on the ground from the 2011 photo to determine if the visual classification matched the actual cover type on the ground. Accuracy was assessed by calculating the percentage of points correctly classified within each cover type category and out of the entire sample of points visited (overall accuracy). An overall accuracy of $\geq 85\%$, and within-cover type accuracies $\geq 70\%$ were the criteria used to establish whether or not the cover type classification method was sufficiently accurate (Thomlinson et al. 1999).

Cover types included immature aspen (<2m tall), mature aspen (>2m tall), conifer, alder, willow, surface water, or sagebrush-grasslands (McColley et al. 2012). The percentages of each cover type were determined for each sample by dividing the number of points in each cover type category by the total number of points (300 total points per sample). The percentages from each sample were compared between the 1990, 2005, and 2011 photos to detect changes in the percentage of each cover type over time.

Aspen Responses to Beaver Disturbance

In an effort to monitor beaver and ungulate herbivory on aspen, forest managers established 31 permanent vegetation plots throughout the Eagle Creek drainage in 1997, six years after the initial beaver reintroduction (Map 4, Appendix A). Twenty plots were established along the drainage in 1997, ten in 1998, and one in 2001. These plots were visited each spring from 1997 to 2012 after snowmelt but before leaf-out of the aspen stems. At each plot, a measuring tape was used to establish a 4 m radius circle from the center stake, and the presence or absence of beaver cutting or ungulate browsing on each aspen tree within the circle was recorded. Though a $1/20^{th}$ acre plot (8-m radius circle) was initially established according to previous aspen research methods (St. John 1995), the copious amounts of sprouts and saplings in the aspen stands following beaver disturbance made counting the trees in this larger plot extremely time-consuming. The smaller 4-m radius plot size was used (one half of a standard $1/20^{th}$ acre plot) so that small trees could be counted accurately and efficiently, but all size classes were recorded. In order to accurately capture the density of larger trees, each circular plot also contained an extended radius of 8 meters, and only mature trees were recorded within this extension area between the 4 and 8 meter radius (Figure 1). Beaver cutting or ungulate herbivory on mature trees was recorded in the same categories as the trees within the 4 meter radius circular plot.

Figure 1. Schematic of aspen circular plots used to monitor long-term trends in aspen stands of Eagle Creek.

All sizes of cut and uncut aspen trees in these circular plots were recorded each year from 1997 to 2012. As an aspen tree grows older, its diameter also increases (Jones and Schier 1985). Diameter at breast height (DBH) measurements are commonly used to categorize trees into size classes that indicate the approximate age of the tree (Ripple and Larsen 2000). Trees felled by beaver can be categorized into size classes based on their diameter at stump height, which is their basal diameter at ~30 cm above ground (Johnson and Naiman 1990). The vegetation plots in this study contain trees felled by beaver and many aspen stems that have not yet grown tall enough to have a measurable diameter at breast height, so size classification according to basal diameter was used for all trees in the plots. The basal diameter size classes were as follows: Sprout (<1 cm), Sapling (1-2 cm), Pole (>2<12.5 cm), or Mature (>12.5 cm) (Hann and Jensen 1987). The number of sprouts, saplings, and pole trees (sprouts and saplings that have reached recruitment height) in a plot indicates whether or not that area of the aspen clone is producing immature aspen that can regenerate the clone.

For each tree, observers determined if the tree had been cut by beaver, browsed by ungulates, or not utilized by herbivores at all. Beaver cuts are recognizable by the conical, smooth-surfaced cut stumps. Ungulate browse is recognizable by the frayed, broken branch tips of live aspen trees. Other herbivores that might consume aspen (such as snowshoe hares, cottontail rabbits, pocket gophers, and porcupines; DeByle 1985*b*) are either not common in the Eagle Creek study area or do not produce the distinctive browsing patterns resulting from beaver and ungulate herbivory. For live trees, observation of browsing included only the current year's browse so that data reflects annual ungulate utilization. For trees cut by beaver, the number of cuts (divided into fresh and old cuts) and resprouting responses from cut stumps were recorded.

Monitoring these aspen plots for 15 years provides information about when beavers started cutting trees in each plot (some were cut before the plots were established in 1997), how this affected the number of sprouts and saplings, and whether any of these trees grew into pole trees by 2012. For the 30 plots established in 1997/98, beaver foraging trends were captured during the time period the plots were monitored, or reconstructed using old-cut trees in the plot and historically active beaver lodges and dams. The plot established in 2001 contained a high density of sprouts in 2001 and was adjacent to beaver colony active from 2001-04, indicating that it was cut by beaver very near the time of establishment. Though the years of beaver disturbance differed among plots, all plots used in the study were used to describe changes in aspen stands following beaver disturbance. By quantifying the number of trees in each size class and their utilization by beaver and ungulates each year, we can determine the sprouting response to

beaver activity, browsing pressure from ungulates, and how these factors have influenced

recruitment in each plot. The sprouting response trends for each aspen circular plot were

examined by graphing the number of trees in each utilization category for each year.

Factors Influencing Aspen Sprouting and Recruitment

Data from the long-term circular plots was used to determine what factors

influenced sprouting and recruitment trends in Eagle Creek. The response variable

recorded for each plot in the spring of 2012 was the presence or absence of a recruitment

stem (>2m in height, <5 cm DBH; Kay 1985). Using the information on the aspen trees

within these plots, several variables were determined for each plot that may have

influenced the presence or absence of a recruitment stem within the plot. Only variables

that may have differed between plots were determined, because landscape-scale factors

such as climate indices would not help to explain variation in recruitment among plots.

These variables were: 1) percent of sprouts and saplings browsed by ungulates in 1997,

2) percent of sprouts and saplings browsed by ungulates in 2012, 3) percent of original

overstory stems cut by beavers, 4) number of years beavers cut trees in the area

(longevity), 5) number of overstory stems alive in the plot in 2012, 6) number of pre-

disturbance overstory stems, 7) presence or absence of prolonged flooding on the plot at

any time since 1997, 8) percent of plot in which woody species other than aspen are

growing in 2012, and 9) elevation. Though snow depth could have affected ungulate

access to the aspens within each plot, elevation provides an acceptable surrogate for

variation in snow depth along the elevational gradient of Eagle Creek. The nine factors

listed above were predicted to be the most likely to influence the presence or absence of recruitment stems, and hence, aspen recovery, in each plot.

We hypothesized that higher percentages of sprouts and saplings browsed by ungulates in 1997 and/or in 2012 would be associated with a lack of recruitment stems in the circular plots. We hypothesized that a higher percentage of overstory stems cut by beaver, fewer years of beaver foraging in the area, fewer overstory stems alive in 2012, and more pre-disturbance overstory stems would contribute to aspen recruitment in the plots. We predicted that prolonged flooding, greater percentages of woody competition, and lower elevation would be associated with a lack of recruitment stems in the plots.

This long-term data was also used to calculate the number of live pole trees in each plot for each year after the cessation of beaver disturbance. Percent of sprouts and saplings browsed by ungulates was also calculated for each plot in each year subsequent to initial beaver disturbance. After beaver disturbance, sprouts and saplings that escape ungulate browsing will likely grow into pole trees if beaver do not continue to forage in that plot. The fewer sprouts and saplings that are browsed by ungulates in a plot, the greater likelihood that recruitment stems will be found in that plot. If a plot has experienced lower browsing pressure on sprouts and saplings over time, this trend should be associated with increased recruitment of pole trees.

Effects of Ungulate Browsing on Aspen Recruitment

Research in Eagle Creek by McColley et al. (2012) isolated the effects of ungulate herbivory on the ability of aspen stems to grow to recruitment height by building fourteen

3x3x1.5m fenced ungulate exclosures in 2004/05 throughout the riparian corridor of the Eagle Creek drainage (Map 5, Appendix A). Directly beside each exclosure, a 3x3m unfenced plot was established that was available for herbivores to browse (Figure 2).

Figure 2. Schematic of ungulate exclosure and adjacent unfenced area.

At the time of establishment, the average height of aspen stems inside and outside each exclosure was ~100 cm. The height of each aspen stem in the fourteen fenced exclosures and unfenced areas established in 2004/05 were measured in the fall of 2004/05 at establishment and again in the fall of 2006, 2007, 2009, 2011, and 2012. Four additional exclosures were established in 2006, the height of each aspen stem in these exclosures and adjacent unfenced areas were measured in 2006, 2007, 2009, 2011, and 2012. The average height of aspen stems inside and outside these exclosures was ~130 cm at the time of establishment in 2006. Lack of ungulate browsing within these exclosures during the study indicated that the exclosure fence height of 1.5 meters was sufficient to exclude ungulate access to the enclosed aspen stems.

The live stem height was determined for each stem in the fenced and unfenced areas each year. The average stem height was calculated for each fenced and unfenced area for each year. The average height of aspens that are exposed to browsing (unfenced

area) and aspens that have received no browsing pressure for 6-8 years (fenced exclosures) will show whether ungulate herbivory is still preventing aspen stems from reaching recruitment height (>2m), in what areas of the drainage aspens are recruiting, and when recruitment started. Aspen recruitment was determined by graphing the average heights of each paired plot (fenced exclosure and juxtaposed unfenced area) over the six years the aspens were monitored.

Spatial Variation in Ungulate Browsing

In order to determine the browsing pressure aspens are exposed to along the elevational gradient of Eagle Creek, the drainage was divided into four elevational zones with an average elevational change of 91 meters (Map 6, Appendix A). Browsing utilization was evaluated for at least 500 individual trees within each of the zones each spring from 2001-2012. Trees were not marked, so the sample of trees was different for each year of the study. Trees were arbitrarily selected by field technicians, and thus are not a random sample. However, the large sample size of trees for each elevational zone greatly increases the likelihood that trees from all stands in all parts of the drainage were sampled. For example, field technicians sampled trees from both the inside of aspen stands and along the edges, and trees located both far and near to the stream to avoid sampling areas more likely to be browsed by ungulates. Only trees in the sprout (<1 cm) or sapling (1-2 cm) basal diameter size classes were investigated because these smaller trees are within the browsing zone between ground-level and 2 meters tall. Browsing utilization was estimated by the percentage of a tree's twigs that have been browsed by ungulates. Browsing percentage categories were 0-25%, 26-50%, 51-75%, or 76-100%.

Browsing included only those twigs that had been bitten in the current year, or freshly

browsed. Because this sampling was completed in the spring of each year, the browsing

measured reflects mid and late-winter browsing. Twigs browsed earlier in the winter may

have appeared as browsed in earlier years, and thus may have not been counted as current

years' browse. The percentage of trees in the lightly browsed (0-25%) and heavily

browsed (76-100%) categories was compared among all elevation zones to determine if

there was any variation in browsing pressure throughout the drainage that may influence

recruitment trends.

Browsing data from the trees sampled within the elevational zones of Eagle Creek

indicated that browsing utilization declined markedly for all elevational zones in the

study period 2010-12. To investigate this trend, the percentage of trees in each browsing

category was compared between the 2001-09 and 2010-12 study periods within each

elevational zone. This was a post-hoc analysis, but it served to differentiate changes in

browsing trends over time.

Ungulate Density Transects

McColley et al. (2012) recorded ungulate sightings on ground surveys completed

twice each month for the winter of 2005-06 to determine ungulate density in Eagle Creek.

To determine how ungulate density may have changed since 2005, this method was

repeated for the winter of 2011-12. The length of the stream reach was travelled twice

every month from December through March and the number of ungulate sightings was

recorded by species. Ungulate density was calculated by dividing the number of

individuals of each species counted in 8 observation periods by the total area of the Eagle

Creek drainage (4.92 km^2). Density was calculated separately for elk, mule deer, white-tailed deer, and bison.

This method of determining ungulate density is limited because it was only performed two days of each month and is a relative measure of density. The ungulates encountered on each survey depended on a number of uncontrollable factors (weather, herd movements, other wildlife in the area), and some animals may not have been visually detected. Variations of distance sampling methods attempt to account for observer inability to visually detect animals further away from the line or point transect, detection error as a function of habitat heterogeneity, and response of the wildlife species to observers (Buckland et al. 2009). We did not attempt to account for these variables, instead using the same ungulate density estimation method and density calculations employed by McColley et al. (2012) for previous research in Eagle Creek in order to facilitate comparison between studies. These estimates would miss any fine scale changes in ungulate abundance, but we felt they would be sufficient to detect large changes in the ungulate populations frequenting the Eagle Creek drainage.

<u>Statistical Analyses</u>

<u>Vegetation Cover Changes</u>

Samples of each vegetation type for each aerial photograph (1990, 2005, and 2011) were normally distributed except for samples with 0% vegetation cover found in that year (alder and surface water were not detected in the 1990 photograph). Many pairwise comparisons between 1990, 2005, and 2011 samples within each cover type

displayed unequal variances, so Welch two-sample t-tests were used to account for

unequal variances between samples. All pairwise comparisons between years within each

vegetation type were investigated.

Factors Influencing Aspen Sprouting and Recruitment

Recruitment in each circular aspen plot was represented by a binary variable:

presence of a recruitment stem in the plot in 2012 (1) or absence of a recruitment stem

(0). Aspen stems >2m and <5 cm in DBH were considered recruitment stems (Kay 1985).

One plot contained no sprouts or saplings when it was established in 1997, so sprouting

and recruitment could not be assessed for this plot and it was not included in analysis.

The factors affecting sprouting and recruitment in the remaining 30 plots were evaluated.

There did not appear to be spatial correlation in recruitment of plots located near each

other. This is probably because most plots were located on average 35-50 meters apart,

and most of the factors that may affect recruitment operate at a very fine scale ($\leq$20

meters) in the riparian corridor. For example, a plot in the floodplain may be located near

a plot further up the streambank, but the two plots are subjected to very different

environmental conditions. Fine-scale environmental variation indicates that recruitment

responses between plots are generally independent. However, some of the plots are

probably located within the same aspen clone. Trees in these plots are connected by the

clonal root system and are not completely independent observations. Due to the binary

distribution of the response variable, there were no outliers.

A generalized linear model (GLM) was fit to the regression of recruitment (1 or 0)

on eight explanatory variables: 1) percent of sprouts and saplings browsed in 1997

(br.97), 2) percent of sprouts and saplings browsed in 2012 (br.12), 3) number of overstory stems cut by beavers (cut), 4) number of years beavers cut trees in the area (longevity), 5) number of overstory stems alive in the plot before beaver disturbance (overstory.pre), 6) presence or absence of prolonged flooding on the plot at any time since 1997 (flood), 7) percent of plot in which woody species other than aspen are growing in 2012 (woody), and 8) elevation. The number of overstory stems alive in the plot in 2012 could not be tested because it perfectly predicted the response, which would not normally be the case with a larger sample size. The Drop-In-Deviance test was used to compare models and arrive at the final inferential model. No significant interactions were found among explanatory variables. Though each explanatory variable was checked for a nonlinear relationship with the response variable, no evidence suggested the use of higher-order terms. The full inferential model used was the regression of br.12, br.97, flood, cut, longevity, overstory.pre, woody, and elevation on the binary recruitment response variable (using the binomial distribution).

In addition, correlations between recruitment and browsing intensity were investigated for each circular plot using simple linear regression. The recruitment response variable was represented by the number of pole trees in each of twenty-five of the circular plots. Five plots had no pole trees growing after beaver disturbance, so correlations could not be investigated. The browsing intensity (percent of sprouts and saplings browsed in each plot each year) was the explanatory variable. Because beavers cut pole trees in many plots, only the years following the cessation of beaver activity in each plot were used in correlations. This resulted in an average sample size of 10 years.

Residual plots from the exploratory linear model for the regression of browsing intensity on recruitment (for each circular plot) indicated that the residuals met the normality and constant variance assumptions for simple linear regression. Measures of browsing intensity each year were independent observations. The linear model for the regression of browsing intensity on recruitment was fit for each plot separately. The R^2 and p-value associated with each regression model was used to evaluate the strength of the relationship between number of pole trees and browsing intensity.

Variation in Ungulate Browsing

The percentage of trees in lightly browsed (0-25%) and heavily browsed (76-100%) categories were compared between elevational zones of the drainage using multiple linear regression. Percent of trees was the response variable, and year and elevational zone were the explanatory variables. Year was used as a factor variable with 12 levels, and elevational zone was a factor variable with four levels. Residuals from the full linear model for the regression of year and elevational zone on percent of lightly browsed trees indicated that residuals were normally distributed around the mean and had constant variance. This full model was compared to the reduced linear model for the regression of year on percent of lightly browsed trees, which does not account for differences between elevational zones. The F-statistic was used to determine whether elevational zone (zone.f) improved the reduced model.

The percentage of trees in the lightly browsed category was compared between elevational zones for the study periods 2001-09 and 2010-12. This was done because the data showed that these study periods demonstrated different browsing trends. All samples

were normally distributed, but many samples that were compared had unequal variance. All pairwise comparisons between elevational zones were investigated using Welch two-sample t-tests to account for unequal variance.

The percentage of trees in the lightly browsed category was compared between the study period 2001-09 and 2010-12 within each browsing zone. These samples were normally distributed but did not have equal variance, so Welch two-sample t-tests were used to investigate differences between sampling periods. Sample sizes of the study periods 2001-09 (n=9) and 2010-12 (n=3) were not equal. Though this does not invalidate using a t-test to detect differences in means, the mean for the 2010-12 study period is derived from only three years and is therefore not as accurate as the mean for the 2001-09 study period. Sample means are reported in conjunction with results of the t-test to account for the inequality of sample sizes. The percentage of trees in the heavily browsed category was also compared between study periods within each browsing zone. All statistical tests were performed using "R" version 2.13.1 (R Development Core Team 2009). P-values were considered significant at the $p<0.06$ alpha level.

RESULTS

Historical Beaver Structure Inventory

Two beaver family groups (~8 individual beavers) were reintroduced into the Eagle Creek drainage in 1991. The number of active beaver lodges in Eagle Creek fluctuated from one in 1991 to a peak of 13 in 2003 (Figure 3). After this peak, active lodges declined, and none were found in 2008 and 2010. However, one active lodge and two active dams were located in Eagle Creek in 2011 and 2012.
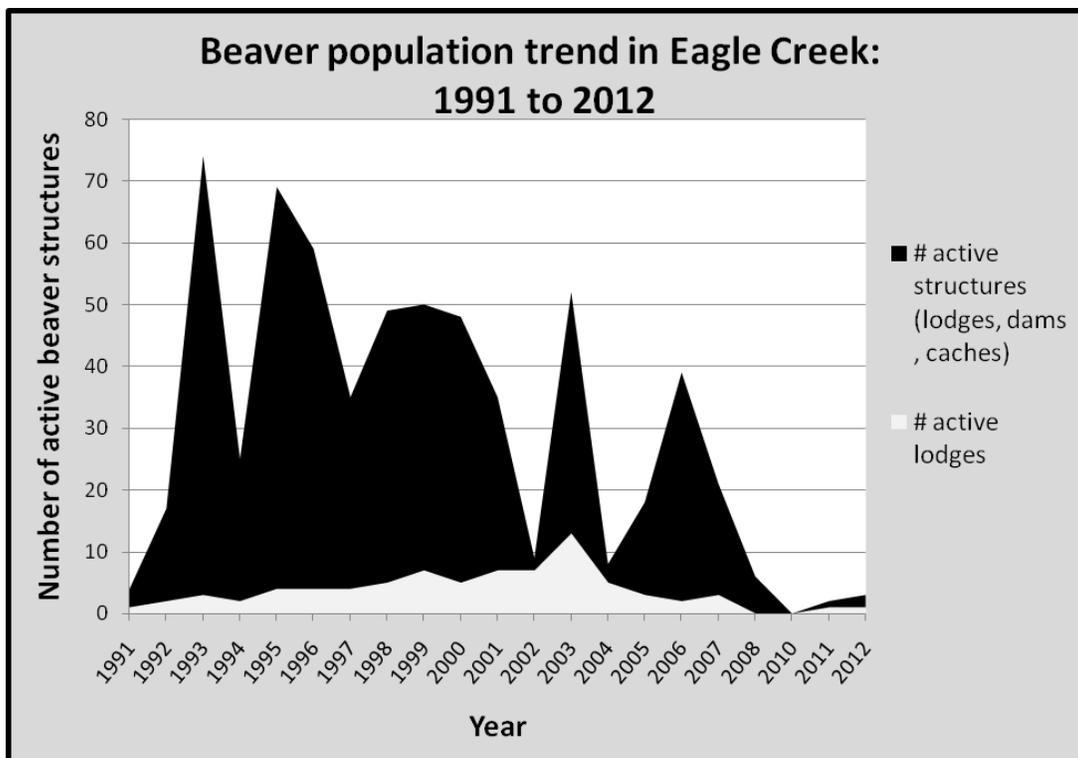

Figure 3. Annual inventory of active beaver structures in Eagle Creek from 1991 to 2012. Number of lodges reached a peak of 13 in 2003, and has declined to one active lodge in 2012.

Vegetation Cover Changes

Overall accuracy of assigning points on the aerial photos to the correct cover type classification was 87% (Table 1). Classification accuracy exceeded the criteria established by Thomlinson et al. 1999, which indicates a minimum overall accuracy of 85% and within-class accuracies ≥70%. This method appears to be sufficiently robust for determining vegetation cover types. Accuracy of classifying surface water could not be determined because the 100 points visited were randomly selected, and none were in the surface water category. Willow and alder have slightly lower accuracies because these points were sometimes misclassified as immature aspen. Points occurring on the edge of vegetation cover types were more often misclassified than points occurring in the center of a vegetation type.

Table 1. Classification accuracy for each vegetation cover type in Eagle Creek.

	Number of points	Number of points correct	% Accuracy
Mature Aspen	18	16	89%
Immature Aspen	7	6	86%
Willow	21	16	76%
Alder	15	12	80%
Conifers	13	13	100%
Riparian Herbaceous Plants	13	11	85%
Sagebrush Grasslands	32	30	94%
Surface water	N/A		
Total	119	104	87%

Mature aspen cover decreased from 1990 to 2005 (p<0.05; Figure 4). However, immature aspen, alder, willow, riparian herbaceous plants, and surface water all increased from 1990 to 2005 (p<0.05). Mature aspen cover, immature aspen, willow, and riparian herbaceous plants did not change from 2005 to 2011 (p>0.05). Alder canopy cover increased and surface water cover decreased from 2005 to 2011 (p<0.001). Conifer and sagebrush-grassland cover did not change at all during the study period 1990 to 2011 (p>0.05).

Figure 4. Changes in dominant riparian cover types in the Eagle Creek drainage from 1990 to 2005 and from 2005 to 2011. All cover types (except conifers) changed from 1990 (before beaver reintroduction) to 2005 (14 years after beaver reintroduction; p<0.05). Alder and surface water were not detected in the drainage in 1990. Alder cover increased (p<0.05) and surface water decreased (p<0.05) from 2005 to 2011, but all other cover types remained constant.

Aspen Response to Beaver Disturbance

Most areas (71% of aspen plots) with beaver disturbance exhibited a similar sprouting response. The initial beaver cutting of mature overstory stems stimulated a dramatic increase in the number of sprouts the year following the disturbance, but sprout numbers then declined to pre-disturbance densities. In a few areas, beaver disturbance did not result in increased sprouts (13% of plots). In some areas, notable fluctuations in the number of sprouts and saplings were unrelated to beaver disturbances (16% of plots). Of the 31 circular plots established in 1997 to monitor the effects of beaver cutting and ungulate herbivory on aspen in Eagle Creek over time, 24 of the plots (77%) had at least one recruitment stem (>2m in height) in 2012. Seven of the plots (23%) had no recruitment stems.

Factors Influencing Sprouting and Recruitment

Two factors that were associated with the absence of recruitment stems in the circular plots were prolonged flooding and high browsing intensity in 2012 ($p<0.05$; Table 2). Other factors tested (browsing intensity in 1997, amount of overstory disturbance, woody competition, elevation, and overstory stems before beaver disturbance) did not contribute to explaining the recruitment response. No significant interactions between explanatory variables were found by comparing models using the Drop-In-Deviance test.

Table 2. Analysis of Deviance Table for the Generalized Linear Model for the regression of recruitment on br.12, br.97, flood, cut, longevity, overstory.pre, woody, and elevation. The binomial distribution and logit link were used for this model. The binary response was regeneration (1) or none (0). Variables were added sequentially. Asterisks (*) represent a significant p-value at the 0.05 alpha level.

	Degrees of Freedom (d.f.)	Deviance	Residual d.f.	Residual Deviance	p-value
NULL	N/A	N/A	29	30.02	N/A
Br.12	1	4.3156	28	25.709	0.038*
Br.97	1	0.2306	27	25.478	0.631
Flood	1	4.5102	26	20.968	0.034*
Cut	1	0.1367	25	20.831	0.712
Longevity	1	1.2474	24	19.584	0.264
Overstory.pre	1	0.4630	23	19.121	0.496
Woody	1	0.0433	22	19.077	0.835
Elevation	1	1.0014	21	18.076	0.317

All plots clear-cut by beaver (all mature overstory stems cut) had no recruitment in 2012 (6 plots), and all plots with at least one recruitment stem also had at least one overstory stem (Table 3). This suggests that mature overstory stems may increase the likelihood of sprouting and recruitment in an area with beaver disturbance. Plots with no recruitment stems seemed to have higher average percentages of sprouts and saplings browsed in 1997 and 2012 than plots with recruitment stems.

Table 3. 77% of long-term circular aspen plots had ≥1 recruitment stem in 2012 (n=31). Plots that lacked any mature overstory stems, were exposed to prolonged flooding conditions, and/or sustained high levels of browsing from 1997 to 2012 were associated with a lack of recruitment stems in 2012.

	Flooded	% sprouts/saplings browsed in 1997	% sprouts/saplings browsed in 2012	Ave. # overstory stems in 2012
≥ 1 recruitment stem	3/24 (13%)	68%	28%	12 stems
No recruitment stems	4/7 (57%)	85%	65%	0 stems

Of the plots with no recruitment stems, 57% (4 of 7 plots) experienced prolonged flooding at some point between 1997 and 2012. Only 12.5% of the plots with a recruitment stem (3 of 24 plots) experienced prolonged flooding. Odds ratio calculations indicate that the odds of recruitment in areas that do not experience prolonged flooding are 9.3 times as large as the odds of recruitment in flooded areas.

Lower browsing intensity was associated with more pole trees in 13% of the circular plots (R^2>0.41, p<0.05). However, 70% of the plots did not show any relationship between browsing intensity and recruitment, and R^2 values were generally very low. In five plots (17%), no pole trees have grown since the plot was initially cut by beaver, so no correlation was possible.

Ungulate Density Transects

Densities of almost all ungulate species were lower in 2011 than in 2005 (Table 4). Most ungulate groups were observed in the middle sections of the drainage for the

winter of 2011-12. Elk were the most common potential browser in Eagle Creek for the

winter of 2011-12, and mule deer were most often encountered in the drainage.

Table 4. Winter ungulate densities in Eagle Creek. Densities of all ungulates except white-tailed deer were lower in the winter of 2011 than in the winter of 2012.

	2005	2011
Elk	8.3/km^2	6/km^2
Mule deer	7.3/km^2	2/km^2
White-tailed deer	0.1/km^2	0.15/km^2
Bison	4/km^2	0.1/km^2

Effects of Ungulate Browsing

The aspen exclosures constructed in 2004/05 indicate that ungulate browsing is no

longer preventing aspen recruitment in Eagle Creek. Two exclosures experienced site

changes since they were constructed in 2004/05 that were not representative of aspen

stands, so the remaining 16 exclosures were used to evaluate recruitment trends. In 2012,

75% of the unfenced areas (exposed to herbivory) had an average stem height ≥2 meters.

Most exclosures reached an average stem height ≥ 2 m in 2009. The average height of

aspen stems in Eagle Creek that were protected from herbivory was 326 cm, and aspen

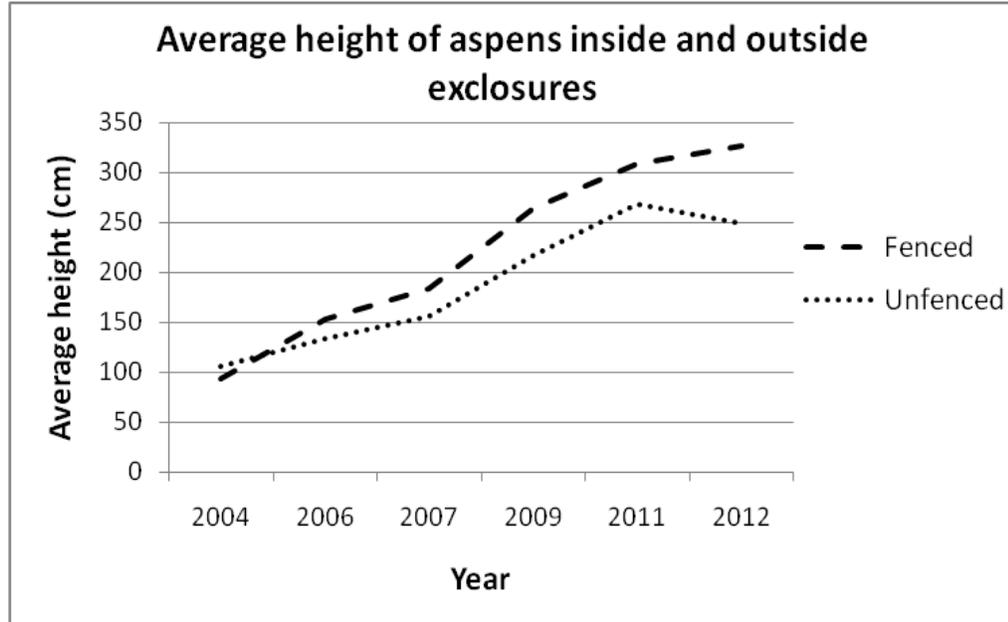stems exposed to herbivory had an average height of 248 cm (Figure 5).

Figure 5. Most aspens inside fenced exclosures and in the unfenced area juxtaposed to the exclosure (n=16) reached recruitment height (>2 meters) in 2009. The average height of aspens exposed to herbivory (unfenced) was 248 cm in 2012.

Variation in Ungulate Browsing

Aspen at the top of the drainage (7100 m) and the bottom (6200 m) experienced less intense browsing pressure than the middle of the drainage for the study period 2001-2009 ($p<0.05$; Figure 6). However, this trend was not observed in the study period 2010-12. There were no differences in browsing intensity among any areas for 2010-12 ($p>0.05$).
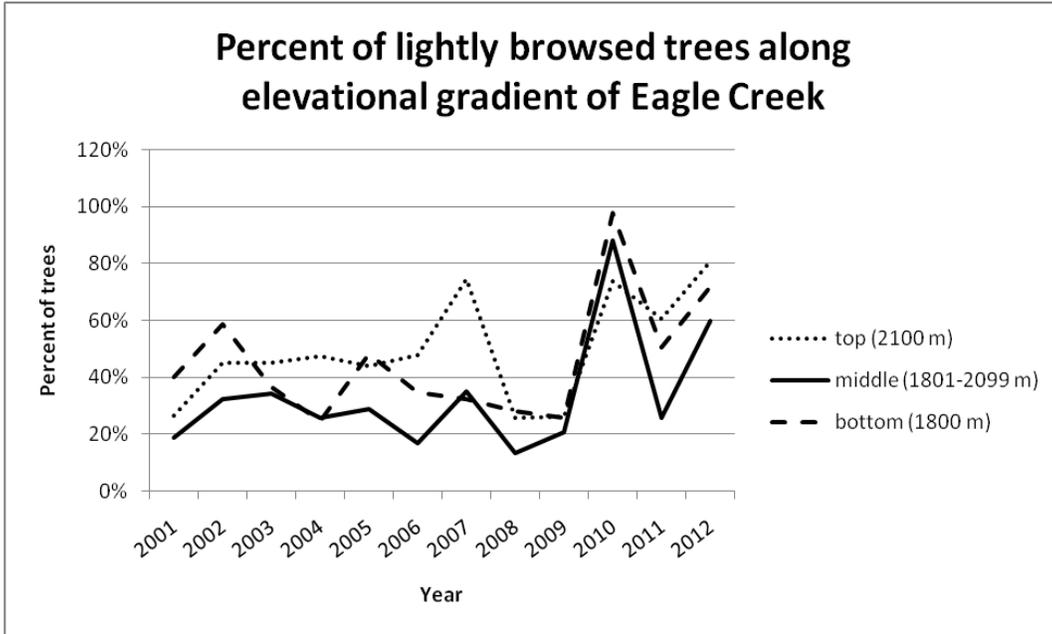
Figure 6. Percentage of sampled trees that were lightly browsed in each elevational zone. The top and bottom of the drainage generally have more lightly browsed trees than the middle sections. There is a sharp increase in lightly browsed trees across all elevational zones in 2010.

Evidence suggests that most areas of the drainage have experienced less intense browsing pressure in 2010-12 than in 2001-09 ($p<0.06$; Table 5).

Table 5. Percentage of lightly browsed (0-25% browsed) sprouts and saplings increased for each browsing zone in 2010-12, indicating a decrease in browsing pressure in recent years.

	Zone 1 (top of drainage)	Zone 2	Zone 3	Zone 4 (bottom of drainage)
2001-09	42%	26%	24%	37%
2010-12	72%	51%	65%	73%

DISCUSSION

Weather records show that average temperature, total annual precipitation, and total annual snowfall have not fluctuated dramatically throughout the study period 1990-2012 (Weather Source, LLC; data from Mammoth Weather Station). Mean temperature ranged from 3-7°C for this 22-yr period, total annual precipitation ranged from 23 to 43 cm, and total annual snowfall ranged from ~1 m in 1992 to ~3 m in 1996. Aspen communities often thrive where total annual precipitation is ≥ 38 cm, and can survive all temperature ranges common in mountainous areas but the most extreme (-57°C to 41°C). Aspen are dormant during winter months, so young aspen trees can survive deep snow conditions. Though temperature and precipitation were not measured in Eagle Creek during the study period, it is unlikely that fluctuations in weather patterns have influenced sprouting and recruitment trends in Eagle Creek because aspen clones are able to withstand wide fluctuations in temperature and moisture conditions.

Mature aspen cover decreased from 1990 to 2005 because the beavers that were reintroduced to the drainage in 1991 cut down many mature aspen trees to use for food and structure material. This removal of overstory aspen trees stimulated the growth of aspen root suckers and contributed to an increase in immature aspen from 1990 to 2005. However, the canopy cover of mature overstory has not increased since 2005, indicating that immature aspen have not yet replaced the mature stems cut by beaver.

Willow, alder, and riparian herbaceous plant cover increased in Eagle Creek from 1990 to 2005, most likely because beaver activity elevates the water table of riparian areas, so many places near beaver dams were suitable habitat for these hydrophilic

species. Though willow and riparian plant cover has not continued to increase from 2005

to 2011, alder cover has increased during this time period, indicating that alder is still

expanding into suitable areas.

Though surface water cover increased from 1990 to 2011 due to the creation of

beaver ponds, water cover decreased from 2005 to 2011. Historical beaver structure data

shows that the beaver population has declined from 3 active lodges in 2005-07 to only

one active colony in 2011 and 12, so there are fewer beaver ponds holding water now

than in 2005.

Conifer and sagebrush grassland cover remained constant during the study period

1990 to 2011. This is not surprising because beavers in this drainage do not cut conifer

trees or utilize sagebrush. Removal of mature aspen overstory can provide an

opportunity for conifer encroachment, but this trend was not observed in Eagle Creek as

of 2012. Kay (1990) found that 57% of the aspen stands in Eagle Creek contained no

conifers in 1985 and concluded that these stands are potentially stable climax

communities. The lack of conifer encroachment in Eagle Creek aspen stands indicates

that many of these aspen stands are most likely climax communities that are not seral to

conifers or upland-sagebrush.

Height trends observed in trees in aspen exclosures, monitored from 2004 to 2012

suggest that many saplings (both protected and unprotected from herbivory) in Eagle

Creek have now exceeded recruitment height (>2m). Some aspen sprouts grew taller

than 2 meters as early as 2000-2004, but the majority of saplings reached recruitment

height in 2009-11. Both browsed (unfenced) and unbrowsed (fenced) aspens exhibited

these recruitment trends. However, some browsed aspens had still not reached recruitment height in 2012. Some exclosure plots showed that browsed and unbrowsed aspens reached recruitment height in the same year, but generally browsed aspens grew to recruitment height about 3 years after the unbrowsed aspens at each paired plot.

Literature suggests that if aspen saplings are able to grow into the mature overstory, it can be replaced 20-30 years after beaver disturbance under moderate to low herbivory conditions (Warren 1926; Jonas 1955). Aspens in Eagle Creek took on average 11 years to grow to recruitment height after initial beaver disturbance. Aspen trees usually do not reach maturity until they are $\geq$ 30 years old (Jones and Schier 1985). Ripple and Larsen (2000) created a linear regression model to predict aspen tree age from DBH based on increment core data collected from aspen trees on the NYWR, including Eagle Creek. This model predicts that aspen trees in this area reach a DBH of 20 cm when they are around 30-40 years old. Since some recruitment began as early as 2000, the mature overstory of aspen in Eagle Creek will probably not begin to be "replaced" until at least 2030. Though browsing has probably inhibited vertical growth of aspen suckers, recruitment has been occurring in some areas despite elk densities 6-8 times higher than 1 elk/km^2 (density proposed by White et al. 1998 that may promote aspen regeneration).

Sprouting responses to beaver disturbance varied throughout the drainage. Most places exhibited prolific sprouting following beaver cutting of the overstory, though this trend was not observed in some areas. These responses indicate that beaver disturbance has stimulated sprouting in many Eagle Creek aspen stands. Some aspen stands had

sufficient sprouting to regenerate the clone without overstory disturbance. This is probably because seasonal fluctuations in auxin production allow sprouting even when mature overstory stems are not disturbed (Eliasson 1971), and is supported by research indicating that aspen in the GYE can regenerate without overstory disturbances (Kay 1985).

Though some studies suggest that removing all mature overstory stems can result in high stem densities, results of beaver clear-cutting were mixed. Beaver clear-cutting stimulated a significant sprouting response in some areas, though these sprouts declined rapidly. In other areas, beaver clear-cutting did not result in increased sprouting. Many of these areas were flooded during beaver disturbance due to dam-building activity in the area. Lack of mature overstory stems was associated with lack of recruitment stems in the aspen circular plots. Plots lacking mature overstory stems probably still maintained a living root system via root connections with live trees in the clone (DeByle 1964).

However, prolonged flooding or competition with other woody species probably contributed to poor sprouting and survival in clear-cut plots. These observations suggest that in patchy aspen stands exposed to poor growing conditions, clearcutting the mature overstory may lead to limited sprouting and recruitment. However, fluctuations in the water table were not measured for the duration of this study, which limits inferences about the effects of ground water on aspen suckering in Eagle Creek. Beaver-created flooding only affected a small portion of the aspen resources in Eagle Creek (23%) because aspen clones are not restricted to growing directly adjacent to the stream in the floodplain, but extend up the bank slopes of the riparian area and into the uplands. This

spatial pattern of aspen distribution along the riparian corridor is apparent in most western streams (Hall 1960), indicating that prolonged flooding will usually only decrease aspen sprouting and recruitment for a small portion of riparian aspen resources.

High proportions of overstory disturbance were not associated with aspen recruitment, indicating that even low levels of beaver disturbance can stimulate sprouting and increase recruitment. Beaver utilized aspens in different areas of the drainage anywhere from 2 to 16 collective years (with an average of 11 years), but the duration of beaver foraging did not affect recruitment of aspen sprouts in Eagle Creek. Though beavers returned to harvest trees in areas previously harvested, this subsequent foraging in circular plots did not seem to inhibit aspen sprouts from growing to recruitment height. This is likely because beavers only harvested a few trees each time they returned to an area, so some sprouts escaped beaver herbivory to reach recruitment height.

Beaver structure records indicate that the beaver population in Eagle Creek has fluctuated between 2 and 7 active lodges most years since their reintroduction in 1991, but in 2008 and 2010, no active lodges were found. One active lodge was found in 2011 and 2012. The lack of active beaver lodges in 2008 and 2010 may be a result of beaver emigration from Eagle Creek, who then may have recolonized the drainage in 2011. Aspen resources were heavily utilized by beaver in Eagle Creek since 1991, and depletion of this preferred food may have contributed to the decline of beaver (Hall 1960). Silting-in of beaver ponds can also limit the suitability of colony sites for continued occupation, which may have also contributed to beaver declines since 2003 (Westbrook et al. 2011). Bears and wolves can prey upon beavers (Smith et al. 1994),

usually by digging into beaver lodges. However, no lodges in Eagle Creek were disrupted in this way, indicating that bear and wolf predation is probably not a significant source of beaver mortality in Eagle Creek. The beaver-structure survey in this study is based on observations conducted on foot, so beaver activity may have been present but overlooked in 2008 and 2010. The recent decline in beaver activity may have contributed to the increase in recruitment since 2008 by decreasing the herbivory pressure on immature aspen trees.

The long-term circular aspen plots were established in 1997 in areas with aspen as the dominant vegetation type. Some areas had large proportions of alder, willow, or other woody vegetation (up to 70% of the plot) in 2012. However, woody competition is not associated with absence of recruitment stems in Eagle Creek. Alder and willow have expanded considerably in many areas of Eagle Creek since beaver reintroduction, and though competition with these species may prevent aspen recruitment in some areas, there is no evidence at this time that aspen regeneration is inhibited by alder and willow expansion at the drainage scale.

The long-term effects of alder and willow expansion depend on the trajectory of riparian succession in different areas of Eagle Creek, which is influenced by changes in the fluvial disturbance regime, soil moisture, and topography (Villarin 2009). If beaver recolonize the area just above the Eagle Creek campground, where most alder expansion has occurred, the ongoing fluvial disturbance caused by beaver activity will likely favor the maintenance or expansion of a predominantly alder plant community (Villarin et al. 2009). However, if this area remains abandoned by beaver, the braided stream that now

flows through this site will probably reunite to form a larger, narrower stream course. The associated lowering of the water table will provide an opportunity for riparian succession to willows and sedges common to beaver meadow communities (Hay 2010; Westbrook et al. 2011). In addition, the nitrogen-fixing ability of alder can actually stimulate the growth of other woody dominants such as willow and aspen (Densmore 2005). Because the areas of Eagle Creek dominated by alder also currently contain aspen recruitment stems, a lower water table may create conditions in which alder facilitates the increase of aspen in these areas of the drainage.

Higher elevations were not associated with increased aspen recruitment in the circular plots or the aspen exclosures, even though there was lower browsing pressure at the top of Eagle Creek than the rest of the drainage. There was no evidence that spatial variation in ungulate distribution affected aspen recruitment in Eagle Creek. Spatial trends may influence recruitment at the landscape scale, but these forces are not evident at the drainage-scale in Eagle Creek.

High 1997 browsing intensities in aspen circular plots were not associated with a lack of recruitment stems. However, high browsing intensities (80-100% of sprouts and saplings browsed) in 2012 were associated with lack of recruitment stems. Areas with very high browsing intensity in 2012 often had high browsing levels since 1997, and this constant browsing pressure has probably inhibited sprouts and saplings from growing to recruitment height. Many plots experienced a decline in browsing pressure around 2010, but contained recruitment stems in 2012 that must have been growing despite higher levels of browsing from 1997-2009. This indicates that even high levels of browsing did

not inhibit some stems from reaching recruitment height. The correlative relationship between lower browsing pressures and increased recruitment was not established in 70% of aspen circular plots, likely because browsing intensity did not decline in many plots until 2010, and more time is needed for a large number of sprouts and saplings that grew after beaver disturbance to reach the pole tree basal diameter of >2<12.5 cm. In many plots, the sample size of years since beaver disturbance may not have been large enough to elucidate the relationship between recruitment and browsing.

Densities of all ungulates except white-tailed deer were lower in 2011 than in 2005. Reasons could be the decline in the Northern Yellowstone elk herd, decline in the mule deer population, a mild winter in 2011 that did not force many bison to migrate out of the Park, and the movement of ungulates to different areas of the winter range (such as Dome Mountain WMA). Our method for determining ungulate density may not have been able to accurately capture density changes because we did not account for variation in observer ability to detect ungulates as a function of distance, habitat, or animal response to observers. A more robust density estimation method would be needed for an accurate density estimate, but this method allows comparison with density estimates from McColley et al. (2012). Though the difference between 8.3 elk/km^2 in 2005 and 6 elk/km^2 in 2011 may not reflect a true decline in elk browsing pressure in Eagle Creek, this estimate in conjunction with declines in all other ungulate species from 2005 to 2011 suggest that there were probably fewer ungulates browsing aspen saplings in Eagle Creek in 2011. This is one factor contributing to the increase in aspen recruitment since 2008.

According to Halofsky and Ripple (2008*b*), the Eagle Creek riparian corridor would be considered an area with a high risk of wolf predation. Eagle Creek should have experienced an increase in aspen recruitment due to modified elk foraging behavior, resulting in lower browsing pressures, after wolf reintroduction. However, high ungulate density estimates and a lack of aspen recruitment in 2005 indicate that risk of wolf predation in Eagle Creek had not modified elk foraging behavior enough to reduce browsing pressure on aspens at that time. It is also possible that the riparian aspen and conifer forests in Eagle Creek are less risky than open grasslands (Kauffman et al. 2007; Creel et al. 2005), and that risk of predation has historically caused elk to use forest edges more often, resulting in higher browsing pressure on the aspen stands in Eagle Creek prior to 2005. Aspen recruitment was not observed throughout the drainage until the elk population declined significantly from 2005 to 2012. These observations support the theory that ungulate density, rather than changes in ungulate behavior due to predation risk, have decreased the browsing pressure in Eagle Creek and allowed aspen stems to reach recruitment height. These findings are consistent with those of Shafer (2011), who found evidence of a density-mediated trophic cascade effect on aspen in the Gibbon drainage of west-central Yellowstone National Park. Predation risk probably plays some part in shaping ungulate-browse interactions in Eagle Creek, but more research is needed to understand how this trophic cascade mechanism affects aspen recruitment.

Beaver populations on the northern range have increased since the 1990's due to reintroduction efforts in the Absaroka-Beartooth Wilderness area north of Yellowstone and increases in the Yellowstone beaver populations (Smith and Tyers 2012). It is likely

that these populations will continue to expand and that more streams on the NYWR will be colonized by beaver. As beaver and ungulate herbivory affect more riparian systems on the NYWR, managers will need to continue to study the mechanisms by which these wildlife species affect riparian vegetation and watershed functions.

CONCLUSION

Beaver reintroduction has stimulated aspen regeneration in Eagle Creek, and aspen saplings are reaching recruitment height. Though the mature overstory has not been replaced in many aspen stands disturbed by beaver, it is likely that it will be replaced because aspen clones are successfully regenerating in this drainage. This study suggests that a decrease in browsing intensity, probably due to decreases in local ungulate populations, has facilitated increased recruitment of aspen saplings in Eagle Creek. This was postulated by McColley et al. (2012), Kimble et al. (2011), Kauffman et al. (2010), Ripple and Beschta (2012), and Winnie (2012). However, browsing intensity is not the only important factor that can limit aspen regeneration. Lack of mature overstory stems and prolonged flooding can also inhibit recruitment by preventing the growth of aspen sprouts in the floodplain of the riparian corridor. In addition, high browsing intensity does not necessarily prevent all saplings from growing to recruitment height. Though exactly how much browsing aspen saplings can sustain and still reach recruitment height is unknown, this study does suggest that even if an area is highly browsed by ungulates some saplings may still be able to escape browsing and prolong the life of the aspen clone. Lower ungulate densities increase the likelihood that saplings will survive to reach recruitment height.

This study describes the effects of beaver reintroduction and ungulate herbivory on aspen in one drainage located on the NYWR, and cannot be replicated due to the unique wildlife community found in Eagle Creek. Though these limitations preclude extrapolation of our results to the rest of the northern range, the interactions between the

plant and animal communities of Eagle Creek will likely operate similarly in comparable streams on the NYWR. The results of this study indicate that beavers can stimulate aspen regeneration in 1st and 2nd order streams on the NYWR under the lower ungulate densities occurring on the northern range since 2005. Ungulate numbers are controlled by predation and hunting throughout many areas of Montana and other western states, so beaver reintroduction or recolonization in these areas may benefit riparian aspen regeneration.

MANAGEMENT IMPLICATIONS

Beaver reintroduction in Eagle Creek has facilitated aspen regeneration by stimulating the suckering of aspen clones, and these suckers have begun to reach recruitment height under lower ungulate densities on the northern range since 2005. Beavers can be used to restore aspen forests in riparian ecosystems that contain suitable beaver habitat, if aspen sprouts are not exposed to intense ungulate herbivory or prolonged flooding. Suitable beaver habitat includes riparian areas with a sustained supply of water, low-gradient stream sections ($\leq$7% slope), sufficient woody resources, and accessibility to other drainages for dispersal and expansion of the beaver population. Trapping can be used to manage reintroduced beaver populations once they are well-established in the drainage.

Beaver reintroduction will be an effective tool to aid regeneration in riparian aspen forests under the following conditions: 1) there are low ungulate densities in the area and limited livestock grazing, 2) the aspen stands are not seral to conifers or upland habitat, 3) most of the aspen clones are not located in the floodplain and/or at risk of being flooded during beaver activity, and 4) there are woody riparian plant species for beaver to browse other than aspen and other drainages for beaver to disperse into when aspen resources are depleted. In areas of high ungulate densities, increasing the number of hunting permits available may help to control ungulate populations. Long-term monitoring of aspen sprouting and recruitment is essential for determining the effects of beaver and ungulate populations on aspen regeneration.

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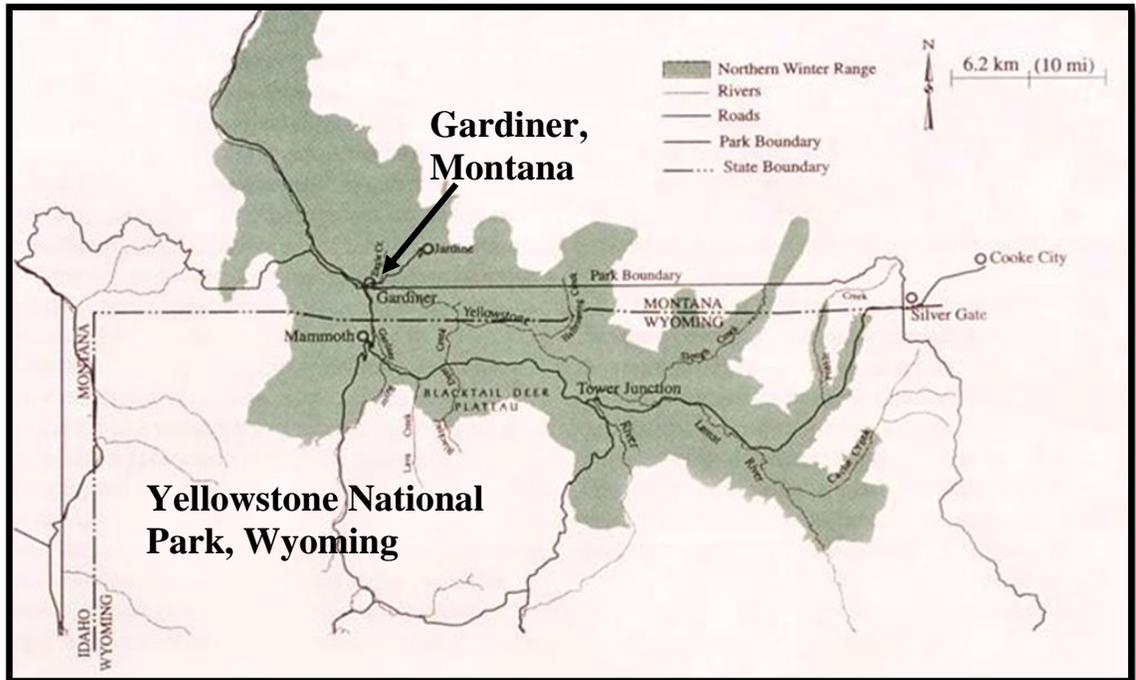Smith, D.W., and D.B. Tyers. 2008. The Beavers of Yellowstone. *Yellowstone Science* 16(3): 4-15.

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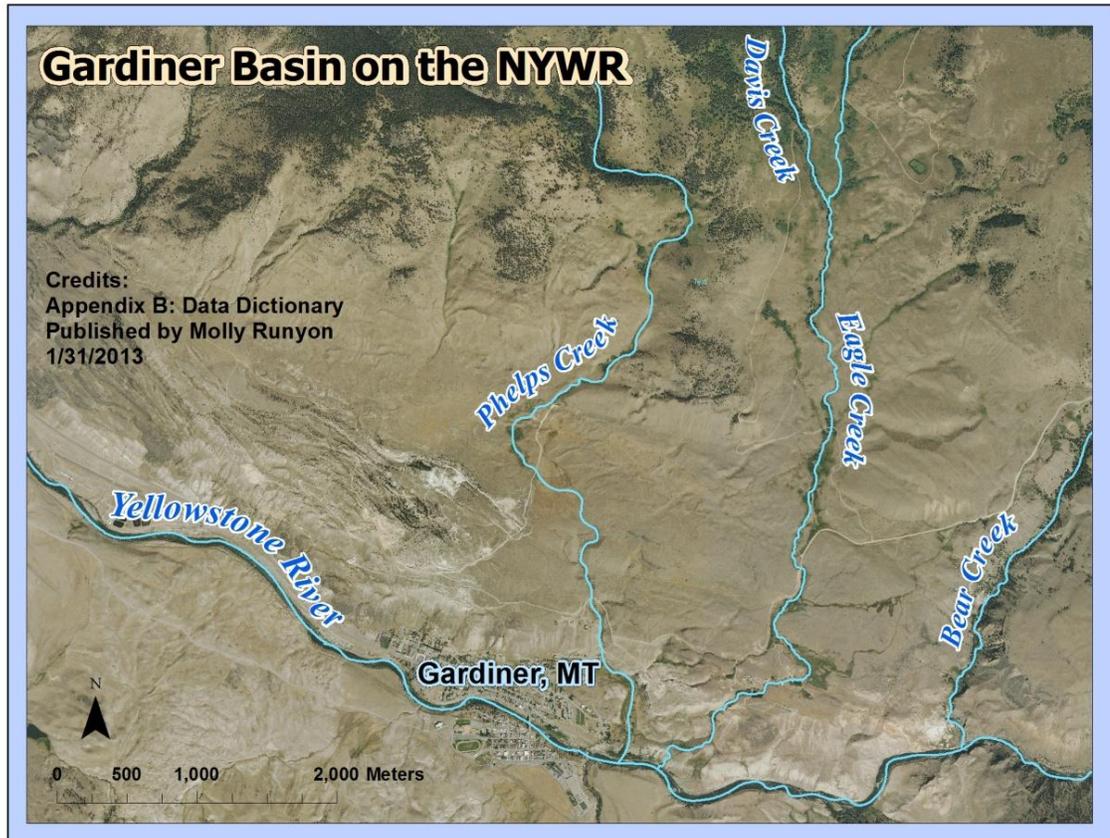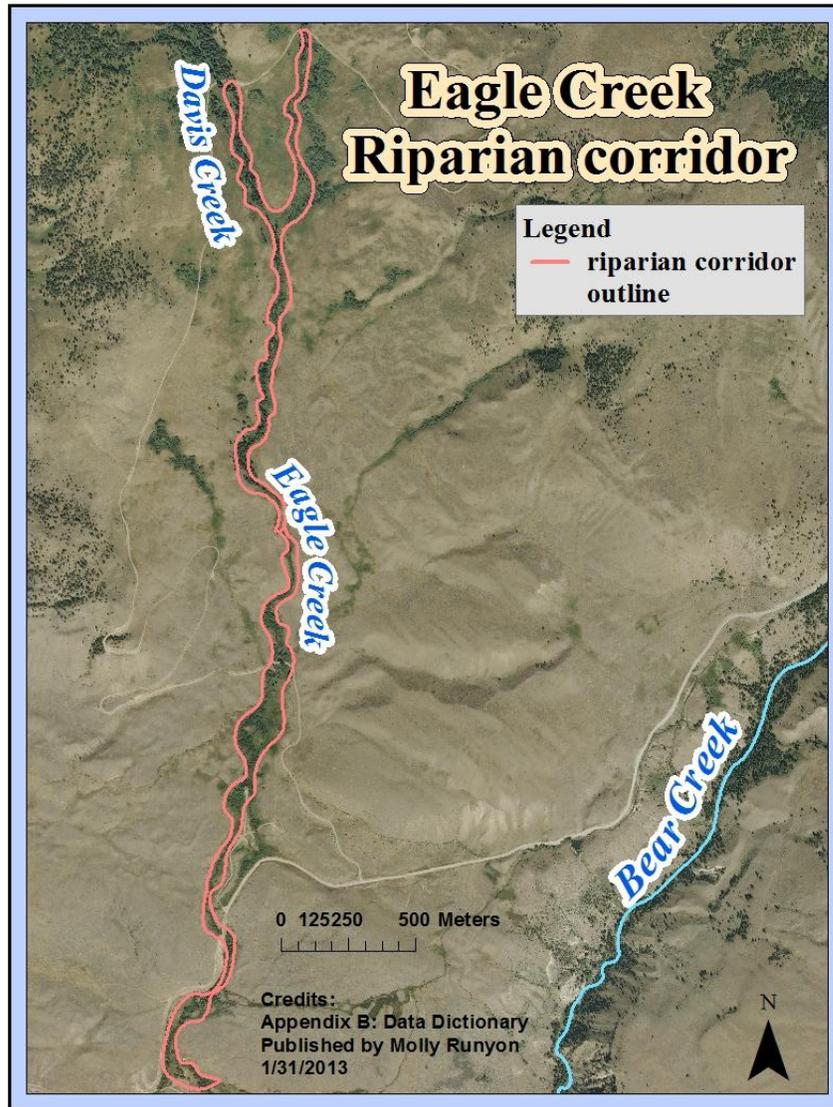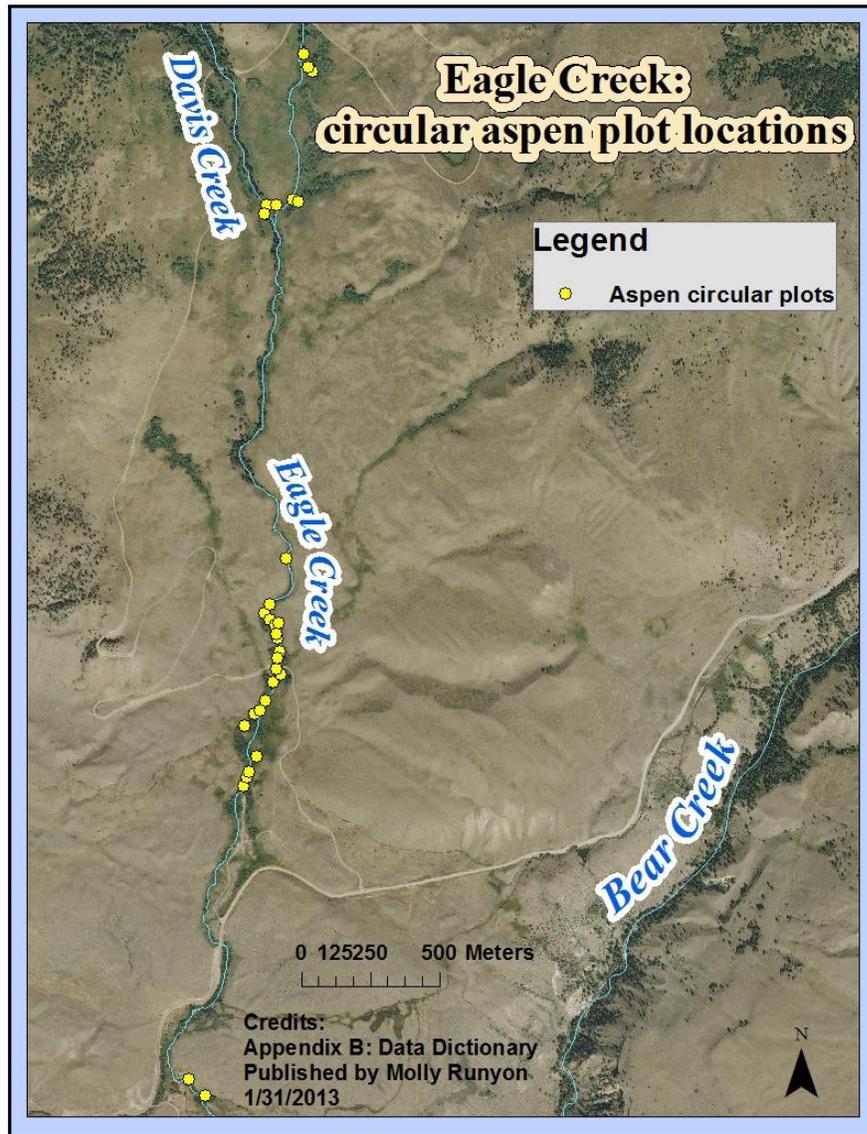
APPENDICES

APPENDIX A

MAPS

Map 1: Location of Gardiner, Montana on the Northern Yellowstone Winter Range (NYWR; shaded green).
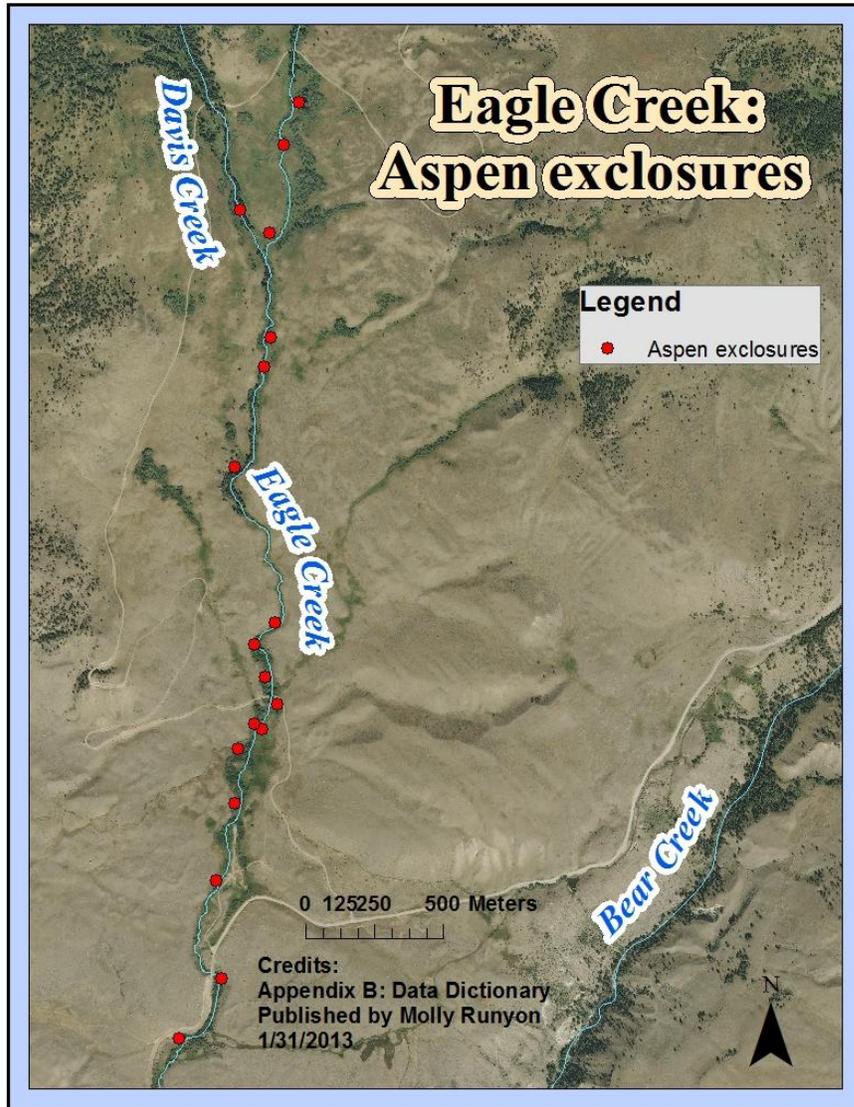
Map 2. Location of Eagle Creek northeast of Gardiner, MT on the Northern Yellowstone Winter Range.
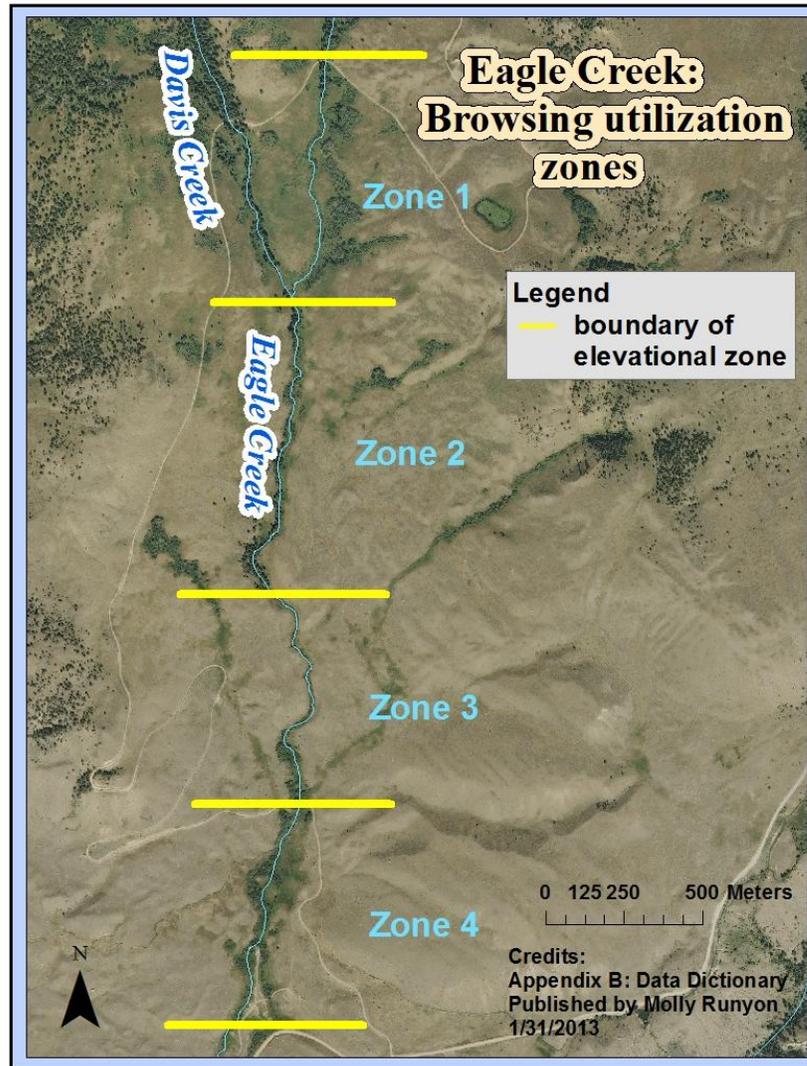
Map 3: Polygon used to delineate the riparian corridor of Eagle Creek; vegetation cover analysis sampled from within this polygon.

Map 4. Circular plot locations established in the Eagle Creek drainage in 1997 and monitored annually until 2012 (n=31).

Map 5. Locations of aspen exclosures established in Eagle Creek in 2004/05 and monitored annually until 2012.

Map 6: Four elevational zones of Eagle Creek, used to investigate the effects of spatial variation in ungulate browsing on aspen recruitment. Yellow bars represent the boundaries of each area. The lower boundary of Area 4 is 6200 feet in elevation, and the top boundary of Area 1 is at 7100 feet (900 feet total elevational change).

APPENDIX B

DATA DICTIONARY

Dataset;   2011 Aerial Photo of the Eagle Creek Drainage
Source;   Montana State Library Natural Resource Information System
Description;   Aerial photograph of the Eagle Creek Drainage and adjacent surrounding
                area near the town of Gardiner, Montana, from the United States Farm
                Services Agency National Agricultural Imagery Program (NAIP), one
                meter resolution, five meter accuracy, published on February 4, 2012,
                projected in GRS_1980_HARN_Montana State Plane Coordinate System.

Dataset;   Eagle Creek Drainage Riparian Area Polygon
Source;   Research Article: McColley, S.D., D.B. Tyers, and B.F. Sowell. 2011.
                Aspen and Willow Restoration Using Beaver on the Northern Yellowstone
                Winter Range. *Restoration Ecology* 20:450-455.
Description;   Polygon used to depict the riparian corridor and study area of the Eagle
                Creek Drainage, one meter resolution, from Samuel McColley,
                Department of Cell Biology and Neuroscience, Montana State University,
                Bozeman, Montana, U.S.A. Published on September 21, 2006, projected
                in NAD_1983_UTM_Zone_12N, grid coordinate system used was
                Universal Transverse Mercator (UTM).