AN ABSTRACT OF THE DISSERTATION OF

Luke E. Painter for the degree of Doctor of Philosophy in Forest Resources presented on May 30, 2013.
Title: Trophic Cascades and Large Mammals in the Yellowstone Ecosystem

Abstract approved:

William J. Ripple

Reintroduction of wolves to Yellowstone National Park (YNP) in 1995-96 provided a rare opportunity to observe the response of an ecosystem to the return of a top predator, including possible reversal of decades of decline of aspen, cottonwood, and tall willows suppressed by intensive herbivory on elk winter ranges. To investigate changes in aspen stands in northern Yellowstone since the return of wolves, I compared browsing intensity and heights of young aspen in 87 randomly selected stands in 2012 to similar data collected in the same stands in 1997-98. I also measured the spatial density of elk and bison scat piles as an index to relative population densities, and used annual counts of elk to calculate trends in elk density. In 1998, browsing rates averaged 88%, heights were suppressed, and no tall saplings ($\geq$200 cm) were found in sampling plots. In 2012, browsing rates in 2012 were much lower averaging 44%, and 28% of plots had at least one sapling $\geq$200 cm, tall enough to escape browsing and therefore more likely to survive to replace dying overstory trees. Heights of young aspen were inversely related to browsing intensity, but not significantly related to leader length, suggesting that differences in height were primarily due to differences in browsing, not factors related to productivity. Aspen recovery was patchy, possibly due in part to locally high elk or bison densities in some parts of the winter range. These results of reduced browsing with increased sapling recruitment were consistent with a trophic cascade from wolves to elk to aspen resulting in a widespread and spatially variable recovery of aspen stands.

There was wide variation in browsing intensity and aspen height between sectors of the Yellowstone northern ungulate winter range (northern range). The east sector generally had lower rates of browsing and more stands with tall saplings than the central and west sectors, a pattern that matched recent trends in elk population densities. Only a

small minority of stands in the west sector had tall saplings, consistent with higher elk densities in the west. Densities of elk in winter on the northern range recently have been highest in the northwest sector outside the park boundary, where elk benefit from lower wolf densities and milder winters. Aspen stands did not recover at a comparable range-wide elk density when elk were culled in the park in the 1950s and 1960s, suggesting that the influence of wolves may be an important factor in the recent redistribution and reduction of herbivory impacts by elk.

To examine the relationship between elk and aspen outside of YNP, I assessed browsing intensity and sapling recruitment in 43 aspen stands in the Shoshone National Forest east of the park, compared to data collected in the same stands in 1997-98. As in northern YNP, results were consistent with a trophic cascade with reduced browsing and increased recruitment of aspen saplings, but aspen recovery was patchy. Elk densities were moderate to high in most of the area, suggesting that the partial aspen recovery may involve a behavioral response to predation or other factors resulting in local variation in browsing impacts. Livestock may also have limited aspen recruitment. Recovery of some aspen stands in the Shoshone National Forest may provide some of the first evidence of a trophic cascade from wolves to elk to aspen outside of a national park, a trophic cascade possibly weakened by the influence of another large herbivore (cattle).

Like cattle, bison in northern Yellowstone may have an effect on woody browse plants. Bison have increased in number and may prevent recovery of some aspen stands in places of high bison density. I also examined browsing impacts of bison on willow and cottonwood in the Lamar Valley. To distinguish the effects of bison from those of elk, I compared browsing at different heights on tall willows, below and above the reach of bison. Because elk were absent from the area in summer when bison were present at high density, I also measured browsing that occurred in the summer. I found high rates of summer browsing, and growth of willows and cottonwoods was suppressed in the Lamar Valley. Above the reach of bison (>100 cm), growth was not suppressed and browsing rates were low, suggesting that these plant species have been released from suppression by elk but bison have compensated for some of the reduction in elk browsing. This study provided the first evidence of significant herbivory by bison of woody browse plants in Yellowstone, and revealed some of the complexity of the Yellowstone food web.

In summary, these research results support the hypothesis of a trophic cascade resulting from large carnivore restoration and subsequent changes in elk population densities and distribution. The return of wolves may have combined with other factors such as changes in hunting and land ownership, and increased predation by bears, to result in large-scale shifts in the distribution of elk in northern Yellowstone and greatly reduced elk densities in some areas. If these trends continue, the result may be a new alternative state with lower elk densities, and potential for enhanced biodiversity through reduced herbivory of woody browse species.

Trophic Cascades and Large Mammals in the Yellowstone Ecosystem

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Luke E. Painter, Author

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CONTRIBUTION OF AUTHORS

Dr. William J. Ripple was involved in the design and writing of Chapters 2-5. Dr. Robert L. Beschta was involved in the design and writing of Chapters 2 and 3. Dr. Eric J. Larsen contributed data for Chapters 2, 3 and 4 and reviewed the drafts.

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1. INTRODUCTION

Deciduous trees and shrubs are an important component of habitat diversity in the northern Rocky Mountains, particularly in riparian areas. In northern Yellowstone National Park (YNP) during the 20th century, aspen (*Populus tremuloides*) and cottonwood (*Populus angustifolia* and *P. trichocarpa*) declined as older trees died and were not replaced (NRC 2002). Willows (*Salix* spp.) also declined in height and cover, and with the decline of these plant species on which beavers depend, beavers disappeared from most streams in northern Yellowstone (NRC 2002, Smith and Tyers 2012). Loss of beavers resulted in further loss of willow habitat as streams became incised (Wolf et al. 2007). These changes were driven primarily by overbrowsing of willow, aspen and cottonwood by elk during winter (White et al. 1998, Barmore 2003, Singer et al. 2003, Wagner 2006, Ripple and Beschta 2012b). Effects were greatest inside the park boundary, but aspen recruitment was also suppressed on elk winter ranges in surrounding areas (Larsen and Ripple 2005). Some ecologists as early as Aldo Leopold (1949) attributed the abundance of elk and the resulting decline of woody browse plants to the absence of wolves, an important predator of elk. If this hypothesis is correct, the return of wolves could restore a trophic cascade resulting in a reduction in browsing and reversal of the decline of willow, cottonwood and aspen. Browsing intensity could be reduced through a reduction in elk population density, but could also be affected by changes in elk foraging behavior in response to predation risk (White et al. 1998, Ripple and Beschta 2007).

Annual culling combined with hunting harvests outside the park limited elk density between 1938 and 1969, but did not result in a reversal in the decline of woody browse plant species. The reintroduction of wolves to YNP in 1995-96 provided an opportunity to test the idea that wolves can have a positive effect on woody browse plants. Other factors besides browsing such as site productivity and climate fluctuations also affect plant growth, and elk distribution could be influenced by other factors as well such as increasing bison and bear populations, and changes in hunting and land use outside the park (White and Garrott 2005b, White et al. 2012).

I carried out three research projects to investigate the effects of browsing by ungulates on woody browse plants on two elk winter ranges, the northern Yellowstone ungulate winter range (northern range), and the Sunlight/Crandall ranges in the Shoshone National Forest (Fig. 1.1):

- I measured browsing intensity and heights of young aspen on the northern winter range within the park, and compared these data to similar data obtained in 1997-98 (Larsen 2001), allowing an analysis of change over time. I analyzed spatial variation in browsing and height in relation to site characteristics and ungulate fecal pile density, and analyzed trends in elk density over time using data from annual aerial counts.
- Using the same methods, I measured browsing intensity and heights of young aspen on an elk winter range east of YNP in the Shoshone National Forest compared to similar data from 1997-98, and analyzed spatial variation in browsing and height in relation to site characteristics, ungulate fecal pile density, and the presence of livestock.
- I assessed the possible impact of the increasing bison population in northern YNP on willow and cottonwood in the Lamar Valley.

These projects provided unique contributions to the study of trophic interactions in the Yellowstone ecosystem. Changes in the grouping behavior and habitat selection of elk following wolf reintroduction have been extensively studied (Mao et al. 2005, White et al. 2009, White et al. 2012), but the extent of cascading effects to plants has been more controversial. The possibility that bison could significantly affect the growth of woody browse plants has not been previously considered in YNP, and no other study within YNP has made use of baseline data on aspen growth and browsing intensity from near the time of wolf reintroduction to compare with later conditions. Also, previous studies of aspen on the Yellowstone northern range since the return of wolves have focused only on a portion of the Yellowstone northern range, or had a very limited sampling of aspen stands. Hunting and livestock grazing were allowed in the Shoshone National Forest study area, creating a system where a trophic cascade from top predators may be affected by anthropogenic factors more strongly than in YNP. A trophic cascade involving wolves, elk and aspen has not previously been demonstrated in a multiple-use landscape such as this (Kimble et al. 2011).

In Chapter 2 of this dissertation, I present evidence of decreased browsing and increased young aspen height on the Yellowstone northern range following the return of wolves, consistent with a trophic cascade resulting in a patchy recovery of aspen stands. In Chapter 3 I discuss the patterns and possible causes of spatial variation in aspen stand recovery and elk and bison distribution in northern Yellowstone since wolf reintroduction. In Chapter 4, I present similar results from the Shoshone National Forest, consistent with a top-down trophic cascade affecting aspen recruitment. Sampling locations and summary data for these two aspen studies are listed in Appendix A. In Chapter 5, I present evidence that bison can and do limit growth and recruitment of willow and cottonwood in northern Yellowstone. Chapter 6 is a synthesis of these results in the larger context of research on the ecology of wolves, elk, bison and woody browse plants in the Yellowstone ecosystem. These papers were written with coauthors (see Contribution of Authors), and Chapter 5 on the ecological effects of bison has been previously published.

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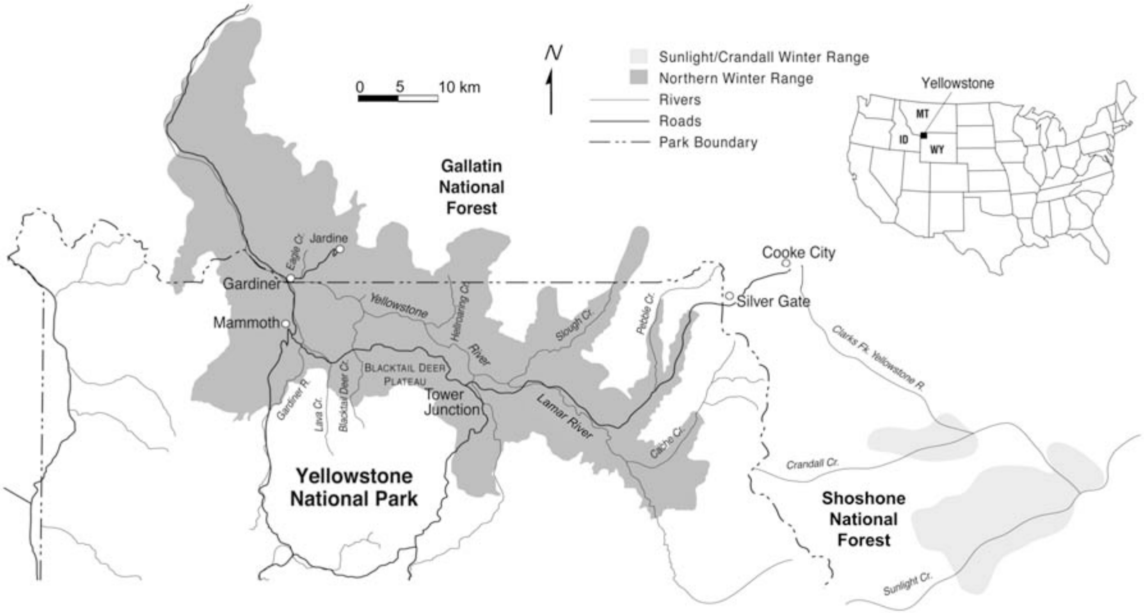

Figure 1.1. Ungulate winter range study areas in northern Yellowstone National Park (dark gray shading) and the Shoshone National Forest (light gray shading). Adapted from Larsen (2001).

2. ASPEN RECOVERY FOLLOWING THE RETURN OF WOLVES TO YELLOWSTONE

2.1. Abstract

On the northern winter ungulate range of Yellowstone National Park, aspen stands were dying out during the late 20th Century following decades of intensive browsing by elk. We hypothesized that with the restoration of large carnivores, including the return of wolves in 1995-96 after 70 years of absence, browsing would be reduced and young aspen would grow taller due to effects of predation on elk. Variation in height would also be expected to increase, due to differences in stand productivity and timing of release from browsing. In 2012, we sampled 87 randomly selected stands in northern Yellowstone and compared our data to baseline data collected in the same stands in 1997-98, soon after the return of wolves. In 1997-98, browsing rates (the percentage of leaders browsed annually) were consistently high, averaging 88% of stems browsed; only 1% of young aspen in sample plots were taller than 100 cm and none were taller than 200 cm. In 2012, browsing rates were much lower averaging 44%, the percentage of young aspen taller than 100 cm and 200 cm averaged 34% and 5%, respectively, and variation increased in both browsing and height. Browsing intensity explained 62% of the variation in height of young aspen in 2012, but height was not related to annual leader growth (an index of site productivity), contrary to what would be expected if height differences were due to differences in site productivity. In 2012, 25% of stands had at least five saplings ($\geq$200 cm) in the entire stand and 46% had at least one sapling, indications of recent growth above the browse level of elk that will likely result in regeneration of overstory trees. Aspen recovery was patchy, with wide variation in browsing and height; browsing rates were >60% in about 40% of stands. Aspen recovery did not begin until after a substantial reduction in elk population density. Our results support the hypothesis that a trophic cascade initiated by the return of wolves has begun to reverse the decades-long trend of aspen decline on the Yellowstone northern range.

2.2. Introduction

In northern Yellowstone National Park (YNP) during the 20th century, stands of quaking aspen (*Populus tremuloides*) declined as mature trees died but were not replaced. This lack of new aspen recruitment was primarily due to intensive browsing by elk (*Cervus elaphus*) on the northern Yellowstone ungulate winter range ("northern range", Fig. 2.1a) (NRC 2002, Barmore 2003, Larsen and Ripple 2003, Kauffman et al. 2010). Reintroduction of wolves (*Canis lupus*) to Yellowstone in 1995-96 and a concurrent increase in grizzly bears (*Ursus arctos*) (Barber-Meyer et al. 2008) provided an opportunity to observe the effects of large carnivore restoration on elk and possible cascading effects on plants, with the potential to increase survival and height of young aspen. After the return of wolves, Ripple and Beschta (2007, 2012b) found a decrease in browsing associated with "the first significant growth of young aspen in the northern range for over half a century." Kauffman et al. (2010), using different methods, did not find evidence of reduced browsing or aspen recovery; these disparate results and the ensuing debate demonstrated a need for further investigation (Winnie 2012, Beschta and Ripple 2013).

Trophic cascades involving wolves, elk and aspen have been observed in other places in the Rocky Mountains besides YNP, attributed to a combination of predation-risk avoidance behavior and reduced elk densities (White et al. 1998, 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007, Hebblewhite and Smith 2010). Bears were present in these areas as well, but it was the presence of wolves in addition to bears that had a significant effect on elk densities and aspen recruitment (NRC 1997). The Yellowstone northern range is well-suited to observe the possible effects of wolves on aspen in that elk population densities prior to wolf reintroduction were very high, wolves were completely absent, and elk browsing overwhelmed other factors affecting aspen regeneration (Barmore 2003, Wagner 2006). Since the late 1990s and the return of wolves, elk numbers have declined substantially on the northern range (Fig. 2.1b), so it is reasonable to expect some response in plants browsed by elk (White and Garrott 2005b, White et al. 2012). Conversely, relatively low elk numbers in the 1950s and 1960s did not result in aspen recovery (YNP 1997, Wagner 2006), so aspen recovery with recently reduced elk numbers is not a foregone conclusion.

If browsing pressure on aspen has decreased since wolves returned, and young aspen have begun to grow above the browse level of elk (increasing the likelihood they will survive to become overstory trees), this would support a hypothesis of a trophic cascade whereby wolves have initiated a transition from aspen decline to aspen recovery through a reduction in elk herbivory. Stands with lower browsing rates would also be expected to have greater variation in height, due to differences in the amount of time since release from browsing and differences in stand productivity. In the summer of 2012 we evaluated aspen stand conditions in 87 randomly located stands on the YNP northern range, compared to 79 of the same stands measured in 1997-98 (Larsen 2001, Larsen and Ripple 2005). This study had the benefit of comparison with the 1997-98 baseline to assess changes in aspen since the return of wolves, with more extensive random sampling of aspen stands than in other recent studies of northern range aspen (Kauffman et al. 2010, Ripple and Beschta 2012b). We used two different sampling methods within stands: 1) measuring young aspen in random plots as an indication of general conditions, and 2) measuring the five tallest young aspen in the entire stand as an indication of the "leading edge" of stand regeneration. We also considered the possible effects of site productivity (indexed by annual leader growth) and annual snowpack accumulation on browsing intensity and aspen height.

2.3. Study Area

Valleys of the upper Yellowstone River and its tributaries are wintering grounds for elk, bison (*Bison bison*), deer (*Odocoileus* spp.), and small numbers of pronghorn (*Antilocapra americana*) and moose (*Alces alces*). In these valleys, dry grasslands and sagebrush (*Artemisia* spp.) steppe are interspersed with groves of aspen, bordered by forested slopes of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) and Engelmann spruce (*Picea engelmannii*). Aspen and willows (*Salix* spp.) are often found along streams, and cottonwood trees (*Populus angustifolia* and *P. trichocarpa*) along the larger rivers (Houston 1982, 1997, NRC 2002). The northern ungulate winter range extends outside of YNP north along the Yellowstone River basin (Lemke et al.

1998, White et al. 2012), but our sampling was limited to the portion within the park (Fig. 2.1a).

Quaking aspen stands enhance wildlife habitat and species diversity, though they occupy only a small portion of the landscape in the northern Rocky Mountains (White et al. 1998). Trees in a stand often share a single root system, with most reproduction in the form of clonal root sprouts (suckering). Stands in the Yellowstone area are often small and widely separated, and may persist for thousands of years where moisture is sufficient, often in wetlands or riparian areas. Fire may stimulate aspen reproduction, but in the absence of fire coniferous trees may invade and replace aspen stands. Aspen is a highly palatable and preferred browse species for elk, and growth and survival of young aspen may be limited by intensive herbivory, eventually killing a stand if new trees cannot be recruited to replace older trees. This was the condition of aspen on the Yellowstone northern range during most of the 20th century (Romme et al. 1995, Kay and Wagner 1996, Renkin and Despain 1996, White et al. 1998, NRC 2002, Larsen and Ripple 2005, Kauffman et al. 2010). As a result of this historical lack of recruitment of trees, aspen stands in 2012 exhibited a gap in recruitment, with an overstory of mature trees and an understory of young aspen, but an absence of intermediate sizes and ages (Fig. 2.2) (Romme et al. 1995, Larsen and Ripple 2003, Kauffman et al. 2010).

Beginning in the 1930s, elk herds in the park were culled to reduce numbers and prevent damage to winter range vegetation, but this did not bring about aspen recovery (Houston 1982, YNP 1997, Barmore 2003, Wagner 2006). After culling ended in 1969, counts of wintering elk on Yellowstone's northern range sharply increased (Fig. 2.1b) from a low of about 3,000 to about 13,000-19,000 elk in 1982 to 1995. These aerial counts indicated minimum numbers of elk, unadjusted for sightability. There were no counts in 1996 or 1997, but the winter of 1997 was unusually severe and many elk died (Garrott et al. 2003), and the next count in 1998 was less than 12,000 elk. By then, wolves were established, and elk numbers continued to decline, due primarily to hunting and predation (Vucetich et al. 2005, White and Garrott 2005a). Recent elk counts have been the lowest since the end of culling in 1969 despite a reduction in hunting after 2005, and the proportion of northern range elk wintering outside the park has increased to more than 50% (Wyman and Smith 2012). Changes in land use and hunting outside the park have worked together with wolves to result in landscape-scale changes in the size and distribution of the northern Yellowstone elk herd (White and Garrott 2005b, White et al. 2010, 2012).

Wolves were extirpated from the Yellowstone area by 1926. After reintroduction in 1995-96, they increased to a population high of 98 in 2003 (Fig. 2.1b), declining to 38 wolves in 2010 and 2011. This decline may be due in part to lower numbers of elk, but disease and conflict between packs also contributed (Smith et al. 2012). Nevertheless, throughout the study period 1997-2012 wolves were the primary predator of elk on the northern range (White and Garrott 2005b, White et al. 2012). Other elk predators included grizzly bears, black bears (*Ursus americanus*) and cougars (*Puma concolor*). Bears take many elk calves in spring and could affect elk recruitment rates (Barber-Meyer et al. 2008), but wolves prey on both young and adult elk throughout the year, and it is wolves that have the greatest potential to affect behavior of elk on winter ranges. Wolves provide food subsidies to bears in the form of carcasses (Wilmers and Getz 2005), and interact with bears and other predators to limit prey population densities (NRC 1997, Ripple and Beschta 2012a).

2.4. Methods

Sampling methods were designed for comparison with data collected by Larsen (2001) in 1997-98, and also to allow a more detailed analysis of aspen conditions in 2012. In 1997-98, Larsen assessed the age structure of 93 randomly selected aspen stands on the northern range (excluding the portion of the range outside the park boundary, Fig. 2.1a) and measured browsing intensity and height of young aspen in 80 of these stands. We excluded one stand on a steep scree slope because this terrain inhibits ungulate access (Larsen and Ripple 2003, Kimble 2007), for a total of 79 stands in our 1997-98 dataset. Between July 24 and September 1, 2012 we revisited 76 of these 79 stands (the ones with GPS locations), plus an additional 11 stands that were marked with GPS in the 1997-98 study (but did not have data for young aspen), for a total of 87 stands sampled in 2012. A stand was defined as a group of aspen separated from other aspen by at least 30 m (Kay 1990). Most stands were relatively small and each was sampled with a single 2x30 m plot, beginning at the closest tree on the perimeter of the closest stand to the GPS location (the “start tree”) and extending toward the centroid of the stand. We defined an aspen “tree”as >5 cm dbh (diameter-at-breast-height); aspen ≤5 cm dbh were “young aspen,” and “saplings” were young aspen ≥200 cm in height, tall enough to escape most browsing by elk (Kay 1990, White et al. 1998).

In each sampling plot, we recorded the dbh of aspen and any other tree species ≥200 cm in height, and the height of coniferous trees <200 cm. For young aspen in the sampling plot, we recorded the height and browsing status (browsed or not) of each plant’s leader for late summer 2012 (fall height, leader held erect), spring 2012 and spring 2011, as indicated by bud scars and browsing scars (Keigley and Frisina 1998). If the righthand side of a plot had 25 or more young aspen older than one year, sampling of young aspen ended with this 1x30 m plot. If a 2x30 m plot had <15 young aspen, the plot was extended in increments of 30 m^2 to reach a count of 15, or until the entire stand was censused. We also located the five tallest young aspen in each stand (within 60 m of the 2x30 m sampling plot) and used bud and browsing scars to measure height and browsing during previous years (Ripple and Beschta 2007). Conifer cover in aspen stands was classified as 0 (none), 1 (<10% cover), 2 (10-50% cover), or 3 (>50% cover).

In the 1997-98 data, fall heights of young aspen were recorded as ≥100 cm or ≥200 cm. We compared heights from 1997-98 and 2012 by calculating the mean percentage of young aspen in these two height categories, and the mean percentage of leaders browsed (browsing rate). Values were first calculated within a stand, and then averaged across stands. Saplings (≥200 cm in height) were not included in calculations of browsing rates. We used bootstrapping to generate bias-corrected confidence intervals (CI) (Efron and Tibshirani 1993) to compare for significant differences in browsing and height between the two time periods. Bootstrapping was used because the 1997-98 data were much more skewed than the 2012 data in both height and browsing rate, precluding the use of analysis methods based on distributional assumptions. A 95% confidence level was used to assess significance in all statistical tests. For calculating the proportion of plots containing saplings, plot size was limited to 2x30 m even if the plot had been extended, to avoid biasing the comparison with 1997-98. To assess changes in overstory we compared the number of trees/plot in 1997-98 and 2012, not including the required start tree.

In the 1997-98 data, new sprouts that had not been exposed to winter browsing were not distinguished from older sprouts that could have been browsed the previous winter, so the calculated browsing rate underestimated the actual annual rate. For further analysis of 2012 data we calculated an adjusted browsing rate that did not include new sprouts. As an index to stand productivity we calculated the mean leader length (current annual leader growth) for each plot as the mean difference between spring height and fall height, the height increase of the stem in the 2012 growing season. Confidence intervals for adjusted browsing, height, and leader length in 2012 were calculated using t-statistics, as the 2012 data had approximately normal distributions. Browsing rates for the five tallest young aspen were calculated from pooled data, rather than the average of the stand browsing rate.

Linear regression was used to test the significance of leader length and browsing rate as explanatory variables for the mean spring height of young aspen, with natural logarithm transformations where needed for constant variance. Coefficients were tested for significance using extra-sums-sums-of-squares F-tests. The fit of regression models was assessed using the coefficient of determination (R^2). For a regression of browsing rates of the five tallest young aspen as a function of annual elk counts, we used elk counts from YNP biologists (Wyman and Smith 2012).

We calculated the annual cumulative daily snowpack water equivalent (SWE_{acc}), summed for the period October 1-April 30 (Garrott et al. 2003) at two Natural Resources Conservation Service (NRCS) SNOTEL stations closest to the study area: Northeast Entrance (MT10d07s) and West Yellowstone (MT11e07S); both began in 1967 (NRCS 2012). We used linear regression to test for an overall trend in annual SWE_{acc} in the years 1967-2012, and a t-test (equal variance) to test for difference between mean SWE_{acc} in the 14 years before the 1998 study (1985-1998) compared to the 14- year period between sampling years (1999-2012).

2.5. Results

Browsing rates of young aspen were generally lower and heights taller in 2012 compared to 1997-98, and both browsing and height in 2012 were more variable (Fig. 2.3a). The percentage of leaders browsed was significantly lower in both 2011 and 2012, compared to1997-98 (95% CI, Fig. 2.3b). Browsing rates in all stands averaged 88% (CI 84, 91) in 1997-98 and 44% (CI 43, 51) in 2012. In 1997-98 browsing rates were consistently very high with a median of 92%; in 2012 the median was 45%. There was no significant difference in browsing rate between 1997 and 1998, or between 2011 and 2012, despite differences in annual snow accumulation (Fig. 2.3b). Young aspen were significantly taller in 2012 than in 1997-98, measured as the mean percentage $\geq$100 cm or $\geq$200 cm (95% CI, Fig. 2.3c). Aspen plots in 1997-98 had no saplings $\geq$200 cm (fall height), but in 2012, 28% of plots had at least one sapling $\geq$200 cm. Most saplings were of small diameter, <3 cm dbh (Fig. 2.3d), and the smallest live aspen tree in the sample plots was 27 cm dbh. The number of aspen trees in sampling plots (not counting the start tree) decreased between 1997-98 and 2012 (t_{102}=8.6, $p<0.001$), from 2.8 trees/plot (n=92 plots) to 0.36 trees/plot (n=87 plots). All stands in 1997-98 contained at least one aspen tree, but 12% of sampled stands in 2012 had no overstory trees remaining. In 1997-98, 6% of plots included conifers $\geq$200 cm tall, but in 2012 this had increased to 26% of plots. Coniferous trees were absent or had <10% cover in 54% of entire stands in 2012, with 18% of stands more than half-covered by conifers.

After removing from the analysis any aspen newly sprouted in 2012, browsing rates in sample plots averaged 67% (CI 62, 72) in 2011 and 52% (CI 46, 58) in 2012 for an average of 59% (CI 54, 65) over both years. Mean heights of young aspen in 2012 were strongly and inversely related to browsing rates (Fig. 2.4a, $p<0.001$, R^2=0.62), but not related to mean leader length (Fig. 2.4b, p=0.2, R^2=0.02).

The five tallest young aspen in each of the 87 stands increased in height concurrent with a decrease in browsing that began about 2003 (Fig. 2.5a). The tallest of these sprouted about 2003, but nearly half (47%) began after 2006. Over the ten years 2003-2012, there was a strong inverse relationship between browsing rate and height (R^2=0.93, $p<0.001$). Browsing rate was also strongly correlated with annual elk counts

(Fig. 2.5b, R^2=0.79, p<0.001), but there was no relationship between browsing rate and annual snow accumulation (Fig. 2.5c, R^2=0.04, p=0.57). In spring of 2012, 46% of stands had at least one sapling ≥200 cm spring height and 25% of stands had five or more saplings ≥200 cm (Fig. 2.5d). Annual leader growth in 2012 averaged 48 cm (range 15, 113) for the five tallest young aspen in a stand versus 30 cm (range 8, 70) in sampling plots. Mean heights of young aspen in sampling plots were correlated with the mean heights of the five tallest in a stand (Fig. 2.7); R^2=0.64, p<0.001. Mean SWE_{acc} for the period 1999-2012 was 17% less than in 1985-1998, but the difference was not statistically significant (t_{26}=1.6, p=0.12) despite a severe winter in 1997 and mild winters in 1998-2005 (Fig. 2.6). There was an overall downward trend in SWE_{acc} in the period 1967-2012 (R^2=0.24, p<0.001), but this trend was not significant over the period 1985-2012 (R^2=0.03, p=0.37).

2.6. Discussion

Compared to stand conditions in 1997-98 immediately following wolf reintroduction, browsing was reduced and young aspen were taller in 2012, consistent with a trophic cascade involving wolves, elk and aspen (Fig. 2.3). The size distribution of saplings demonstrated recent increases in survival and height compared to a complete absence of saplings in 1997-98 (Fig. 2.2a, 2.3d). While the long-term decline of aspen stands on the northern range appeared to be reversing, the changes in browsing and aspen height were highly variable (Fig. 2.2a, b, 2.3a). There was a strong inverse relationship between browsing rate and height in 2012, indicating that young aspen grew taller where browsing intensity was less (Fig. 2.4a). The height increase indicated that the browsing reduction was a multi-year trend, because greater height resulted from the cumulative effect over time (Fig. 2.3c, 2.3d, 2.5a, 2.5d).

Could climate or other factors affecting productivity have caused the recent increase in young aspen height? Drought and high summer temperatures are likely to inhibit aspen recovery (Hanna and Kulakowski 2012), but if aspen were growing at a faster annual rate in recent years due to longer growing seasons (Wilmers and Getz 2005) or increases in atmospheric CO_2 (Cole et al. 2010) they could exceed the reach of elk more quickly. The comparison with 1997-98 is based on fall height, so a general increase in annual leader growth could cause an ephemeral difference in the percentage of tall young aspen in the fall even if the leaders continued to be annually browsed; however, increases in sapling recruitment (>200 cm) indicate a multi-year trend of increasing height. If aspen release depended upon the amount of annual growth, then the most productive stands with the longest leaders would escape browsing first and would have the tallest aspen; however, there was no relationship between leader length and spring height (Fig 2.4b). Browsing appeared to be the primary factor limiting young aspen heights, explaining 62% of height variation (Fig. 2.4a). A reduction in browsing is the reason aspen in many stands have grown taller, not factors related to productivity. Where browsing is reduced, differences in stand productivity may contribute to the variation in height between stands, but differences in the length of time since a stand was released from browsing would also be important.

Deep snowpack can increase browsing of aspen by covering up other forage (Christianson and Creel 2008), but can also decrease herbivory where snow is locally deep or if snow causes elk to move to other areas (Brodie et al. 2011). We found no evidence for a relationship between browsing and amount of snowpack (Fig. 2.5c), despite the fact that a greater proportion of the herd winters outside the park in years of deep snow (White and Garrott 2005a, White et al. 2012). Height could perhaps be influenced by changes in annual snowpack accumulation since it can affect moisture availability to plants and browsing accessibility, but average snow accumulation was not significantly different in the 14 years before 1998 compared to the following 14 years (Fig. 2.6), and the long-term regional trend toward decreasing snowpack was not significant over this 28-year period. There was no evidence that the changes in browsing and heights of young aspen we observed were due to differences in annual snowpack depth.

Because randomly placed plots often did not include the tallest saplings in a stand, the five tallest young aspen in each stand provided a more direct measure of the potential for saplings to replace overstory trees, and the height of the tallest in a stand was positively related to height in sampling plots.. The tallest saplings showed a steady decline in browsing rates after about 2003, followed by a steady height increase after about 2005 (Fig. 2.5a, 2.5d), similar to the findings of Ripple and Beschta (2012b) who used this method. This relatively late timing of height increase for the tallest saplings may explain why Kauffman et al. (2010), sub-sampling a small number of aspen stands with small random plots, did not detect sapling recruitment in 2004-07. Our results confirm that a general aspen recovery was just beginning at that time. Similarly, Kimble (2007) did not find recruitment sufficient to replace overstory trees in 2006 north of the park, though other factors such as livestock grazing and locally high elk densities (White et al. 2012) may also be involved there. Like Kimble, we found that few saplings have yet recruited into new trees as aspen overstories have continued to decline; however, recent growth of saplings above the browse level of elk (~200 cm) will likely result in new aspen trees that will ensure the persistence of aspen stands. The percentage of stands with tall saplings has been increasing rapidly (Fig. 2.5d), and further increases in sapling recruitment are likely if future browsing rates remain relatively low.

The fact that a landscape-scale recovery of aspen did not begin until after a substantial decline in the northern Yellowstone elk herd (Fig. 2.1b, 2.5a, 2.5d) suggests that behavioral responses to predation risk alone without population reduction were not sufficient. However, changes in elk grouping behavior and habitat selection at various temporal and spatial scales may have contributed to recovery and caused variation in aspen stand conditions by redistributing the impacts of herbivory on aspen (White and Feller 2001, Fortin et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005, Christianson and Creel 2008, Gower et al. 2009, Proffitt et al. 2009, White et al. 2009, Muhly et al. 2010, White et al. 2012). Prior to wolf restoration, aspen seemed doomed to heavy browsing even when elk numbers were reduced, and culling of elk before 1969 did not result in aspen recovery in the park despite more than two decades with relatively low elk numbers on the northern range (Fig. 2.1b). Following wolf reintroduction, comparable elk numbers since 2003 have been accompanied by new recruitment of aspen saplings (Fig. 2.3d, 2.5d), suggesting that something more than a simple reduction in the elk population was necessary to reverse aspen decline; changes in the distribution or behavior of elk may also have been necessary.

In many of the stands sampled in 2012, browsing rates remained high enough to suppress aspen growth, preventing recruitment of saplings (Fig. 2.2b). This can be seen in the plot of height as a function of browsing rate (Fig. 2.4a). About 40% of stands had browsing rates >60% and young aspen in these stands were short with little variation in height, an indication of suppression of height by browsing. Even with reduced browsing, some stands may not recover if the long-term trend toward declining snowpack and hotter, drier summers increases stress on stands in xeric habitats (Hanna and Kulakowski 2012). Aspen overstory has continued to decline as older trees die without replacement, and some stands have lost all overstory trees. Also, the number of coniferous trees in aspen stands has increased, and forest succession may prevent recovery of some aspen stands. Nevertheless, an important change in aspen stand dynamics has occurred since 1998, to a condition in which many aspen stands are likely to persist on the northern range rather than dying out as was the previous trajectory.

Like aspen, willow and cottonwood were in decline prior to wolf reintroduction due to intensive browsing by elk (Keigley 1998, NRC 2002, Singer et al. 2003, Beschta 2005, Wolf et al. 2007), but heights and canopy cover of these plants have recently increased in portions of the northern range (Beyer et al. 2007, Tercek et al. 2010, Baril et al. 2011, Ripple and Beschta 2012b). In some places willow heights are now more influenced by abiotic factors such as water availability and soil composition (Bilyeu et al. 2008, Tercek et al. 2010, Marshall 2012), evidence of a significant reduction in herbivory compared with past conditions (Singer et al. 2003). With more tall willows, beavers have begun the process of recolonizing the northern range (Smith and Tyers 2012), with the potential to expand willow habitat through a mutualistic interaction. However, bison numbers have increased in recent years, and browsing by bison on cottonwood and willow in the Lamar Valley area has slowed or prevented recovery of these plant species, weakening the effects of the trophic cascade from wolves to plants (White and Garrott 2005b, Painter and Ripple 2012). Bison also browse on aspen (author’s observations), and may compensate for the reduction in elk herbivory in places used intensively by bison.

Are aspen recovering since the return of wolves to northern Yellowstone? Aspen stands have begun to recover, but this recovery is in an early stage, and varies widely between stands. Browsing has been reduced, accompanied by widespread but patchy recruitment of saplings, something that failed to happen before wolf reintroduction despite significant culling of elk herds. Tall enough to escape elk browsing, these new saplings are likely to survive to become the next generation of aspen trees, keeping stands alive into the future. We found no evidence that climate caused these recent changes in aspen and elk dynamics. Prior to the return of wolves, the proportion of elk wintering north of the park boundary increased, but this was without a corresponding decline in elk population density or browsing intensity in the park (Lemke et al. 1998). Recent increases in height and survival of young aspen were associated with a reduction in browsing, linked most plausibly to the return of wolves and subsequent changes in elk population density and distribution (White et al. 2012). The Yellowstone example supports previous research in Canada (White et al. 1998, 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007) suggesting that large carnivores may aid aspen conservation through reduction of herbivory where aspen have been suppressed by elk.

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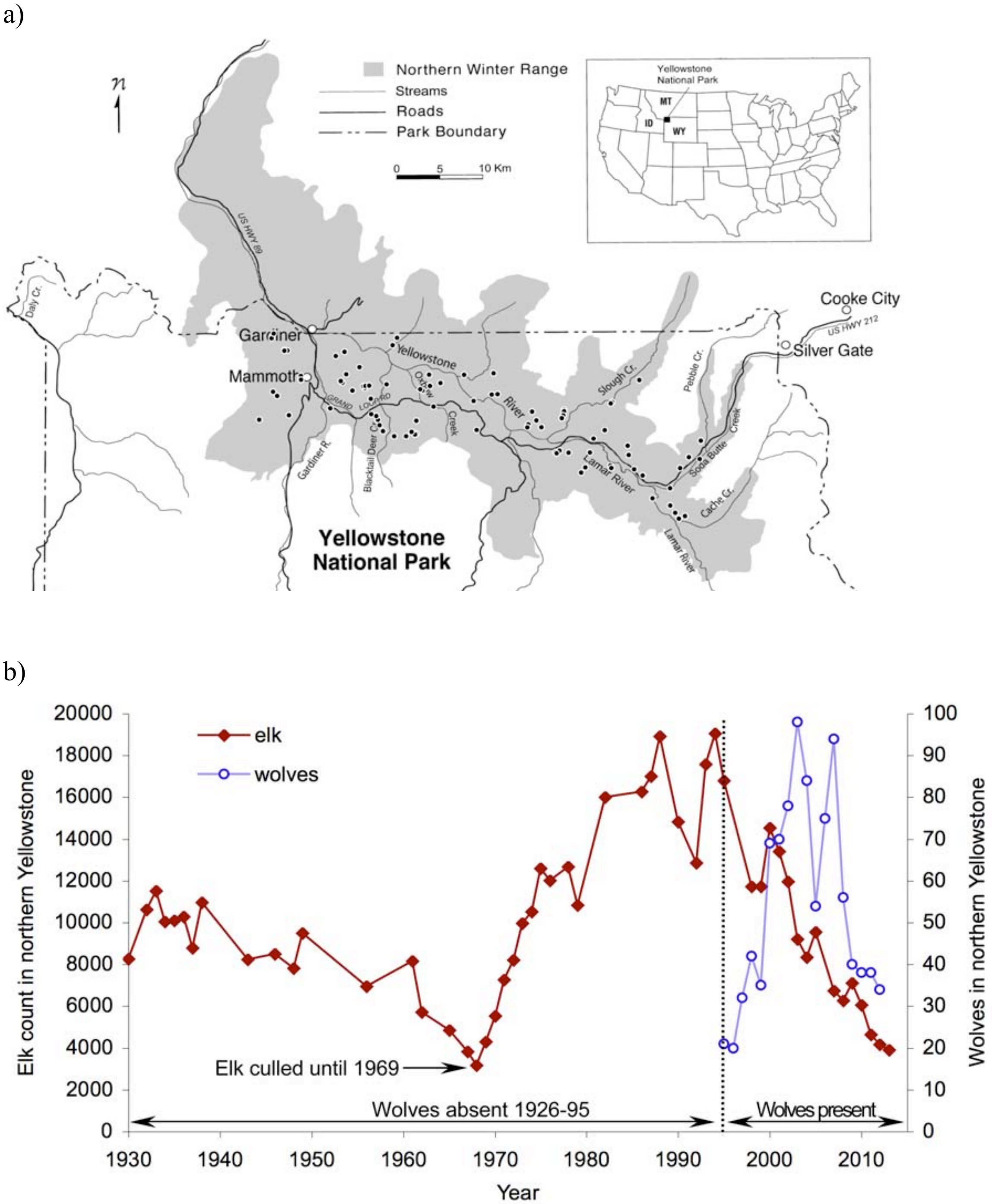

Figure 2.1. Map of study area and graph of elk and wolf population trends.
(a) The Yellowstone northern ungulate winter range; black dots mark sampling locations [adapted from Ripple and Larsen (2000)].
(b) Elk (YNP 1997, Wyman and Smith 2012) and wolf (Smith et al. 2012) counts. Missing elk counts were not done or were unreliable.

a)

b)

Figure 2.2. Aspen stand conditions on the northern range were highly variable.
(a) Northern range aspen stand with mature trees and young saplings but no intermediate size/age classes; tall saplings were about 3 m tall.
(b) Suppressed stand with no saplings; young aspen were repeatedly browsed and did not grow tall.

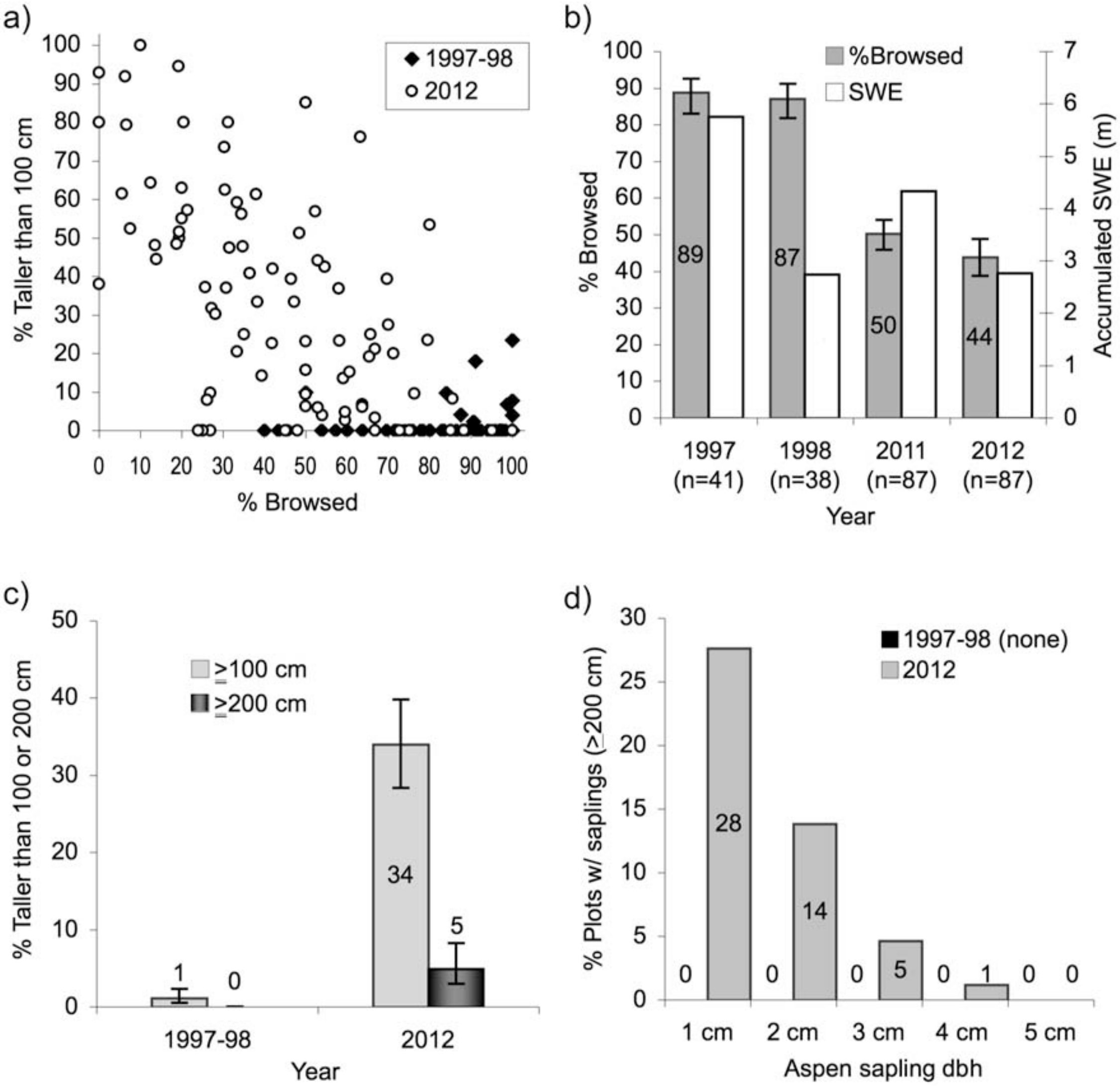

Figure 2.3. Comparison of aspen height and browsing intensity in sampling plots.
(a) Young aspen ≥100 cm (fall height) as a function of browsing rate in sampling plots in 87 aspen stands in 1997-98 and 2012. Browsing rates included new aspen sprouts but did not include aspen ≥200 cm (see methods).
(b) Mean browsing rate in plots (bars show 95% CI), with snow accumulations (SWE_{acc}) for each sampling year; 41 stands were surveyed in 1997, an additional 38 in 1998; browsing for 2011 was assessed in 2012 using browse scars.
(c) Mean percentage of young aspen ≥100 cm or ≥200 cm in sampling plots (95% CI).
(d) Percentage of plots with at least one sapling (≥200 cm) in five dbh classes; there were no saplings in 1998.

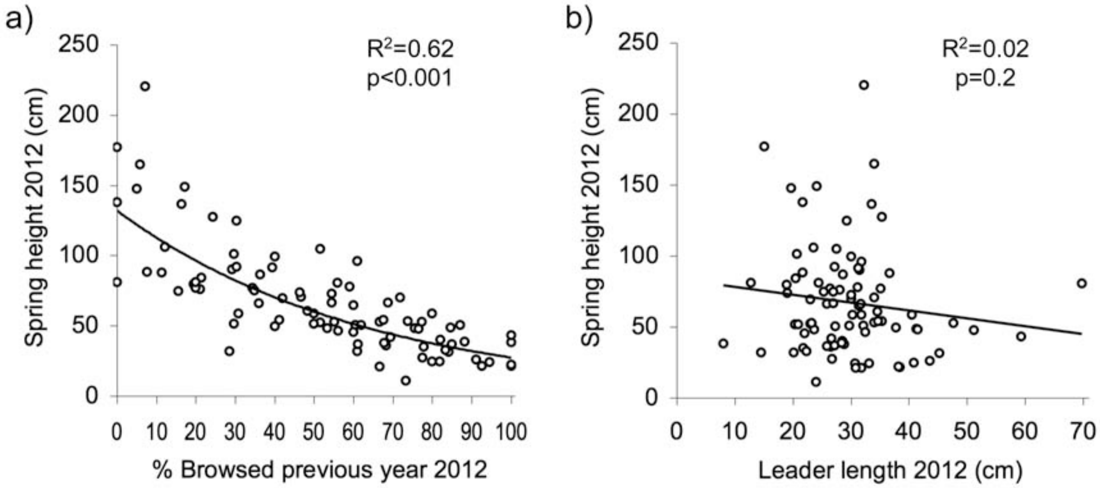

Figure 2.4. Mean height as a function of browsing and leader length in 87 sampling plots; each data point represents an aspen stand. Fitted lines are based on the natural logarithm of height.

(a) Browsing rates were calculated without new sprouts, and so were slightly higher than in Figure 2.3.

(b) Height as a function of leader length, an index for productivity.

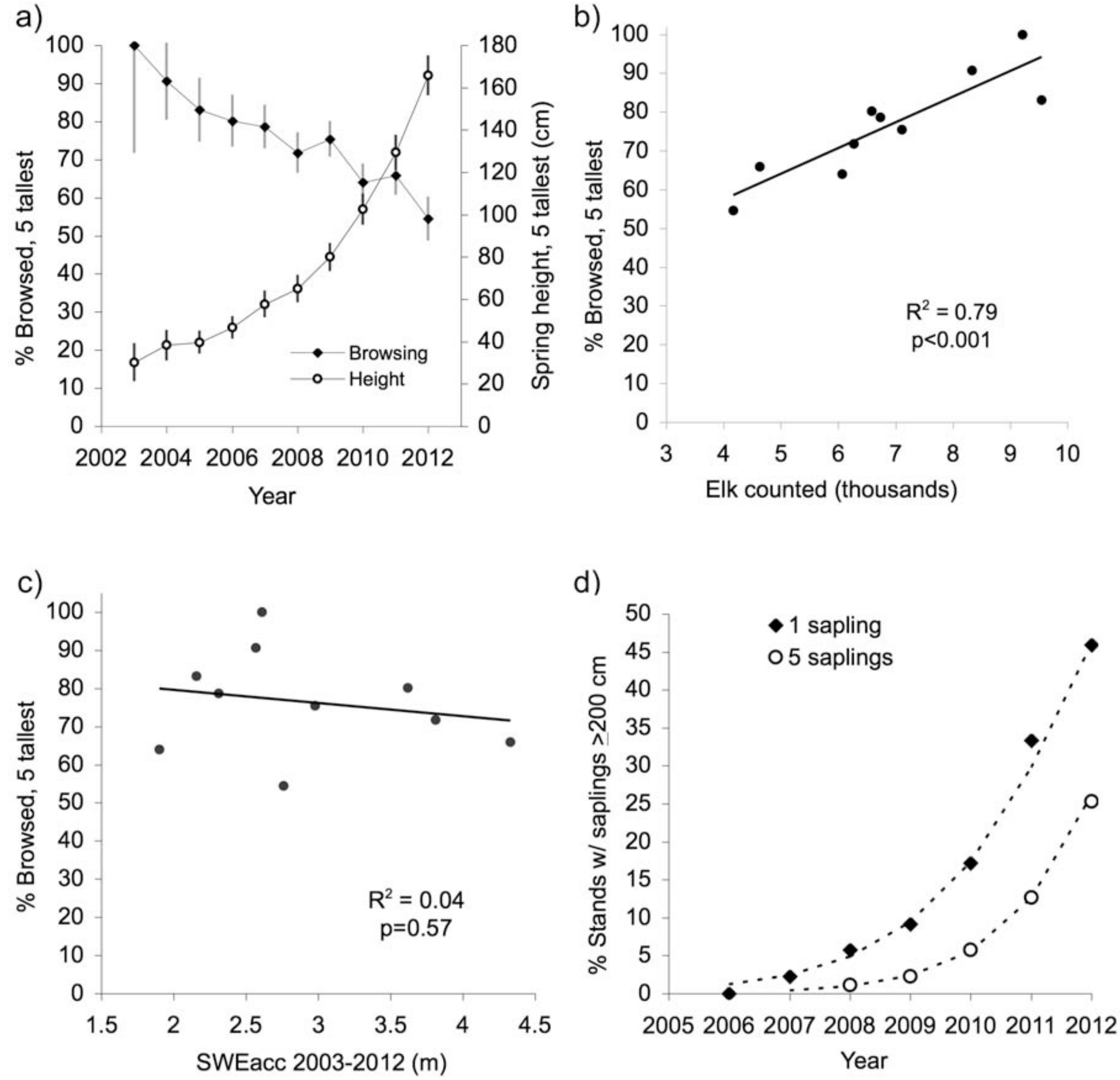

Figure 2.5. Results for the five tallest young aspen in each stand.
(a) Browsing rates and heights (with 95% CI) over time for the five tallest saplings pooled from 87 stands. History was measured by plant architecture.
(b) Browsing rate as a function of annual winter elk count, 2003-2012.
(c) Browsing rate as a function of accumulated snowpack (SWE), 2003-2012.
(d) Percentage of stands with one or five saplings ≥200 cm spring height.

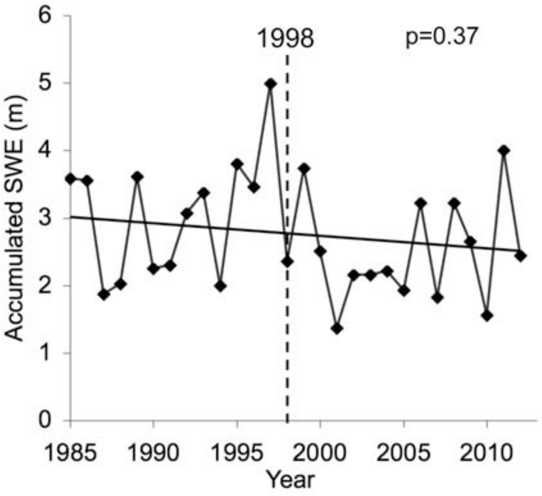

Figure 2.6. Accumulated snow water equivalent (SWE_{acc}) averaged for two SNOTEL stations near the West and Northeast park entrances, 1985-2012. There was no significant trend in this period ($p=0.37$), and no significant difference in mean SWE_{acc} before vs. after 1998 ($p=0.12$).

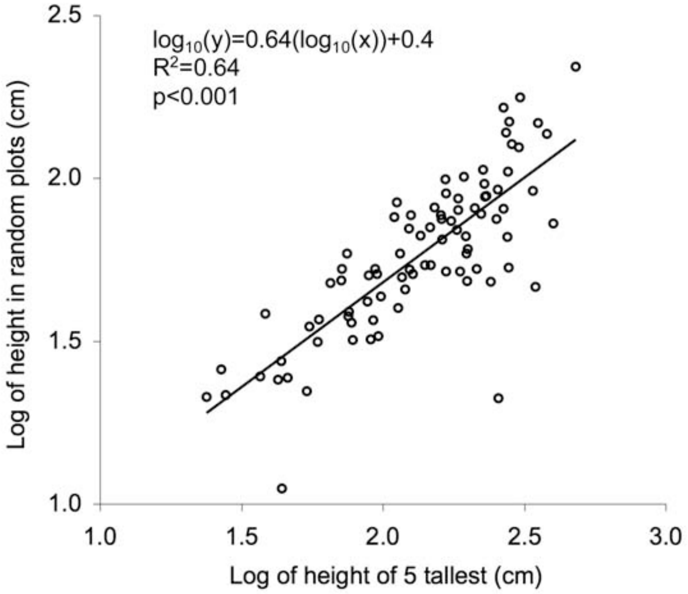

Figure 2.7. Relationship between mean height of the five tallest young aspen in a stand and young aspen in random sample plots, suggesting the five tallest could be used as an indication of the average height of young aspen. Correlation was strongest for five-tallest heights <200 cm (log<2.3).

3. SPATIAL DYNAMICS OF ASPEN, ELK AND BISON IN NORTHERN YELLOWSTONE

3.1. Abstract

In northern Yellowstone National Park, aspen stands began to recover from decades of decline following wolf reintroduction, but this recovery has been patchy and highly variable. To investigate the possible causes of spatial variation in aspen recovery, in 2012 we measured browsing intensity and height of young aspen in 87 randomly selected aspen stands on the Yellowstone northern ungulate winter range, and compared our results to similar data collected in 1997-98. We also analyzed annual elk count data and ungulate fecal pile densities to examine the relationship between aspen recovery and the distribution of elk and bison. The height of young aspen in a stand was inversely related to browsing intensity, with the greatest change in both browsing and height on the eastern side of the range, corresponding with recent changes in elk population distribution. The greatest densities of elk recently have been in the west sector of the range and the northwest sector outside the park boundary, with relatively few elk wintering in the east sector. This is in contrast to historical elk distribution, and may be the primary reason why aspen stands in the park have begun to recover. The recent decline in elk density within the park suggests that the recovery of aspen stands may be just beginning with elk densities <3 elk/km^2 in much of the winter range in the park, and <1 elk /km^2 in the east sector of the range. Topography explained little of the variation in aspen height or browsing intensity, though location in riparian areas and number of fallen logs were positively related to the height of the five tallest young aspen in a stand. Aspen have begun to recover in northern Yellowstone in association with a large-scale redistribution of elk that may be driven by a combination of factors, including increased mortality from predation and behavioral responses to predation risk.

3.2. Introduction

Quaking aspen stands (*Populus tremuloides*) declined in northern Yellowstone National Park (YNP) during the 20th century, due primarily to intensive browsing of young aspen by elk (*Cervus elaphus*) in winter (White et al. 1998, NRC 2002, Larsen and Ripple 2005, Kauffman et al. 2010). Following the return of wolves to YNP, researchers reported a reversal of this decline with reduced browsing and increased height of young aspen in some aspen stands, attributed to the influence of wolves on elk (Ripple and Beschta 2012). In 2012, we examined browsing intensity and height of young aspen on the northern ungulate winter range ("northern range") of YNP, compared to baseline data collected in the same stands in 1997-98 (Chapter 2, this dissertation). We found that some aspen stands have begun to recover with reduced browsing and increased recruitment of saplings, but this recovery was patchy and highly variable. In this paper, we examine the patterns and possible causes of variation in aspen stand conditions on the northern range, including large-scale changes in ungulate distribution as well as small-scale factors that could affect foraging behavior and responses to predation risk.

In 2006 and 2010, Ripple and Beschta (2007, 2012) found that young aspen in some stands in the eastern portion of the northern range were growing significantly taller with reduced browsing, a significant change from past conditions. They hypothesized that, in addition to reduced elk density, behavioral responses by elk to predation risk may have contributed to a trophic cascade benefiting aspen. Most of the browsing reduction occurred in riparian (streamside) stands, while non-riparian stands "generally showed continued suppression with only a slight decrease in browsing intensity" (Ripple and Beschta 2007). Riparian areas were often associated with complex terrain that could discourage ungulate access. Stands with many fallen trees also showed signs of aspen recovery suggesting that downed logs might be avoided by ungulates as impediments to access or escape.

Kauffman et al. (2010), working at about the same time as Ripple and Beschta (2007), reported that "aspen are not currently recovering in Yellowstone, even in the presence of a large wolf population." To measure behavioral responses by elk to predation and possible cascading effects on aspen, Kauffman et al. (2007, 2010) developed a map-based model of predation risk based on kill sites and topographic features, but found no relationship between this model and the amount of browsing in aspen stands. The model could not be tested as a predictor of aspen height or recruitment of saplings because all young aspen in sampling plots were short. Kauffman et al. (2010) concluded that no trophic cascade benefiting aspen was yet occurring, whether behaviorally or density mediated.

These two aspen studies differed significantly in study design (Beschta and Ripple 2013). Ripple and Beschta (2007, 2012) measured the five tallest young aspen in a stand as an indication of the potential for new sapling recruitment. They sampled 98 aspen stands in the eastern portion of the northern range near the Lamar Valley. Selection of stands by topographic position ensured that riparian stands, some of the first to recover, were included in the sample, as did the intensive sampling of a limited area. Kauffman et al. (2010) measured young aspen in only 16 stands, but covered the whole northern range within the park by randomly selecting four stands in each of four sections of the range, assessing height and browsing of young aspen in random sampling plots. While this sampling was limited it could have detected a strong, widespread recovery of aspen stands; however, no saplings >200 cm in height – the height at which saplings begin to escape from elk browsing – were found in sampling plots. Given the difference in sampling methods the findings of these studies were not as contradictory as they may at first appear; however, the fact that Kauffman et al. (2010) did not find evidence of aspen release from browsing raised questions about the extent of aspen recovery on the landscape. In 2010, on the Gallatin River elk winter range in northwest YNP, Winnie (2012) found high browsing rates in aspen stands and few saplings >200 cm, raising further questions about the ability of wolves to trigger a recovery of aspen in Yellowstone.

Our sampling of 87 randomly selected aspen stands on the YNP northern range updated and expanded information about the condition of aspen stands, and had the advantage of comparing to a similar dataset collected in 1997-98. We used two different methods to sample young aspen in aspen stands: 1) randomly placed sampling plots, and

2) selecting the five tallest young aspen in a stand. We analyzed variations in browsing intensity, aspen height, and ungulate distribution to answer the following questions:

- How do changes since 1998 in browsing intensity and height of young aspen vary spatially, and what does this variation reveal about the extent and timing of aspen recovery? We expected changes in aspen stands to be associated with changes in elk distribution following wolf restoration.
- What factors explain the spatial variation in browsing rates and heights and in 2012? Browsing intensity may be related to the large-scale distribution of elk and bison, and may also vary in response to site characteristics that could affect ungulate herbivory including topographic location, number of logs on the ground (Ripple and Beschta 2007) and openness of view (Ripple and Beschta 2006).
- Are bison browsing on aspen? If so, we would expect more browsing at heights accessible to bison (<100 cm) in areas of high bison concentration in the eastern part of the range. We also would expect a higher rate of summer browsing in the eastern part of the range due to large herds there in summer, if browsing occurs in summer.
- How are elk and bison distributed across northern Yellowstone? We mapped the density distribution of elk and bison scat, and used aerial count data to calculate trends in elk population density for four sectors of the northern ungulate winter range.

3.3. Study Area

Elk densities were relatively low from about 1950 to 1970 due to culling in the park (Fig. 2.1b in Chapter 2) yet no evidence of aspen recovery was found (Houston 1982). This suggests that the current aspen recovery was aided by something more than simple population reduction (Chapter 2). The difference could be due to behavioral responses to predation at small spatial scales (White et al. 2003, Fortin et al. 2005, Ripple and Beschta 2007), or the result of large-scale shifts in elk distribution (White et al. 2012), a change that could also have a behavioral component (Gower et al. 2009b, Proffitt et al. 2009). White et al. (2009) reported that "Elk apparently minimized predation risk during winter by selecting portions of the landscape that increased their probability of escape if attacked, while still providing relatively high quality vegetation and snow characteristics that allowed access to forage." Such behavioral responses to predation may work in combination with decreased elk density to influence aspen recovery (White et al. 2003, Fortin et al. 2005, White and Garrott 2005b, Hebblewhite and Smith 2010).

White et al. (2012) examined changes in elk density in four sectors of the Yellowstone northern range which we have called east, central, west, and Northwest (Fig. 3.1a). The northern Yellowstone elk herd is composed of two herd segments, which are exposed to different levels of predation and hunting. Some elk vary their migration strategies and there is some mixing between segments (White et al. 2010). The "Lamar River" segment winters in the upper-elevation Lamar River valley and surrounding area (east sector), while the "Yellowstone River" segment winters in the lower-elevation Gardiner River and Yellowstone River valleys (central, west and Northwest sectors), both in and out of the park. Prior to the return of wolves winter elk densities were usually greatest in the east and central sectors, with high densities in the west sector in severe winters (Houston 1982, White et al. 2012). Elk densities in the park stayed relatively high even as the proportion wintering outside the park increased with the overall increase in elk numbers in the 1980s and 1990s (Lemke et al. 1998).

After wolves returned to Yellowstone in 1995-96, the proportion of the elk herd wintering in the Northwest sector increased despite significant removals by hunting, but elk densities and the proportion of the herd wintering within the park boundary decreased (White et al. 2012). Hunting harvests were an important factor in the Northwest sector until 2005 (White and Garrott 2005b), then were much reduced in response to declining elk numbers. One reason for a higher rate of decline in the Lamar River herd segment was a higher rate of mortality from predation by wolves and bears (*Ursus* spp.) (White et al. 2012). In addition to differences in mortality and recruitment between herd segments, behavioral changes may have played a role in shifting the population center of northern Yellowstone elk distribution (Gower et al. 2009). There are many benefits for elk wintering in the lower elevation range outside the park including cultivated hay fields, less snow and earlier spring, but these advantages did not result in higher elk densities prior to wolf reintroduction. The disadvantage for elk outside the park is that they are exposed to hunting seasons in fall and winter, and hunting can influence the timing and location of elk winter migrations (Houston 1982, Proffitt et al. 2009, White et al. 2010). Before the return of wolves, predation risk for wintering elk was primarily from humans and may have influenced elk to winter inside the park. Now, the balance of predation risk has shifted. Outside the park there are fewer wolves, hunting has been reduced and occurs in limited seasons, and some private lands provide a partial refuge from hunting (Haggerty and Travis 2006). Furthermore, increasing numbers of bison (*Bison bison*) on the northern range in the park may be competing with elk (White and Garrott 2005b), particularly in the east sector where bison densities have been high (Wallen 2012). Bison numbers have increased on the northern range and in recent years have been comparable to the number of elk wintering inside the park (Wallen 2012, Wyman and Smith 2012). Elk may avoid domestic cattle and may avoid bison as well (Stewart et al. 2002), though avoidance of wolves has been found to be a more important driver of elk movement patterns (Proffitt et al. 2010).

The selection of winter range by elk is probably a response to many factors including quality of forage, risk of wolf attack, depth and timing of snows, risk of human hunting, and tendency to return to areas used in the past (Mao et al. 2005, White and Garrott 2005a, Haggerty and Travis 2006, Proffitt et al. 2009, White et al. 2009). Before wolf reintroduction, elk migrating out of the park in response to heavy snows encountered higher risk of hunting and without wolves the park was relatively safe. In central Yellowstone, elk home ranges increased in size after wolves returned, and elk movements were more dynamic with some elk dispersing to new areas (Gower et al. 2009). White et al. (2010) found that 39% of cow elk tracked on the northern range during 2000-03 and 2007-08 changed the location of their winter range by 8-55 km. Researchers have also found a strong correlation between the depth of snowpack and the number of northern Yellowstone elk migrating to lower elevation ranges north of the park (Houston 1982, White and Garrott 2005a, White et al. 2012). Movements of elk in response to winter severity, predation and hunting pressure demonstrate the possibility of large shifts in the selection of winter range.

3.4. Methods

In 1997-98, Larsen (2001) randomly selected 88 aspen stands on Yellowstone's northern ungulate winter range and marked them with GPS. In 2012 we revisited 87 of these aspen stands, excluding one stand on a steep scree slope because these conditions inhibit ungulate access (St. John 1995, Larsen and Ripple 2005). Larsen (2001) measured browsing intensity and heights of young aspen and in 79 stands, and we used these data as a baseline for change over time. See Chapter 2 of this dissertation for further description of the study area, wolf and elk population trends, a map of sampling sites, and details of aspen sampling. In each stand, young aspen were sampled with a randomly placed 2x30 m plot. An aspen "tree" was defined as >5 cm dbh (diameter-at-breast-height); "young aspen" were ≤5 cm dbh including "saplings" which were young aspen ≥200 cm in height. For young aspen in the sampling plot, we recorded the height and browsing status (browsed or not) of the tallest leader for fall 2012 (top height), spring 2012, and spring 2011, as indicated by bud scars and browsing scars (Ripple and Beschta 2007). We also located the five tallest young aspen in each stand and used plant architecture to assess height and browsing status over all previous years (Ripple and Beschta 2007). Because we were interested in the effects of herbivory, aspen that were protected by a physical barrier and had no evidence of browsing were not included. For each stand we recorded slope, aspect, and topographic position classed as "riparian" (associated with a stream) or not riparian. We counted the number of fallen trees and boulders >30 cm above the ground within 3 m of sampling plots, and also within 3 m of each of the five tallest young aspen (Ripple and Beschta 2007).

As an index to ungulate use of the area near a stand (Ripple et al. 2001, White et al. 2003), ungulate fecal piles including elk, bison, deer (*Odocoileus* spp.) and pronghorn (*Antilocapra americana*) were counted in four 2x50 m plots spaced 7 m apart, placed outside of the stand perimeter in the nearest open area within 10 m of the stand. Sampling plots for fecal piles were not placed within aspen stands because many stands were wet or mesic with very dense ground cover, some with standing water for part of the spring and summer; scat piles were unlikely to persist and difficult to detect in these conditions. Placing the scat plots outside of the stands in the adjacent grassland resulted in more consistent scat persistence and detection; scat densities are also expected to be higher in these locations compared to the interior of a stand, based on past research (White et al. 2003). This method provided an index to relative ungulate densities across the landscape, but elk scat densities were partially decoupled from some small-scale site factors such as the number of logs near the plot or complex terrain in the interior of many riparian stands (White et al. 2003). Elk pellets may persist for five years or more in xeric grassland (author's unpublished data). An index for openness of view was calculated from the average distance at which view was obstructed (to 900 m, the limit of the rangefinder) in the four directional quadrants (Ripple and Beschta 2006), viewed from the origin of the ungulate scat plots.

For each sector of the northern range, an annual browsing rate (percentage of top leaders that were browsed in the previous year, summer through spring) and mean young aspen height were calculated, first within each stand and then averaged across all stands within a sector. Browsing rate calculations did not include saplings (≥200 cm tall). We compared browsing rates between 1997-98 and 2011-12 by estimating 95% confidence intervals (CI) for the mean value for each sector using bootstrapping (10,000 iterations); data from 1997-98 were too skewed for distributional analysis methods. In the 1997-98 data, new aspen sprouts that had not been exposed to winter browsing were not distinguished from older sprouts, so the calculated browsing rate underestimated the actual browsing rate for the previous year in stands with new sprouts. We followed this method for comparison with 1997-98 (Fig. 3.1b), but for further analysis of data from 2012 we removed new sprouts from the calculations resulting in a slightly higher estimate of the percentage browsed (Fig. 3.2, 3.3a). We calculated 95% CI for mean browsing rate, spring height, and elk or bison scat density in 2012 for each sector. Confidence intervals showed that significant differences between sectors were primarily between the east and west sectors, so t-tests (unequal variance) were used to analyze differences between these sectors, with a 95% confidence level as a measure of statistical significance. We used kriging (ESRI ArcMap v.10, Spatial Analyst) to create a smoothed interpolated map of elk and bison scat density (cell size and search distance 3000 m).

We compared explanatory models for young aspen height (both in plots and of the five tallest), browsing rate in 2012, and elk or bison scat density (Table 3.1). Models were constructed from variables hypothesized to influence these response variables, and were compared using the corrected Akaike information criterion (AICc) (Burnham and Anderson 2002). The model with the least number of variables and with an AIC score within 2 units of the lowest value was chosen as the best model. A natural logarithm transformation of variables was used where needed to meet the assumption of constant variance. To limit the number of parameters in model comparisons, we first compared models using variables for basic landscape attributes and ungulate distribution including range sector (east, central, west), slope, aspect (south or not, where south includes southwest and southeast), leader length (for browsing rate and height only), elk scat density, bison scat density, and browsing rate (for height in sampling plots). We expected an inverse relationship between browsing and height. Gentle slopes, southerly aspect, and location in the western range sector were expected to be positively related to ungulate scat density and browsing rate, and hence negatively related to aspen height. We selected the best model using these variables, and then added variables hypothesized to affect small-scale predation risk (or convenience of access) including: number of logs and boulders (logs), topographic position (riparian or not), and openness of view. Browsing was expected to decrease and height to increase with number of logs and riparian position. Browsing was expected to be inversely related to openness of view. We estimated the topographic kill-site value assigned by the model from Kauffman et al. (2010) by locating our aspen sites on published maps (Kauffman et al. 2007, 2010). We tested this variable for influence on browsing, height, or elk scat density separately from other risk variables.

We devised two tests to assess the possible effect of bison browsing on aspen. First, we hypothesized that high densities of bison in the east sector have resulted in more browsing of aspen in summer in that sector, and tested this by comparing mean summer browsing rates of top leaders between east and west sectors. Second, we hypothesized that bison browsing in the east would result in significantly more browsing of plants <100 cm (spring height) compared to taller plants *in the same plot*, because most browsing by bison occurs at heights <100 cm (Painter and Ripple 2012); we tested this hypothesis using a t-test for paired values, including only those plots that had three or more young aspen >100 cm. We expect the difference in browsing rate between tall and short aspen to be smaller in stands in the west sector because bison densities have been lower there.

To assess trends in elk densities over time for the northern range, we calculated elk population density by sector (Fig. 3.1a) for all years for which these data were available, 1987-2012 (White et al. 2012). Annual winter elk count data by count unit were obtained from YNP staff (unpublished data), including the area of each count unit. Elk counts were totaled for each sector, then divided by the total area for that sector. An F-test was used to test the significance of the slope of elk density over time. Counts in the Northwest sector were not adjusted for hunter harvest, which was reduced after 2005 (Lemke et al. 1998, White et al. 2012). We averaged elk density for the years 1987-1994 and 2005-2011 by unit and created maps displaying average elk density in each unit for these time periods.

3.5. Results

In 1997-98 shortly after the return of wolves to the Yellowstone northern range, browsing rates were consistently high, near 90% in all range sectors (Fig. 3.1b), and aspen were consistently short (Fig. 3.1c). Browsing rates were lower and more variable across the northern range in 2011 and 2012 compared with 1997-98 (Fig. 3.1b). There also was wide variation within sectors in 2012 (Fig. 3.2), but the stands with the lowest browsing rates and tallest young aspen were mostly in the east sector. Comparing the east and west sectors, browsing rates in 2012 were significantly lower (Fig. 3.3a; t_{58}=3.9, p<0.001) and spring heights significantly taller in the east (Fig. 3.3b; t_{58}=4.0 p<0.001); variance in height was also greater in the east ($F_{36,22}$=2.84, p=0.006). The summer browsing rate in 2012 was 15 percentage points higher in the west (20% of leaders browsed in summer) compared to the east (5% of leaders browsed in summer), more than half of the 26-point difference in browsing for the entire previous year. The five tallest aspen were older (t_{58}=4.0, p<0.001) and taller (t_{57}=4.9, p<0.001) in the east than in the west (Fig. 3.4a), with more sapling recruitment (Fig. 3.4b) in the east, matching the pattern seen in the sampling plots. There were few stands with saplings (i.e., $\geq$200 cm tall) in any sector in 2007 (Fig. 3.4b).

The east sector had greater bison scat density than the west (t_{37}=8.7 p<0.001), but elk scat density was greater in the west than the east (t_{25}=4.6, p<0.001). The interpolated density map showed the greatest elk scat density in the park near the border of the Northwest sector, and the greatest bison scat density in the east sector and southern part of the central sector (Fig. 3.5; t_{26}=2.1, p=0.001). Summer browsing rates were significantly lower in the east than the west (Fig. 3.3a) despite high bison densities in the summer; however, there was evidence that bison have been browsing aspen. In the east browsing was significantly less at heights >100 cm (paired t-test t_{25}=3.7, p<0.001), but in the west the difference in browsing intensity above and below 100 cm was much smaller and not statistically significant (paired t-test t_6=0.6, p=0.56).

The multiple regression model for spring height of young aspen explained 67% of height variation, but most of this (62%) was explained by browsing rate alone (Table 3.1). The sector of the range was the most influential variable explaining variation in percentage browsed, height, and scat density (Table 3.1, Fig. 3.3). The signs of regression coefficients were as expected (see Methods). For the five tallest saplings, browsing rates were not available for all stands because many of the tallest were beyond the reach of ungulates (>200 cm) and therefore not included in browsing rate calculations.

Elk densities in the four sectors of the northern range continued to follow the same general trends after wolf reintroduction as were previously reported (White et al. 2012), with a significant decline in population density inside the park but stable or slightly increasing density in the northwest sector (Fig. 3.6). Winter elk densities in 2012 by sector were: east, 0.2 elk/km^2; central, 2.2 elk/km^2; west, 2.4 elk/km^2; and Northwest, 6.2 elk/km^2. These corresponded with elk scat densities of: east, 4 groups/100 m^2; central, 11 groups/100 m^2; and west, 17 groups/100 m^2. Scat counts in the central and west sectors may have been inflated relative to elk density due to recent declines in elk density and the persistence of elk pellets. Elk densities in the east sector were <2 elk/km^2 for six of the last seven years, while those in the west and central sectors have been 2-6 elk/km^2.

3.6. Discussion

Spatial variation of aspen recovery in northern Yellowstone supported the hypothesis that a trophic cascade following wolf reintroduction, mediated by recent changes in elk density and distribution, has resulted in a patchy recovery of aspen stands. In 2012, browsing rates were lower and young aspen taller in all range sectors within the park compared with conditions in 1997-98 (Fig. 3.1b, c), with the greatest change in the east sector where aspen recovery was first reported in 2006 (Ripple and Beschta 2007). This pattern was consistent with the fact that elk densities declined earlier and to lower levels in the east than in the central or west sectors of the range (Fig. 3.6). In addition to this landscape-scale gradient in browsing and height from east to west, browsing and height varied greatly within range sectors (Fig. 3.2).

What explains the variations in browsing and height across the landscape, and what caused the additional variation in height between stands with lower browsing rates? The percentage of stems browsed in 2012 explained 62% of height variation in sampling plots (Table 3.1, Fig. 3.2). It would be reasonable to expect some additional variation to be due to differences in stand productivity resulting in different rates of growth following release from browsing. While the rate of growth (indexed by leader length) was included with browsing in the best models for height, this index of productivity explained little additional height variation (Table 3.1). Small-scale topographic variation also had a small influence as represented by openness of view, but browsing intensity was the primary driver of differences in height between stands.

The evidence from annual counts and pellet pile densities suggests that elk have greatly reduced their use of the winter range in the east sector (Fig. 3.5a, 3.6, 3.7). Elk densities have also declined in the central and west sectors, but these sectors continued to have elk densities higher than those in the east (Fig. 3.6). This difference in the timing of elk density decline in various parts of the range may be one reason, perhaps the primary reason, for the variation in height seen among stands with lower browsing rates (Fig. 3.2). If current downward trends in elk density continue, browsing rates may be reduced further in aspen stands in the central and west sectors. Alternatively, elk densities may be leveling off at about 2-3 elk/km^2 on the west side of the range, a threshold below which a similar partial release of aspen has been found in other study areas (White et al. 1998, 2003). A more complete aspen recovery may require lower elk densities of <2 elk/km^2 (White et al. 2003), as recently occurred in the east sector. In contrast with elk distributions prior to wolf restoration, the greatest elk densities were in the northwest sector (Fig. 3.5a, 3.7b), consistent with the generally high browsing rates and lack of aspen sapling recruitment found there in 2006 (Kimble et al. 2011a, Kimble et al. 2011b). Shielding by humans (Berger 2007) may be one factor attracting elk to the northwest sector; for example, elk in the vicinity of the towns of Mammoth Hot Springs, WY, and Gardiner, MT are protected from both predators and hunting and exhibit low levels of vigilance (author's observations). Similarly, after wolves recolonized Banff National Park, Canada, the distribution of elk shifted toward centers of human activity resulting in a trophic cascade benefiting willow and aspen in other areas (White et al. 2003, Hebblewhite et al. 2005).

Elk and bison have been using different parts of the northern range, as evidenced by scat densities as well as annual counts (Fig. 3.5, 3.7). Bison may have been limited by competition with high densities of elk in the past (Houston 1982, White and Garrott 2005b), and bison may now be displacing elk (White and Garrott 2005b), or simply expanding into range vacated by elk for other reasons. Bison concentrations have resulted in high browsing intensities on willow and cottonwood in the Lamar Valley (Painter and Ripple 2012), and we found some evidence of an effect on aspen from bison. Bison may slow or prevent recovery of some aspen stands in the east sector despite the reduction in elk herbivory; however, relatively high densities of bison have not prevented a general trend toward aspen recovery in the east sector.

Most of the variation in browsing intensity between aspen stands remained unexplained (Table 3.1), and the causes of variation are likely to change over time as aspen recovery continues to develop. With reduced browsing, site productivity may become a more important driver of differences in height, and the influence of topographic factors may cause greater browsing in some stands over others. A similar process has occurred with the recovery of tall willows (*Salix* spp.) in northern Yellowstone. In the lower Lamar Valley, browsing by bison kept most willows short (Painter and Ripple

2012), but in some other places browsing has been reduced following the return of wolves so that willow height is now primarily influenced by resource limitations such as water availability and soil composition (Tercek et al. 2010, Marshall et al. 2013).

Changes in elk habitat selection and grouping behavior following wolf restoration have been well documented (Mao et al. 2005, Gower et al. 2009, White et al. 2012), but linking these changes to cascading effects on plants has been more elusive. At the small scale of individual stands, the five-tallest young aspen were taller in riparian stands and stands with more logs, consistent with the findings of Ripple and Beschta (2007, 2012). The influence of these variables could be related to increased risk of predation for elk, or to the inconvenience of accessing young aspen by elk or bison in these conditions. As elk densities decline elk may be less driven to access difficult locations, so both density-mediation and predation risk mediation would be likely to result in a variable release from browsing, and the two causes would be difficult to distinguish.

We tested the kill-site index developed by Kauffman et al. (2007, 2010) as an explanatory variable for height, browsing rate, or elk scat density, but found no evidence for a relationship. This model may not represent predation risk from the perspective of an elk in a way that would be reflected in a trophic cascade to plants, for two reasons: 1) Kills of elk by wolves occur after a chase so the kill location is more informative about where an elk chooses to flee once attacked, rather than where an elk chooses to forage (White et al. 2009). Although Kauffman et al. (2010) found no difference in topography between the start and end of a chase, elk behavior may have been modified by imminent wolf attack before the chase began (Creel et al. 2005, Middleton 2012), or differences may have been undetected due to fine-scale topographic variation or selection of test parameters. 2) Temporal variation in predation risk may not be represented adequately in a map based on kill locations. Predation risk factors such as snow depth, elk condition, time of day, and proximity of wolves are temporally variable and even a short period of browsing can be sufficient to prevent aspen regeneration (Fitzgerald and Bailey 1984). Small-scale temporal variation in predation risk and prey response may be important factors mediating the strength of a trophic cascade (Creel and Winnie 2005, Creel et al. 2005).

Seventeen years after wolf reintroduction, the northern Yellowstone ecosystem is still changing in response to wolves in combination with other influences such as hunting, climate and bears (White et al. 2012). Some general observations about the condition of aspen stands on the northern range are possible from our results:

There was no evidence of a trophic cascade in aspen shortly after wolf reintroduction in 1997-98, with browsing rates >80% in ~80% of stands. Wolves were present on the range beginning in 1995, and wolf numbers in 1997-98 were comparable to those of recent years (Fig. 2.1b in Chapter 2 this dissertation). A strong behavioral trophic cascade might have been detectable in the form of variation in browsing rates between stands, but there was no evidence of this.

By 2006, there were important changes beginning in the east sector in some stands (Ripple and Beschta 2007), but browsing rates were generally high across the range and few stands had saplings (Fig. 3.4; Fig. 2.5a in Chapter 2). The timing of height release from browsing at a large-scale matched the pattern of declining elk densities. The tallest saplings were older and began to increase in height earlier in the east sector than in the central and west sectors (Fig. 3.4).

Aspen recovery has been associated with large-scale changes in elk distribution, but small-scale predation risk effects may be a cause of local variation. Even in the east sector in 2012, some stands had relatively high browsing rates (Fig. 3.2), and 35% of stands in the east had no saplings. Browsing rates were also highly variable in the central and west (Fig. 3.2), and even the five tallest saplings in most stands averaged <200 cm in 2012 (Fig. 3.4) though some stands were much taller. The delayed recovery in the west suggests that a threshold of density must be reached below which recovery can begin. In some Canadian parks, small-scale predation risk responses may have contributed to a patchy release of aspen such as we found in most of the Yellowstone northern range, but only with low to moderate elk densities (White et al. 1998, 2003). Only in portions of the northern range and only since about 2005 (Fig. 3.6, 3.7) have elk densities been comparable to those at which aspen recruitment was observed in those Canadian parks. In places with low elk density such as the east sector, variation in browsing intensity may be due to browsing by bison, or by small numbers of elk focusing on some stands more than others in response to predation risk, accessibility, depth of snow, variations in stand palatability (Wooley et al. 2009), availability of forage, or random chance.

Something more than an overall reduction of the elk herd was required for a general aspen recovery. Before wolf restoration, severe winters drove elk out of the park to the northwest sector, but the shift of range was temporary (Houston 1982). Since the return of wolves, a reduction in the elk herd has been accompanied by a change in elk distribution toward the safer and more snow-free northwest sector, resulting in lower elk densities and reduced browsing of aspen in the park (Fig. 3.6, 3.7). Similar changes in elk distribution were observed following wolf recolonization in Banff National Park, Canada, due in part to human "shielding" from predation (Hebblewhite et al. 2005, Berger 2007, Hebblewhite and Merrill 2009).

Trophic cascades involving wolves, elk and aspen are usually discussed as either density-mediated at a landscape-scale, or behaviorally mediated at the small scale of individual stands, topographic features, or piles of logs (Kauffman et al. 2010, Winnie et al. 2011, Ripple and Beschta 2007). This paradigm may be inadequate to describe recent changes in northern Yellowstone, where large-scale, range-wide changes in elk density and distribution may have a behavioral component, in response to wolves as well as human hunting and human shielding. Predation risk may also operate at an intermediate scale through changes in elk movement patterns, grouping behavior, range size and habitat selection, as were observed when wolves returned to the Yellowstone ecosystem (Mao et al. 2005, Gower et al. 2009b, White et al. 2009, White et al. 2012). A more complete understanding of the interactions of predators, elk and aspen may result from consideration of responses to predation risk at multiple scales.

The complex relationship of wolves, elk and aspen will continue to unfold, interacting with other large predators, an increasing bison population, changing climate, changes in land use and hunting, and other facets of the Yellowstone ecosystem. Many aspen stands have begun to recover, with the greatest and earliest change in the east sector of the range, where elk densities declined more rapidly and to lower levels than in the central and west sectors. Elk densities north of the park boundary have remained little changed even as overall elk numbers have declined, and a greater proportion of northern

Yellowstone elk now winter outside the park than inside. Aspen stands did not recover in the mid-twentieth century when overall elk densities were similarly low due to culling in the park. The difference now appears to be due primarily to a large-scale redistribution of the elk herd, an effect that is unlikely to have occurred without the return of wolves.

3.7. Acknowledgements

We received financial support from the UW–NPS Research Station. Park biologists P.J. White, Doug Smith, and Rick Wallen provided ungulate count data and other helpful information. We thank field technicians Jeff Stephens and Jonathan Batchelor. Ariel Muldoon assisted with the statistical analysis.

3.8. References

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Table 3.1. Selected models (bold type) compared with simplified models for five response variables; the sign for each term indicates the sign of the regression coefficient. Columns list difference in AICc score compared to selected model (dAICc); adjusted R^2; and degrees of freedom (df) for the regression model.

Model	dAICc	adj R^2	df
BROWSING RATE IN SAMPLING PLOTS			
(Browsing)~ +Central +West +(Leader Length)	**0**	**0.23**	**3, 83**
(Browsing)~ +Central +West	4	0.19	2, 84
HEIGHT OF YOUNG ASPEN IN SAMPLING PLOTS			
ln(Height)~ -(Browsing) +(Leader Length) -(Elk Scat) -View	**0**	**0.67**	**4, 82**
ln(Height)~ -(Browsing) +(Leader Length) -View	3	0.65	3, 83
ln(Height)~ -(Browsing) +(Leader Length) -(Elk Scat)	4	0.64	3, 83
ln(Height)~ -(Browsing) +(Leader Length)	6	0.64	2, 84
ln(Height)~ -(Browsing)	9	0.62	1, 85
ln(Height)~ +(Leader Length)	92	0.02	1, 85
HEIGHT OF FIVE TALLEST YOUNG ASPEN IN STAND			
Height~ -Central -West +Logs +Riparian	**0**	**0.32**	**4, 82**
Height~ -Central -West +Riparian	4	0.28	3, 83
Height~ -Central -West +Logs	6	0.27	3, 83
Height~ -Central -West	11	0.22	2, 84
Height~ -(Leader Length)	30	0.004	1, 85
ELK SCAT DENSITY			
ln(Elk Scat)~ +Central +West -View	**0**	**0.36**	**3, 83**
ln(Elk Scat)~ +Central +West	8	0.29	2, 84
ln(Elk Scat)~ +(Bison Scat)	22	0.15	2, 84
BISON SCAT DENSITY			
ln(Bison Scat)~ -Central -West -Slope	**0**	**0.54**	**3, 83**
ln(Bison Scat)~ -Central -West	4	0.51	2, 84

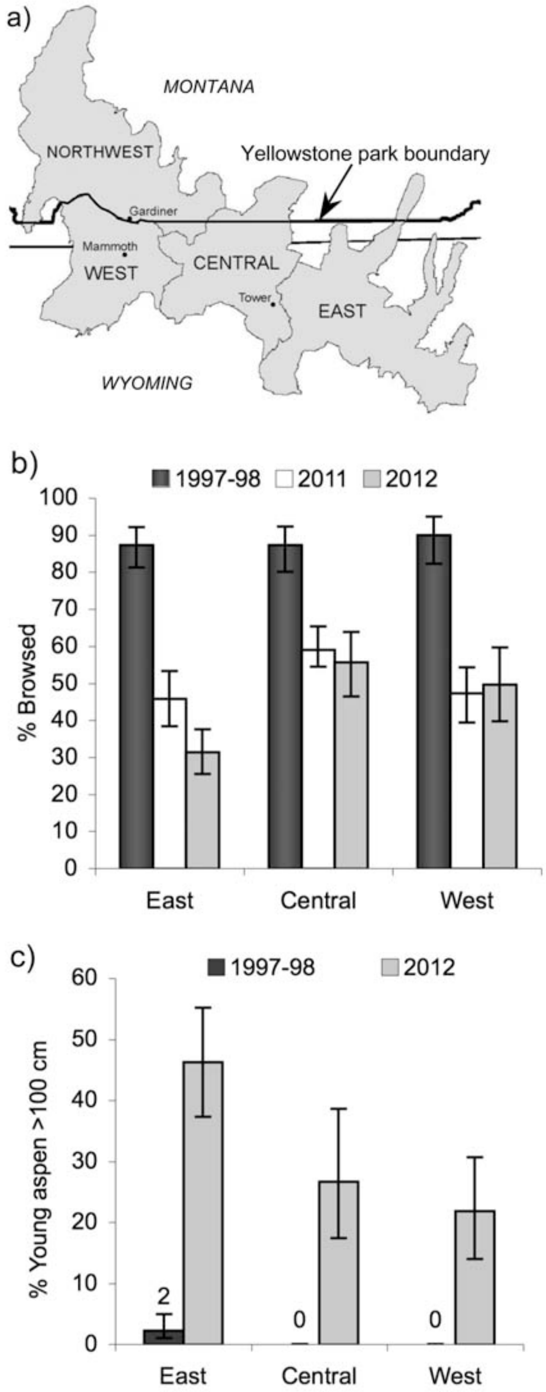


Figure 3.1. Sector map and changes in aspen by sector between 1998 and 2012.
(a) Map of the Yellowstone northern ungulate winter range in gray, with four sectors.
(b) Browsing rates for 87 aspen stands in three northern range sectors in 1997-98, 2011 and 2012; error bars show 95% CI (includes new summer sprouts).
(c) Percentage of young aspen in sampling plots ≥100 cm tall in 1997-98 and 2012, with 95% CI.

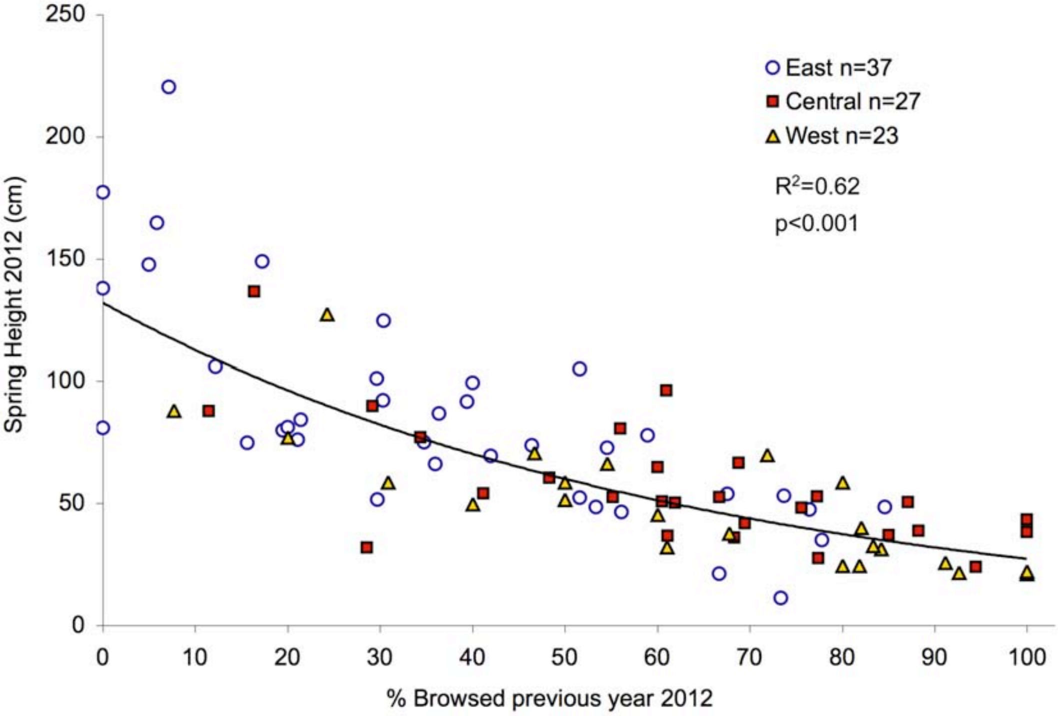


Figure 3.2. Mean spring height of young aspen as a function of browsing rate in 87 aspen stand sampling plots, coded by range sector. Line is fitted to the logarithm of height.

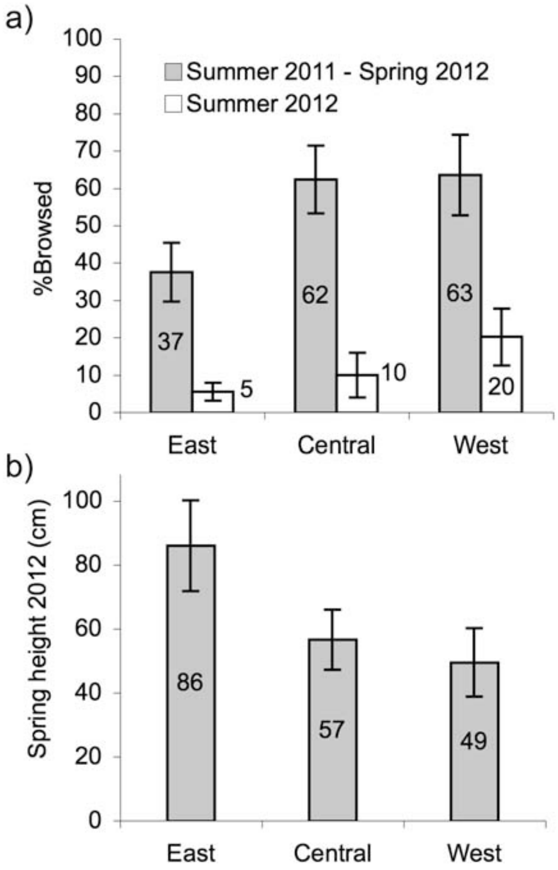


Figure 3.3. Height and browsing in sampling plots by sector in 2012 (with 95% CI).
(a) Browsing rates in three range sectors, including during the growing season in 2012. Both annual (summer 2011- spring 2012) and summer browsing rates were significantly greater in the west than in the east. Browsing rates were calculated without new summer sprouts, and so were slightly higher than in Fig. 3.1.
(b) Spring height of young aspen in sampling plots was significantly taller in the east sector.

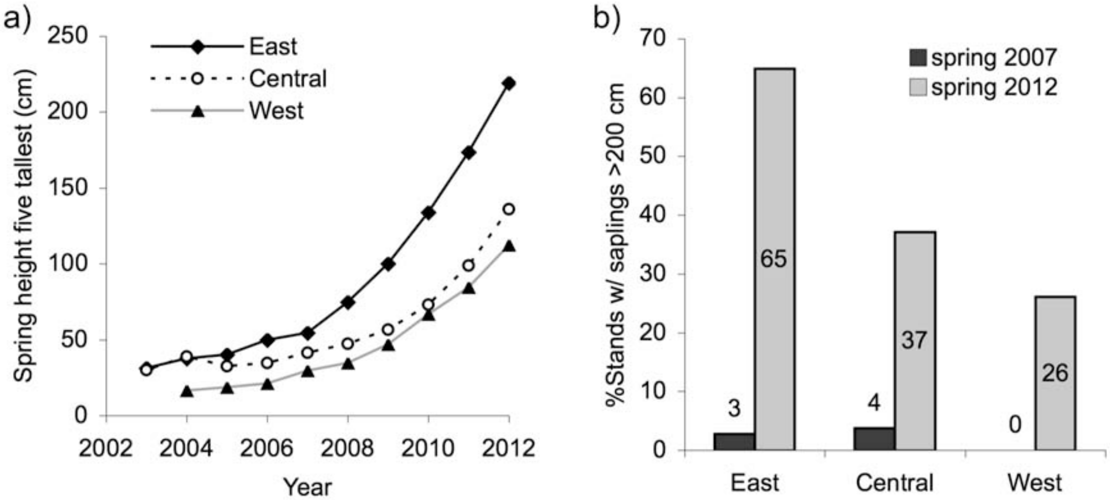


Figure 3.4. Height and recruitment of the five tallest young aspen in each stand (n=87 stands) in three range sectors, based on plant architecture.
(a) Height over time; east and central range values overlapped in 2003 and 2004.
(b) Percentage of stands with at least one sapling ≥200 cm spring height in 2007 and 2012.

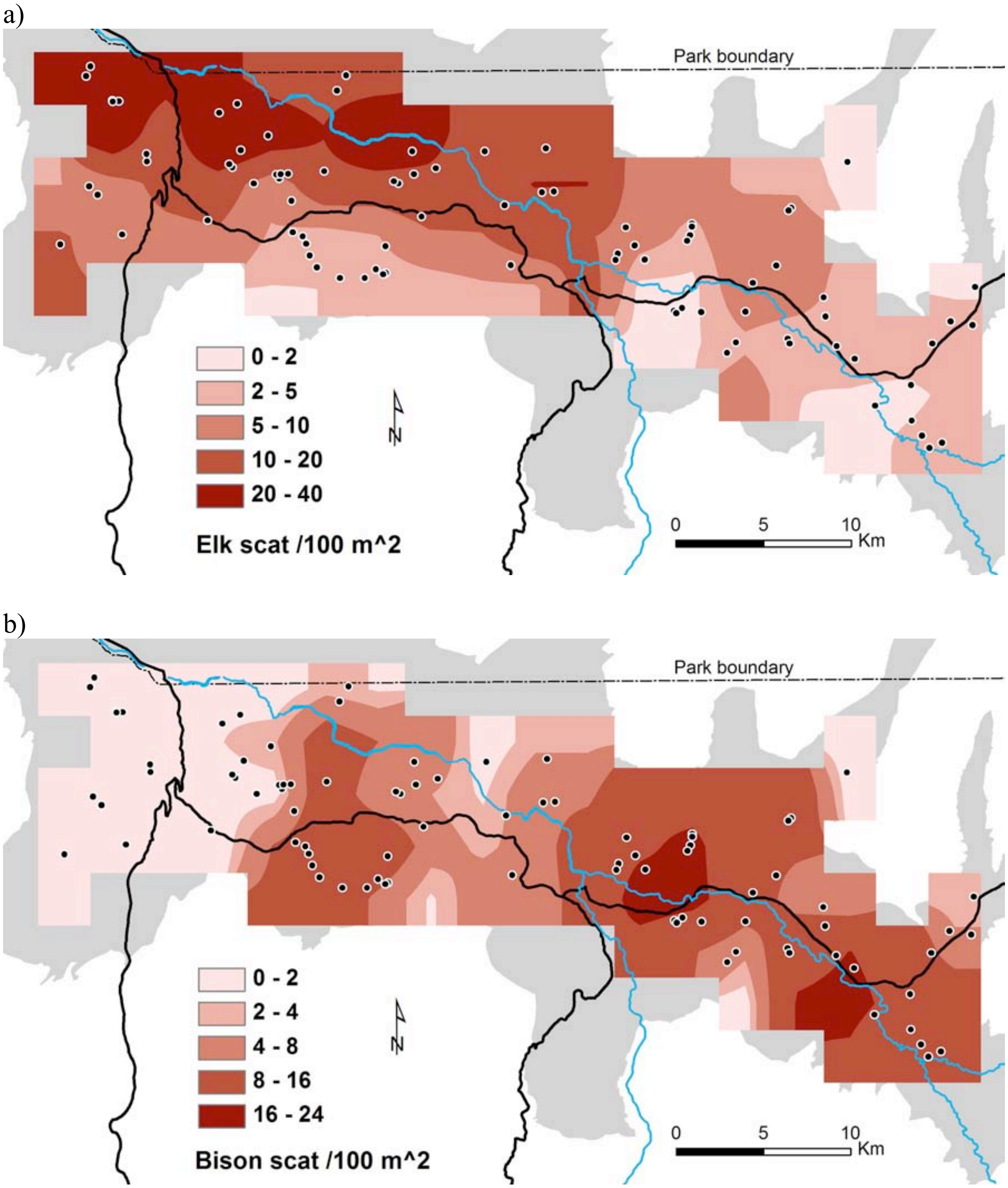


Figure 3.5. Elk (a) and bison (b) scat density distribution in northern YNP in 2012, interpolated from data at 87 aspen stand locations (black dots). Grey background is the Yellowstone northern ungulate winter range. Interpolation did not include consideration of topographic variation.

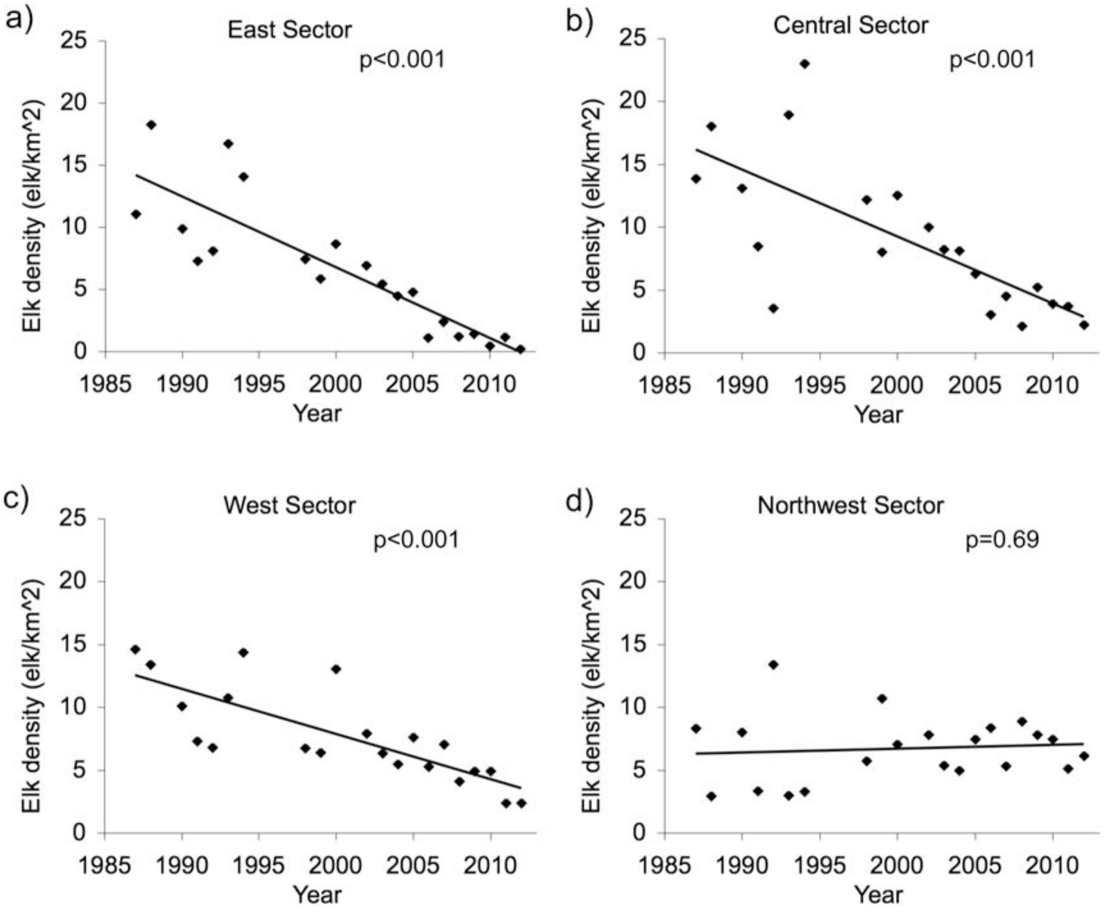
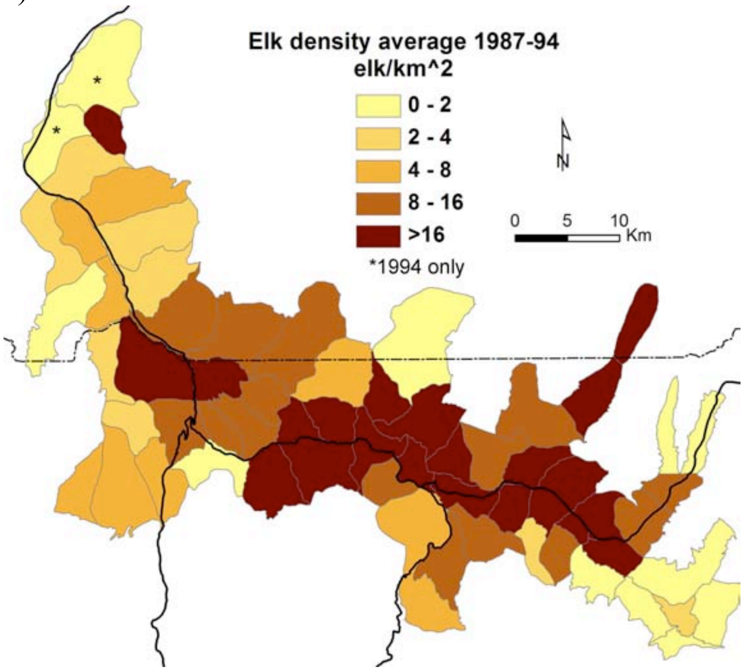


Figure 3.6. Elk population density in the four sectors of the northern range (Fig. 3.1a), estimated from annual winter aerial counts, 1987-2012. Unit count data were not available for 1989, 1995-97 and 2001. P-value is for the F-test for the significance of the regression slope.

a)



b)

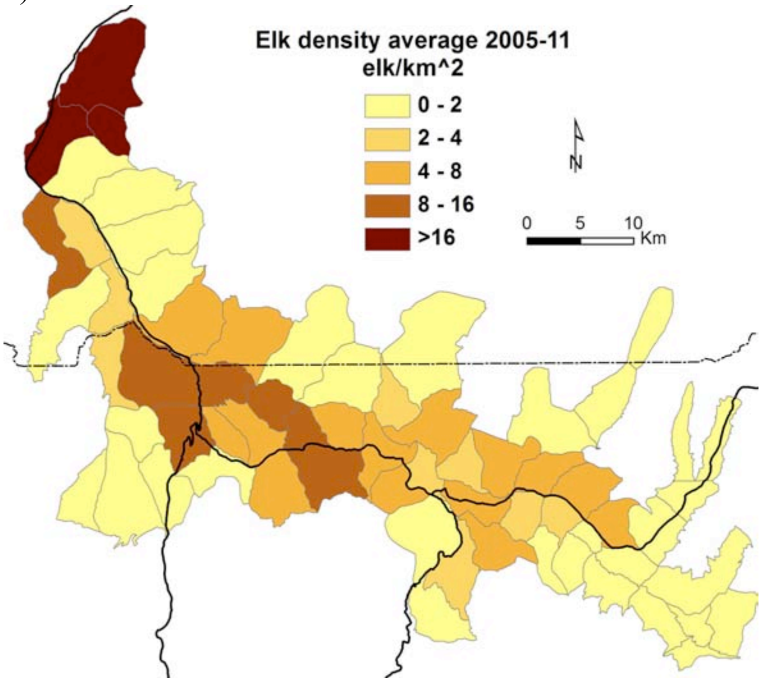


Figure 3.7. Elk population density in each count unit averaged for the years 1987-1994 (a) and 2005-2011 (b). The two northernmost units had no count data prior to 1994 (Lemke 1998).

4. INCREASED ASPEN RECRUITMENT IN A WYOMING NATIONAL FOREST FOLLOWING THE RETURN OF WOLVES

4.1. Abstract

In the Shoshone National Forest east of Yellowstone National Park (YNP), we investigated the possibility that a trophic cascade from wolves to elk to plants has produced a significant reduction in browsing of aspen by elk, resulting in increased heights of young aspen and increased recruitment of aspen saplings. In the summer of 2011, we measured browsing intensity and heights of young aspen in 43 aspen stands in the Sunlight/Crandall area, and compared these data to previous measurements from the same stands in 1998, the year before wolves returned to the study area after being reintroduced in YNP. The percentage of leaders browsed (browsing rate) was consistently high in 1998, averaging 84%, and the percentage of young aspen ≥100 cm tall averaged only 5%. In 2011 the browsing rate was lower at 47%, and the percentage ≥100 cm was higher at 32%. The percentage of plots with saplings ≥200 cm increased from 13% in 1998 to 40% in 2011. Mean height of young aspen was more strongly related to browsing intensity than to annual leader growth. In 2011, 14 stands without livestock had a lower browsing rate (33%) than the 29 stands with both livestock and wild ungulates (61%), suggesting that livestock may have had a significant effect on aspen, adding to the effects of elk. Average elk density in the area has remained moderate to high, with predation losses compensated by reduced hunting, so a trophic cascade may be mediated in part by changes in elk habitat selection, movements, foraging or grouping behavior. Though not all stands were released from browsing, lower rates of browsing on aspen in association with increased height since the return of wolves provides some of the first evidence of a trophic cascade involving wolves, elk and aspen outside of a national park.

4.2. Introduction

In the river valleys of Yellowstone National Park (YNP) and the surrounding area, stands of aspen trees (*Populus tremuloides*) enhance biodiversity and provide vital habitat for many species (DeByle and Winokur 1985). Aspen declined in the 20th century in the Yellowstone area, due primarily to intensive browsing of young aspen by elk (*Cervus elaphus*) (White et al. 1998, Kay 2001, NRC 2002, Barmore 2003). These effects were most pronounced within park boundaries, but aspen were also suppressed by browsing on winter ranges outside the park (St. John 1995, Kay 2001, Larsen and Ripple 2003, 2005). On national forest land, both elk and livestock affected aspen recruitment. Through their effects on elk movements, grouping and foraging behavior, and population density, wolves (*Canis lupus*) may influence the relationship between elk and aspen (White et al. 1998, Ripple and Larsen 2000). The reintroduction of wolves to the Greater Yellowstone Ecosystem in 1995-96 provided an opportunity to observe these interactions. Wolves quickly radiated from their point of introduction in northern YNP and by 1998 breeding packs were established in adjacent areas managed by the Gallatin and Shoshone National Forests (Smith et al. 1999).

In 1997-98, Larsen (2001) examined the age structure of aspen trees, and the height and intensity of browsing of young aspen in elk winter ranges in the Yellowstone area, including the Shoshone National Forest east of the park in Wyoming. Young aspen were intensively browsed, and the ages of overstory trees showed that recruitment of trees declined following the loss of wolves in the early 1900s (Larsen and Ripple 2003, 2005). After wolves returned to YNP, heights of young aspen increased in association with decreased rates of browsing, consistent with a trophic cascade from wolves to elk to aspen (Chapter 2 this dissertation; Ripple and Beschta 2007, 2012b). Similar trophic cascades have been found in other national parks in Canada (White et al. 1998, White et al. 2003, Hebblewhite et al. 2005, Beschta and Ripple 2007). A trophic cascade involving wolves, elk and aspen has not been documented outside the protection of a national park, however, and the question remains whether wolves can have an effect on aspen in a landscape that has elk hunting, cattle grazing, lethal wolf control, and other human activities (Soulé et al. 2003). Kimble et al. (2011) did not find evidence of a widespread increase in aspen sapling recruitment between 1991 and 2006 in the Gallatin National Forest north of YNP. Although there was evidence of a patchy release from browsing suppression, elk browsing in 2006 was intensive enough to inhibit aspen growth in many places in the Gallatin National Forest, with livestock adding to the effects of elk.

Has there been a general reduction in herbivory of aspen and increase in young aspen height and recruitment of tall saplings in the Shoshone National Forest since the return of wolves? Most browsing by elk occurs at heights <2 m, so taller saplings are likely to escape browsing and survive to become trees (White et al. 1998). Is there evidence that wolves have facilitated the regeneration of aspen trees? To begin to answer these questions, in the summer of 2011 we revisited 43 aspen stands previously sampled in 1998 (Larsen 2001), and collected data to compare browsing rates and heights of young aspen across the 13-year period. A reduction in browsing by elk could be caused by a decline in elk population density, but changes in elk habitat selection and foraging behavior might also benefit aspen (White et al. 2003, Fortin et al. 2005, Ripple and Beschta 2007). We also considered other factors that could affect browsing rates and the growth of aspen, including site productivity, livestock grazing, climate, and the number of logs on the ground in aspen stands.

4.3. Study Area

The Sunlight Creek and Crandall Creek basins are located in the Shoshone National Forest, Wyoming, approximately 30 km east of YNP (Fig. 1.1 in Chapter 1). These basins also contain large areas in private ownership, mostly ranches, and the Sunlight Creek Wildlife Habitat Management Area managed by the Wyoming Game and Fish Department (WGFD). Elk use the Sunlight/Crandall area in winter, sharing the range with mule deer (*Odocoileus hemionus*) and a small number of moose (*Alces alces*) (WGFD 2010). Livestock graze much of the area in summer and fall, mainly cattle (*Bos taurus*) but also some horses (*Equus caballus*). In the 1990s, livestock grazed most available areas on national forest land. Between 1998 and 2011, livestock grazing continued near permitted levels in the Sunlight Creek area; however, as predation from wolves and grizzly bears (*Ursus arctos*) increased in the early 2000s, grazing declined in the Crandall basin as ranchers avoided the area to reduce losses to predators (Joe Hicks, Shoshone National Forest Range Management Specialist, personal communication).

The Sunlight/Crandall elk winter range is comprised of valleys of dry grassland dominated by big sagebrush (*Artemesia tridentata*), interspersed with stands of aspen and coniferous trees, bordered by slopes with dry forests of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*). Riparian corridors are dominated by willow (*Salix* spp.), cottonwood (*Populus angustifolia* and *P. balsamifera*), and silverberry (*Elaeagnus commutata*). For further description of the study area, see Larsen (2001) and Larsen and Ripple (2003).

All sampled aspen stands were within Crucial Elk Winter Range and Parturition Areas as mapped by WGFD (Larsen and Ripple 2005, WGFD 2010), and all were on national forest land except for two in the Sunlight Creek Wildlife Habitat Management Area. Aspen trees in a stand are normally clones sharing a root system, and most reproduction is from root sprouts, potentially maintaining an aspen stand for hundreds of years where moisture is sufficient. Stands in the northern Rocky Mountains are often small and widely separated and associated with wetlands and riparian areas (Fig. 4.1) (White et al. 1998). Coniferous trees may invade and eventually replace aspen stands where habitat is suitable, particularly in the absence of fire.

The Sunlight Creek and Crandall Creek valleys are wintering grounds for the Sunlight/Crandall or Sunlight Basin segment of the larger Clark's Fork elk herd. These Sunlight Basin elk are largely migratory, spending summers at higher elevation in YNP and returning to the Sunlight/Crandall winter range with the first snows of fall (Craighead et al. 1972, Houston 1982, Rudd et al. 1983, WGFD 2007). The Clark's Fork herd population estimate averaged about 5500 animals in the years 2005-2010 (WGFD 2010), with the migratory portion estimated to be about 48% of this total (Middleton 2012) or about 2600 animals, most wintering in the Sunlight Creek area. The population estimate for the entire Clark's Fork herd was similar in 1998, 5300 elk (WGFD 1980-2009), down from higher densities in the early 1990s stimulated by the 1988 fires (D. McWhirter, personal communication). Although overall population density did not substantially change, calf/cow ratios declined by more than 50% in the migratory portion of the herd in the decade following the return of wolves. This “dramatic shift” in elk recruitment (WGFD 2007) has been attributed to predation by wolves and bears, combined with low pregnancy rates due to summer drought stress (Middleton and McWhirter 2010, Middleton et al. 2013). Despite increased predation and reduced recruitment, Sunlight/Crandall elk numbers have been fairly stable, due in part to reduced hunting, though low recruitment has caused concern among managers. Harvest declined from from an average of 493 elk in 1998-2000 to 140 in 2008-2010 (WGFD 2010), and in 2006 the WGFD reported an increase in elk numbers in the Sunlight/Crandall area presumably due to the decreased elk harvest (WGFD 1980-2009). In 2010 WGFD (2010) reported that elk numbers in the Sunlight and Crandall management units were probably slightly above management objectives (Stephenson 2010). As predation replaced hunting in the Sunlight/Crandall elk herd and calf recruitment declined, demographics of the herd changed toward an older average age with a higher proportion of mature females (Middleton and McWhirter 2010, Middleton et al. 2013).

In 1998, a pair of wolves from YNP moved into the Sunlight basin, and in 1999 they produced pups. Pack sizes and territories have fluctuated, in part due to lethal control actions following livestock predation, but wolf packs have been present in the study area from 1999 to 2011 (USFWS 2000-2011, WGFD 2007, Nelson et al. 2012), along with bears (*Ursus* spp.) and cougars (*Puma concolor*). Bears are important predators of elk calves in spring and summer, and may affect elk recruitment (Barber-Meyer et al. 2008, Middleton and McWhirter 2010, Middleton 2012). Annual estimates of wolf numbers in packs ranging in the study area including both adults and pups averaged 16 wolves over the period 2000-2010, with a minimum of 9 in 2009, and a maximum of 21 in 2005.

4.4. Methods

Aspen sampling methods were designed for direct comparison with data collected by Larsen (2001) in 1997-98, and to allow more detailed analysis of aspen stand conditions in 2011, similar to methods used in YNP in 2012 (Chapters 3 and 4 this dissertation). In the summer and early fall of 1997 and 1998, Larsen (2001) randomly selected 47 aspen stands in the Sunlight/Crandall elk winter range, marked with GPS. In 2011, between August 14 and September 11, we revisited 43 of these 47 aspen stands and repeated the measurements, excluding one stand with no GPS location and three that were located on steep scree slopes, terrain that partially excludes browsing ungulates (St. John 1995, Larsen and Ripple 2005). Larsen (2001) sampled young aspen in 36 of these 43 stands, so our data include 36 stands from 1997-98 plus an additional 7 stands in 2011. The data from 1997-98 will be collectively referred to as "1998" data. A randomly placed 2x30 m plot was used to sample young aspen in each stand (Kay 1990), most stands being small and widely separated from other stands. If a plot had <15 young aspen >1 year old, the plot was extended in increments of 30 m^2. Conifer cover in each stand was classified as 0 (none), 1 (<10% cover), 2 (10-50% cover), and 3 (>50% cover).

In this discussion, "trees" are >5 cm dbh (diameter at breast height); "young aspen" are ≤5 cm dbh including "saplings" which are ≥200 cm in height but ≤5 cm dbh. For saplings and trees in the sample plot we recorded the species and dbh. For young aspen in the sampling plot, we recorded height and browsing status (browsed or not) of the top leader for fall 2011 and spring 2011. In addition to random plots, we selected the five tallest saplings in each aspen stand and used bud and browsing scars to measure browsing rates and heights for all previous years (Ripple and Beschta 2007). We counted the number of boulders and fallen trees (logs) >30 cm high within 3 m of the sampling plot, and also within 3 m of the five tallest saplings.

As an index to relative use of a site by ungulates – elk, mule deer, moose, cattle and horses – we counted fecal piles in four 2x50 m sampling plots spaced 7 m apart. Plots were placed near the edge of an aspen stand in the closest open area, generally in sagebrush grassland or open woods (see Methods, Chapter 3 this dissertation). Aspen stands were categorized as having "wild ungulates", or "wild ungulates plus livestock" based on presence or absence of livestock fecal piles, and known accessibility to livestock.

In 1998 data, young aspen heights were classified as ≥100 cm or ≥200 cm. We compared heights between 1998 and 2011 by calculating the proportion of young aspen ≥100 cm or 200 cm in a plot. Browsing rate was defined as the percentage of young aspen <200 cm tall that were browsed in the previous year (summer through spring). Annual leader growth or leader length was calculated as the difference between the fall height and spring height in 2011, providing an index for site productivity. Values for mean height, mean leader length, and browsing rate were calculated for each stand as the basic sampling unit, and bootstrapping (Efron and Tibshirani 1993) was used to estimate a bias-corrected 95% confidence interval (CI) for mean values in 1998 and 2011 to compare for significant differences. Bootstrapping was used because the 1998 data distribution was skewed, and the variance was much smaller than in 2011 (Fig. 4.2a). We also compared the proportion of plots containing at least one young aspen ≥200 cm, using logistic regression to estimate the odds ratio between the years and the proportion in each year (plot size was limited to 2x30 m for this calculation to avoid biasing the comparison to 1998). Statistical significance was assumed for p-values <0.05.

In the 1998 aspen data, aspen sprouts that were new in the summer and had not been exposed to winter browsing were not identified. Inclusion of these new sprouts resulted in a slightly lower annual browsing rate estimate than was actually the case. We followed this method for comparison with 1998 data (Fig. 4.2), but for the separate analysis of 2011 data (Tables 4.1 and 4.2; Fig. 4.3) the browsing rate calculation did not include new sprouts or any >200 cm spring height. A t-test for unequal variance was used to test for differences with and without livestock in mean height and browsing rate in 2011, and to estimate CI for these variables.

We used multiple linear regression to select variables in models for browsing and height of young aspen (Table 4.2). Models were composed of variables likely to influence browsing or height including wild ungulate scat density, livestock scat density, leader length, and number of logs. For height in sampling plots we also included browsing rate. Livestock presence was included separately from livestock scat density. Where needed, variables were log transformed (natural log) for constant variance. Preliminary analysis suggested an interaction between logs and livestock presence, so we included this interaction term. Other variables such as aspect, slope and topographic position were not used because they were not well distributed among stands. The model with the fewest parameters and within two units of the lowest Akaike information criterion score (AICc, adjusted for small sample size) was selected as the best model (Burnham and Anderson 2002).

To judge the possible effect of winter severity, we calculated the cumulative daily snowpack water equivalent, SWE_{acc} (Garrott et al. 2003) by water year (Oct 1-Sept 30) for two Natural Resources Conservation Service (NRCS) SNOTEL stations closest to the study area: Wolverine (NRCS station 09E08S) and Evening Star (NRCS station 09E11S) (NRCS 2012). A t-test (equal variance) was used to test for difference between the mean SWE_{acc} in the time period before wolf reintroduction (1983-1998) compared to the period following wolf reintroduction (1999-2011), and linear regression to test for an overall trend. We also used linear regression to assess the trend in annual elk count data between 1992 and 2009 (unpublished data, WGFD), combined for Sunlight and Crandall.

4.5. Results

A scatterplot of height and browsing rate showed a general change toward less browsing and increased height in 2012 compared with 1997-98 (Fig. 4.2a). Mean browsing rate (not adjusted for new sprouts) was 85% in 1998, compared to 47% in 2011 ($p<0.001$, Fig. 4.2b). The percentage of young aspen ≥100 cm tall in a plot increased from 5% to 32% ($p<0.001$, Fig. 4.2b), and the percentage of saplings ≥200 cm increased from 2% to 7% ($p=0.05$); height variance also increased ($p<0.001$). The odds of a plot having at least one aspen sapling ≥200 cm tall were 4 times higher in 2011 than in 1998 ($p=0.01$; CI 2, 15), and the percentage of plots with saplings increasing from 14% to 40%. The distribution of sapling diameters showed an increase in the percentage of plots with saplings, and most were recent recruits of small diameter (Fig. 4.2c).

In 2011, height was inversely related to browsing and there was little variation in height where browsing intensity was relatively high (Fig. 4.3a) regardless of leader length (Fig. 4.3b). Summer browsing rates in 2011 averaged 5% in sampling plots. Spring height of the five tallest young aspen averaged 2.1 m, and increased steadily from 2003 to 2011 (Fig. 4.4). In 2011, 30% of stands had at least five saplings >200 cm in the entire stand, and 60% had at least one sapling. Median age of the tallest saplings (pooled) was 7 years, range (2, 10). We did not analyze browsing rates for the five tallest saplings because many were >200 cm tall. Conifer encroachment was as follows: 0-10% cover, 9 stands; 10-50%, 8 stands; >50%, 26 stands. Accumulated snow water equivalent (SWE_{acc}) for 1983-1998 (Fig. 4.5) was not significantly different from 1999-2011 (t_{27}=1.13, p=0.27,), and a fitted line had no discernible trend (R^2=0.0003, $F_{1,27}$=0.008, p=0.93). Snow accumulation was unusually deep in 1997, slightly below average in 1998, and above average in 2011 (Fig. 4.5).

In 2011, browsing rates were positively related to the density of both wild and domestic ungulates, as well as to leader length (Table 4.2). The best model also included the number of logs and an interaction between logs and livestock presence; this model explained 51% of the variation in browsing intensity (Table 4.2). The best model for young aspen height in sampling plots included both browsing and leader length but most of the variation in height remained unexplained by these variables. For the height of the five tallest young aspen, livestock presence or absence was the best predictor explaining 24% of variation.

Livestock

In 1998, only 4 of 36 aspen stands were free of livestock, compared with 14 stands (of 43) that did not have livestock in 2011. The difference was due to 8 stands in the Crandall Creek area where grazing stopped prior to 2011. All four stands without livestock in 1998 had very high browsing rates >98%, but in 2011 browsing in these four stands ranged from 6-56%, with an average of 30%. In 2011 the mean browsing rate was significantly higher in the 29 stands with livestock compared to the 14 stands without livestock (Table 4.1, Fig. 4.3a), and height variance was also significantly greater.

Ungulate scat counts and population counts

Elk fecal pellet group density averaged 18 groups/100 m^2, median = 12 groups/100 m^2, range (1, 51) (Fig. 4.6a). Livestock scat piles were 91% cattle (Fig. 4.6b) and 9% horse. Wild ungulate scat were 86% elk, 13% deer, and 1% moose. Wild ungulate scat totaled 75% of all counts, livestock 25%. Elk were present in all stands, and some of the stands with livestock also had the highest densities of elk pellet piles (correlation coefficient r=0.50), so it was not possible to clearly separate the effects of livestock from the effects of high elk densities. Stands without livestock also had relatively low elk densities (<12 pellet groups/100 m^2). Between 1992 and 2009, combined elk count numbers for Sunlight and Crandall had no overall trend (n==10, $F_{1,8}$=0.04, p=0.84).

4.6. Discussion

Recovery of aspen stands in the Sunlight/Crandall area was far from complete, but a patchy increase in recruitment has occurred consistent with a trophic cascade from wolves to elk to aspen. Reduced browsing was a likely cause of greater height, based on the evidence of high browsing intensity with suppressed recruitment in 1998 (Fig. 4.2), and the relationship between browsing and height in 2011 (Fig. 4.3a). These changes in aspen stand conditions were similar to changes we found by the same method in YNP (Chapter 2). The mean height of the five tallest young aspen in each stand increased steadily in recent years and averaged 210 cm in 2011, tall enough to escape elk browsing (Fig. 4.4), and 30% of stands had at least five tall saplings. The oldest aspen saplings sprouted about 2002, and half began after 2004, suggesting that herbivory was reduced by that time allowing these sprouts to survive. Recent growth of the tallest young aspen above the reach of elk is a further indication that browsing suppression has released in many stands and the gap in recruitment has begun to close (Fig. 4.1b, 4.2c). These results provide evidence of a trophic cascade benefiting aspen; however, other possible explanations must be considered.

Was the change in height meaningful, and was the change in browsing outside the normal range of annual variation? The height comparison between 2011 and 1998 was based on fall height due to limitations in the 1998 data; changes in climate such as a longer growing season (Wilmers and Getz 2005) could result in an ephemeral increase in fall height even if the leaders are later browsed in winter. However, the increase in sapling recruitment (Fig. 4.2c, 4.4) demonstrated that stands have been released from browsing for multiple years resulting in a significant increase in height. The winter of 1997 had unusually deep snow accumulations (Fig. 4.5) that could perhaps have caused unusual browsing rates in some stands, but browsing rates were consistently high in 1997 and 1998 (Fig. 4.2a) despite large differences in snow accumulation. Deep snows may have actually limited browsing in some stands (Brodie et al. 2011). The high browsing intensity in 1997-98 was consistent with the lack of sapling recruitment at that time, as the lower browsing intensity in 2011 was consistent with the greater height we observed. By similar reasoning, if the increase in height and recruitment of saplings were the result of increased annual growth instead of a release from browsing, then the stands with the tallest young aspen would be the ones with the greatest amount of annual growth, but this was not the case (Fig. 4.3b). Browsing intensity was a more important influence on the height of young aspen in 2011 than leader length, an index of annual growth (Table 4.2; Fig. 4.3). Though much of the variation in height remained unexplained and browsing rates certainly will vary from year to year, our results indicate a significant increase in height has occurred primarily due to a release from browsing.

Besides elk, cattle also can affect the growth of aspen (Kay and Bartos 2000), especially when added to the effects of elk (Fitzgerald and Bailey 1984, St. John 1995, Kimble et al. 2011a). In 1998, livestock grazed in all but four of the sampled aspen stands, but in those four stands browsing rates were very high (100%) suggesting that elk herbivory was intensive across the landscape so that cattle made little difference. In 2011, with lower browsing rates overall, the difference between stands with and without livestock (Table 4.1) and the relationship between browsing and livestock density (Table 4.2) suggest that browsing by cattle may be biologically significant. The interaction of logs and livestock presence as an explanatory variable for browsing suggests that logs inhibit browsing but not in stands with livestock, again pointing to browsing impacts from cattle; however, cattle scat densities were very low in about half of stands (Fig. 4.6b). While cattle may be responsible for some of the continued suppression of aspen and the removal of cattle from the Crandall area may have contributed to aspen recovery, the reduction in cattle grazing in Crandall does not explain the overall reduction in browsing, or the changes in stands that had no livestock in either 1998 or 2011. A substantial difference in browsing and height occurred in stands with or without livestock, pointing to a reduction in elk browsing.

Why was browsing by elk reduced? Were the changes in aspen stands due solely to a reduction in elk numbers, or did behavioral changes play a part? Even moderate elk population densities can result in suppression of aspen (White et al. 1998), and there was no evidence that the elk population in the Sunlight area has fallen to low densities that would likely result in reduced browsing and aspen release based on overall elk population density. The density of elk pellet groups indicated moderate to high densities of elk in most locations, many comparable to pellet count densities (20-40 groups/ 100 m^2) found in northern YNP in 1999 when elk population densities were very high (Ripple et al. 2001).

One possible explanation for the reduction in elk browsing is that wolves may have changed the distribution of elk, resulting in high concentrations in some areas and reduced densities in others. Studies in the Yellowstone area and Canada suggest that when wolves are part of the ecosystem, wintering elk move around more, and are more likely to form large groups in open areas (Hebblewhite and Pletscher 2002, Mao et al. 2005, Garrott et al. 2009, Gower et al. 2009, White et al. 2012). Hunting by humans also has significant effects on elk foraging behavior and habitat selection (Proffitt et al. 2009), and hunting has been reduced in the Sunlight area. Reduced hunting pressure could work together with predation risk from wolves to cause a redistribution of elk on the landscape. For example, some of the stands with the largest reductions in elk browsing and greatest amount of recruitment were located away from main foraging areas where elk congregate and scat densities were high. A greater tendency for elk to form groups and select more open areas since the return of wolves (Mao et al. 2005, Gower et al. 2009, White et al. 2012) could explain much of the reduction in herbivory in these peripheral stands.

Some aspen stands were recovering but others had a browsing intensity sufficient to suppress aspen recruitment; in 2012, ~40% of stands had browsing rates >60% with consistently short average heights (Fig. 4.3a). White et al. (1998, 2003) found sparse and patchy aspen sapling recruitment with “moderate” elk densities of 2-3 elk/km^2, but abundant saplings required low average elk densities of <2 elk/km^2. In northern YNP we found elk scat densities averaging 4 groups/100 m^2 in a sector of the range where elk density was <1 elk/km^2, and 11 groups/100 m^2 in an area of moderate elk density (2-3 elk/km^2) with less aspen sapling recruitment. These scat densities suggest that elk densities in the Sunlight/Crandall range were moderate to high in much of the range and aspen recruitment would be expected to be patchy as we have observed (Fig. 4.3a). Some stands have begun to recover but continued browsing suppression is likely to cause some stands to decline and die. While this does not constitute a full recovery of aspen stands, it is evidence of a trophic cascade from wolves to elk to aspen, and ensures that at least some stands will persist with new trees. Whether or not aspen recovery will expand in the future may depend on the extent to which declining calf recruitment decreases the Sunlight migratory elk herd (Middleton et al. 2013), on the ability of wolves in the area to survive conflicts with humans (Nelson et al. 2012), and on the extent of cattle grazing.

Coniferous trees covered >50% of the area in most aspen stands, suggesting that even with reduced browsing and increased recruitment, encroaching coniferous trees may eventually replace aspen stands if disturbances do not intervene to reset forest succession. Logging and fire are sometimes used as restoration tools to clear conifers and stimulate aspen reproduction, but these efforts are likely to fail if elk or livestock eat most of the new aspen shoots and prevent their growth (Romme et al. 1995, Bartos and Campbell 1998, Bergquist and Bergquist 2006). The recent reduction in browsing intensity in many stands suggests the possibility that predation by wolves could improve the outcome of aspen restoration efforts by reducing browsing impacts on new aspen shoots.

On the northern winter ungulate range in YNP, we found that a general aspen recovery followed a substantial decrease in elk population density resulting from large-scale shifts in population distribution (Chapter 2 this dissertation); however, some aspen stands began to recover much earlier than others (Chapter 3 this dissertation; Ripple and Beschta 2012b). This partial release is similar to what we found in the Sunlight/Crandall area. As in northern Yellowstone, the population distribution of the Clark's Fork elk herd may be shifting toward lower elevation, less risky areas (Middleton 2012), but so far average elk density has remained relatively high in the Sunlight Basin. The patchy release we observed appears to be due to a local rather than large-scale redistribution of elk herbivory impacts, perhaps due to changes in habitat selection or grouping behavior, and possibly influenced by small-scale factors such as logs on the ground or complex terrain.

This survey of aspen in the Shoshone National Forest adds to a growing number of studies that point to the importance of large predators in the ecology of plant communities and the structure of ecosystems (White et al. 1998, Hebblewhite and Smith 2010, Strong and Frank 2010, Ripple and Beschta 2012a). Lower browsing rates and increased heights of young aspen since wolves returned to the Shoshone National Forest support the hypothesis of a trophic cascade from wolves to elk to aspen causing a partial release from browing. This patchy recovery of aspen stands occurred without a substantial decline in average elk population density, suggesting that behavioral responses to predation at various scales may have contributed to aspen recovery through a redistribution of herbivory, reducing browsing in some places while possibly increasing it in others (White et al. 2003). Cattle may also be limiting aspen recovery, and stands without livestock showed the greatest change. Since the return of wolves to the Sunlight basin, browsing pressure on aspen has decreased sufficiently to allow a release of aspen growth and increased aspen recruitment in some aspen stands, providing some of the first evidence of a trophic cascade resulting from wolf restoration outside the boundaries of a national park.

4.7. Acknowledgements

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4.8. References

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Table 4.1. Browsing rates and heights in 2011, with 95% CI. Browsing rate estimate included only young aspen <200 cm spring height, but did not include new sprouts and so was slightly higher than in Fig. 4.2.

	% Browsed mean	% Browsed median	Height mean (m)	Height variance	Plot n
2011 all plots	52 (44, 60)	55	0.69 (0.55, 0.83)	0.213	43
2011 wild+domestic	61 (52, 69)	69	0.57 (0.48, 0.67)	0.058	29
2011 wild ungulates only	33 (19, 47)	30	0.92 (0.52, 1.32)	0.478	14
Test for difference: wild+domestic = wild ungulates?	p=0.001, t=3.6, df=25		p=0.09, t=1.8, df=15	p<0.001, F=8.3, df=13,28	

Table 4.2. Selected models (bold type) and reduced models for browsing and height of young aspen (n=43); the sign for each term indicates the sign of the regression coefficient. Columns list difference in AICc score compared to selected model (dAICc), adjusted R^2, and degrees of freedom (df) for the regression model.

Model	dAICc	adj R^2	df
BROWSING RATE IN SAMPLING PLOTS			
(Browsing)~ +ln(Wild Scat) +(Leader Length) –(Stock Present) –Logs +(Logs*(Stock Present))	**0.0**	**0.51**	**5, 37**
(Browsing)~ +ln(Wild Scat) +ln(Livestock Scat) +(Leader Length)	3.2	0.44	3, 39
(Browsing)~ +ln(Livestock Scat) +(Leader Length)	3.8	0.41	2, 40
(Browsing)~ +ln(Wild Scat) +(Leader Length) +(Stock Present)	4.9	0.41	3, 39
(Browsing)~ +ln(Wild Scat) +ln(Livestock Scat)	7.0	0.37	2, 40
(Browsing)~ +ln(Wild Scat) +(Leader Length)	7.9	0.35	2, 40
(Browsing)~ +ln(Livestock Scat)	10.3	0.27	1, 41
(Browsing)~ +ln(Wild Scat)	13.2	0.27	1, 41
(Browsing)~ +(Leader Length)	12.8	0.27	1, 41
(Browsing)~ +ln(Stock Present)	14.3	0.25	1, 41
HEIGHT IN SAMPLING PLOTS			
ln(Height)~ –(Browsing) +(Leader Length)	**0.0**	**0.27**	**2, 40**
ln(Height)~ –(Browsing)	3.6	0.20	1, 41
ln(Height)~ +(Leader Length)	13.4	0.001	1, 41
ln(Height)~ –(Stock Present)	10.1	0.08	1, 41
HEIGHT OF FIVE TALLEST			
Height~ –(Stock Present) +(Leader Length)	0.1	0.23	2, 40
Height~ –(Stock Present)	**0.0**	**0.24**	**1, 41**
Height~ –(Wild Scat)	6.5	0.11	1, 41
Height~ +(Leader Length)	11.2	0.007	1, 41

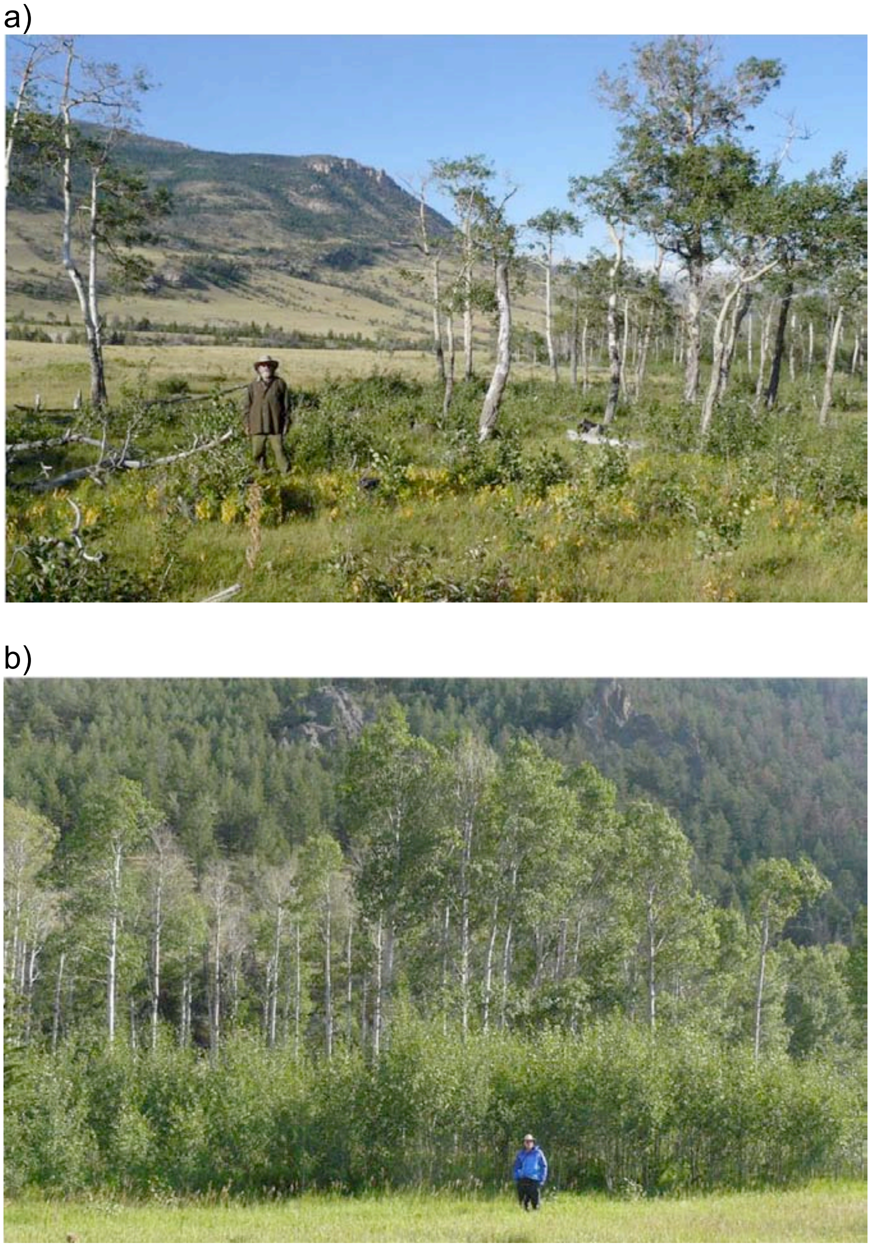

Figure 4.1. Sapling recruitment in aspen stands was highly variable.
(a) Aspen stand with little recent recruitment of saplings.
(b) Aspen stand with a gap in recruitment that has begun to close with new saplings.

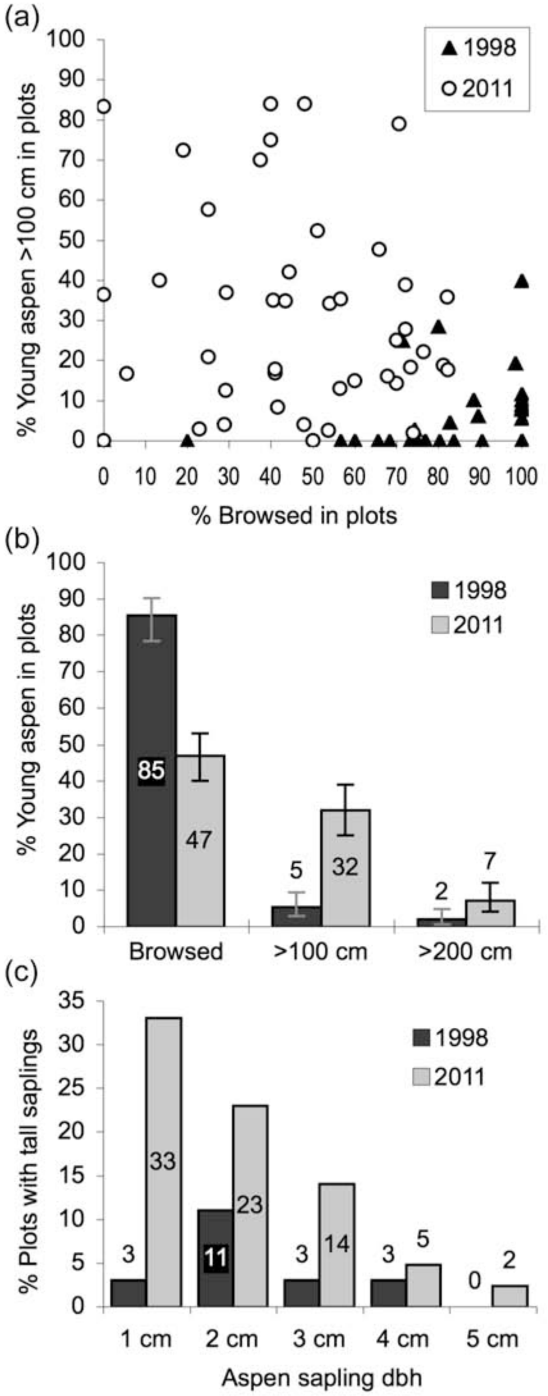

Figure 4.2. Comparison of aspen stand conditions between 1998 (n=36) and 2011 (n=43). (a) Browsing rate and percentage ≥100 cm tall; each point represents an aspen stand. (b) Changes in percent browsed, percent ≥100 cm, and percent ≥200 cm; values were calculated by plot, then averaged across plots. Bars show 95% CI. (c) Percentage of plots with one or more saplings (≥200 cm) in five dbh classes.

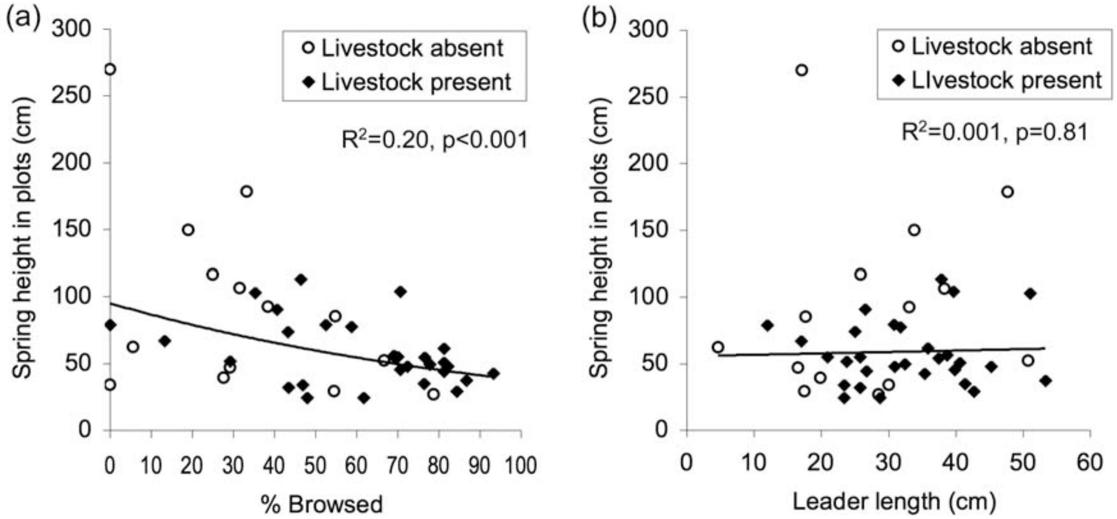

Figure 4.3. Regression lines fitted to the logarithm of height, including 29 plots with livestock and 14 without.
(a) Mean height and height variance in 2011 decreased with increasing browsing intensity.
(b) Height as a function of leader length, an index of site productivity.

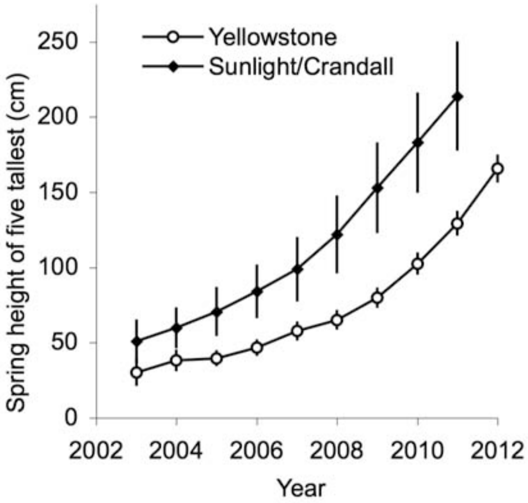

Figure 4.4. Mean spring height of the five tallest young aspen in each stand, using plant architecture to measure past height. YNP data were collected in 2012 (Chapter 2). Height release appears to have occurred about the same time in the two areas, but the rate of height increase has been slower in Yellowstone, perhaps due to higher elk densities and greater suppression before recent changes (Larsen and Ripple 2005). Average leader length of the five tallest was 48 cm in Yellowstone in 2012 and 46 cm in Sunlight in 2011.

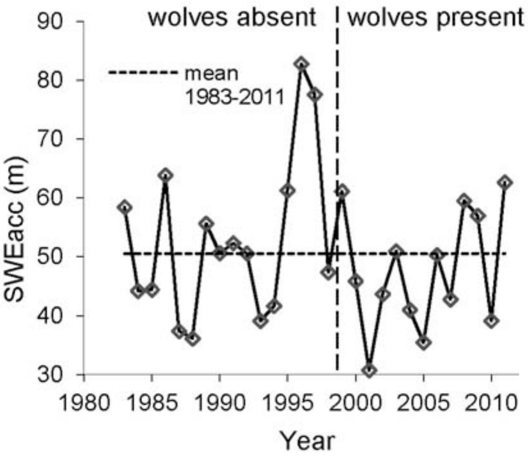

Figure 4.5. Accumulated snow water equivalent (SWE_{acc}) averaged for two SNOTEL climate sites closest to the study area showed no overall trend, and no significant difference before or after 1998.

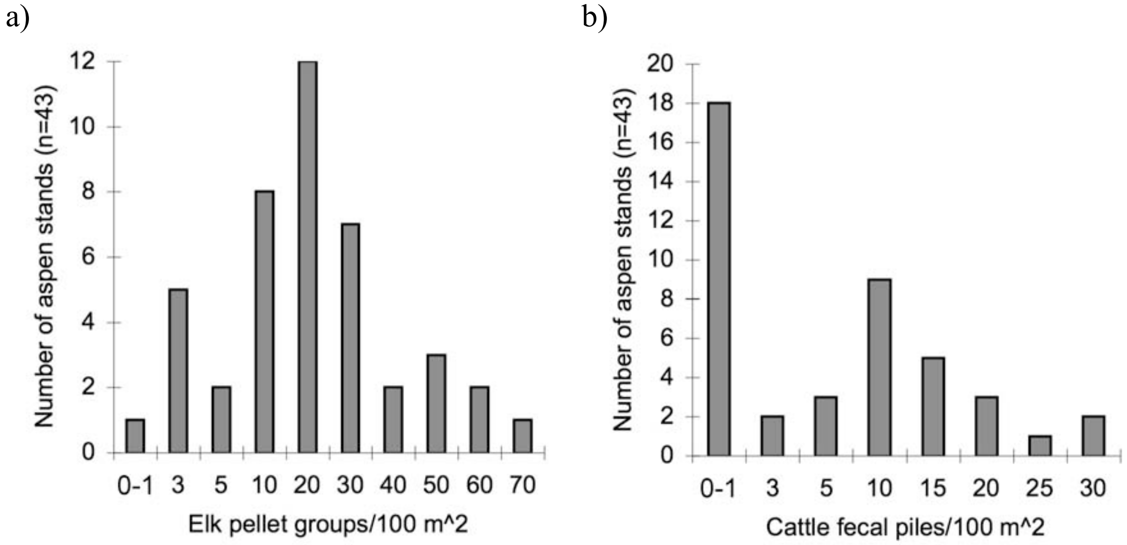

Figure 4.6. Histograms of fecal pile areal densities in 2011 at 43 aspen stands in the Sunlight/Crandall elk winter range for (a) Elk and (b) cattle. Elk were present at all stands, cattle were absent from 14 stands.

5. EFFECTS OF BISON ON WILLOW AND COTTONWOOD IN NORTHERN YELLOWSTONE NATIONAL PARK

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5. EFFECTS OF BISON ON WILLOW AND COTTONWOOD IN NORTHERN YELLOWSTONE NATIONAL PARK

5.1. Abstract

On the northern ungulate winter range of Yellowstone Park, willow and cottonwood have increased in height and cover in some places since the reintroduction of wolves and the subsequent changes in elk behavior and population densities. However, in the Lamar Valley, an important part of this winter range, many plants are still intensively browsed and recruitment has been limited. As elk numbers have declined and their distribution has changed in recent years, bison have increased on the northern range. To distinguish bison effects from those of elk, we measured browsing that occurred in summer. We found average summer browse rates of 84% for willow and 54% for cottonwood seedlings in the summer of 2010, demonstrating that bison have become significant browsers in the Lamar Valley. Plants were increasing in size except where intensively browsed by bison, suggesting that a release from elk browsing has occurred, and that a trophic cascade is occurring from wolves to plants, mediated by both elk and bison. Release of bison from competition with elk, low levels of predation on bison, and lack of opportunity for migration and range expansion may be factors contributing to a high concentration of bison, with resulting effects on plant communities and biodiversity.

5.2. Introduction

Some ecosystems of western North America were shaped in the past by bison (*Bison bison*) and the ecological effects of these iconic animals may again be a factor, with recent efforts to restore them to portions of their former range (Sanderson et al. 2008, Gates et al. 2010). In Yellowstone National Park, elk (*Cervus elaphus*) numbers have decreased following wolf (*Canis lupus*) reintroductions in 1995 and 1996, but the bison population has continued to grow, maintained below a peak of about 5000 by large-scale culling when bison leave the park in winter (White and Garrott 2005b, Plumb et al. 2009, White et al. 2010, 2011). White et al. (2011) reported that current management practices, in which bison are kept close to park boundaries in winter and hazed back into the park in early spring, are likely to lead to high population densities and density-dependence among bison, possibly causing deterioration of range resources and ecological processes.

Valleys in the northern part of Yellowstone National Park are used as winter range by elk, bison, and other ungulates (Singer and Norland 1994). In this area, called the northern ungulate winter range, or "northern range," willow (*Salix* spp.), cottonwood (*Populus angustifolia* and *P. balsamifera*) and aspen (*Populus tremuloides*) declined in the 20th century, primarily due to browsing by elk in winter (Kay 1994, Chadde and Kay 1996, Singer 1996, Keigley 1997, 2000, Romme et al. 2001, NRC 2002, Barmore 2003, Singer et al. 2003, Beyer 2006, Wagner 2006). Beaver (*Castor canadensis*), which depend on these plants, also declined in number and range resulting in loss of wetlands and further decline of willows (Wolf et al. 2007, Bilyeu et al. 2008, Smith and Tyers 2008). Since the return of wolves to the northern range, elk population size, spatial distribution, and foraging behavior have changed (Laundré et al. 2001, Hernandez and Laundre 2005, White et al. 2010, 2012). Probably as a result of these changes, woody browse plants have increased in height and cover in some places (Ripple and Beschta 2006, Beschta and Ripple 2007, Beyer et al. 2007, Ripple and Beschta 2012), and beaver have increased in number and range (Smith et al. 2003, Smith and Tyers 2008). For example, few cottonwood trees grew to maturity on the northern range after the early 20th century (Beschta 2005), and cottonwood saplings were kept short (<1 m) by browsing

(Keigley 1997, Beschta 2003). Between 2001 and 2006 cottonwoods again began to grow tall enough to begin to escape elk browsing (>2 m) in places along the east edge of the Lamar Valley, on an island in the Lamar River, and on Soda Butte Creek (Ripple and Beschta 2003, Beschta and Ripple 2010). Willows also increased in height in some places (Ripple and Beschta 2006, Beschta and Ripple 2007). However, in most of the Lamar Valley, west of the Soda Butte Creek confluence (Fig. 5.1), the median cottonwood sapling height remained the same or decreased, and many willows and young cottonwoods were intensively browsed (Beschta and Ripple 2010).

Use of the Lamar Valley by wintering elk has declined since wolf reintroduction, due to lower elk numbers and a decrease in the proportion of the elk population wintering on the east side of the range (White et al. 2010, 2012). Meanwhile, bison on the northern range increased from 455 in the summer of 1997 (following the removal of 725 the previous winter), to 2070 bison in 2007, the highest count on the northern range in the history of the park (Meagher 1973, White et al. 2011). Since 1984 bison have congregated in the Lamar Valley in summer as well as winter, and some bison have moved from central Yellowstone to the northern range (Taper et al. 2000, Gates et al. 2005, Fuller et al. 2007). Ripple et al. (2010) hypothesized that the bison increase on the northern range may be part of a secondary trophic cascade, where wolves reduced elk density, thereby releasing bison from interspecific competition, resulting in higher bison densities and greater effects from bison on forage plants. Researchers reported seeing bison browsing in the summer season (Beschta 2003, Beschta and Ripple 2010), and found willow height to be inversely related to the density of bison fecal piles (Ripple and Beschta 2006). Significant browsing in summer on the northern range had not previously been reported, nor has browsing by bison (winter or summer) been regarded as an important factor in the ecology of the area by most researchers, who have generally assumed that bison had little effect on browse plants (Singer et al. 1994, Singer and Norland 1994, Keigley 1997).

Are bison affecting the growth of willow and cottonwood in the Lamar Valley? Summer browsing can distinguish the effects of bison from those of elk, because elk are scarce in the valley in summer. Also, tall willows may be used to compare browsing between heights accessible only to elk, and heights accessible to both bison and elk (Fig. 5.2). We measured the effects of browsing, differentiated by height and season, to answer three questions regarding willow and cottonwood in the Lamar Valley: 1) are these plants suppressed by browsing, 2) how much browsing occurs in summer, and 3) what proportion of browsing can be attributed to bison?

5.3. Study Area

The northern ungulate winter range in the Greater Yellowstone Ecosystem is comprised of open valleys with steppe and sagebrush-steppe vegetation, bordered by slopes with coniferous forest interspersed with aspen groves (Singer and Norland 1994, Barmore 2003, Gates et al. 2005). Willow bushes are present in riparian areas and wet meadows throughout the northern range, but cottonwood trees are limited to the larger river valleys (NRC 2002, Beschta 2005, Beyer 2006, Beschta and Ripple 2010). Elk and bison share the winter range with smaller numbers of moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and bighorn sheep (*Ovis canadensis*) (Singer and Norland 1994, Barmore 2003).

Study sites were located in the Lamar Valley, a floodplain of the Lamar River about 1 to 2 km wide, extending about 9 km from the area of the confluence with Soda Butte Creek on the east to a small canyon called Lamar Canyon on the west (Fig. 5.1). All study sites were west of the Soda Butte Creek confluence. Willow study sites were in wet meadows on the river floodplain, with an additional site along Oxbow Creek about 20 km west and north of Lamar Valley, near where the creek crosses Grand Loop Road (Fig. 5.1, 5.3). Cottonwood study sites were within the active channel of the Lamar River, where thousands of cottonwood seedlings grow on gravel bars in the wide, shallow, meandering river bed, flanked by meadows of grasses and sedges on the sides of the river (Fig. 5.4). All study locations were within the winter ungulate range.

5.4. Methods

Field data were collected between August 20 and September 9, 2010. Plant measurements were similar for willow and cottonwood, but sampling methods were different. Browsing intensity was measured by the percentage of browsed leaders (browsing rate) in the current summer and previous year, the mean length of leader growth since last browsing (growth-since-browsing), and for cottonwood saplings, the mean spring height. We also noted damage from horning (bison thrashing bushes with their horns), and the height of browse-killed stems, defined as a dead stem with at least three terminal twigs at least one of which was pruned by browsing (Keigley 1997). Season of browsing and growth-since-browsing were determined by examining plant growth architecture, following Keigley and Frisina (1998) and Keigley et al. (2002). Season of browsing was determined by counting the terminal bud scars on the stem. Growth-since-browsing (Keigley's Live-Dead index) was calculated as the difference between the spring height of a stem (the base of current annual growth) and the most recent browse height of the stem, as indicated by the browsed stub (spring height – browse height = growth-since-browsing). Growth-since-browsing compares the current (spring 2010) height of the plant to the height at which it was previously clipped by browsing. This indicator of growth suppression is independent of the height or age of the plant. A strong positive number indicates plants that are growing larger and not suppressed, whereas a negative or small positive number indicates plants suppressed by browsing, because the new growth is lower than or similar to the previous browse height. This occurs when a stem starts a new leader below a leader that was killed by browsing.

Willow Methods

There were few tall willows in the Lamar Valley, so it was possible to locate all willows taller than 2 m on the Lamar Valley floor (between Lamar Canyon and the confluence with Soda Butte Creek, to the toe of the slope around the valley), and collect data on growth and browsing for all that met the sampling criteria. Height was measured as the spring height, at the base of current annual growth. Willow sites, both in Lamar Valley and Oxbow Creek, were in flat, wet meadows watered by groundwater. Willows within 20 m of a road, in the active channel of the river, or in areas inundated by recent spring river floods were not included, because these factors could affect accessibility and browsing, and flood damage could obscure browsing effects. Most tall willows had a large canopy, but some had few live stems, or were severely damaged by horning, and these were not included. For comparison to the Lamar Valley, we also measured willows on Oxbow Creek, where summer bison use appeared to be very slight (confirmed by scat counts, see Results). All willows shorter than 1 m within the tall willow sites were also measured, using the same methods detailed above for tall willows. Willow bushes in a clump were sampled as a unit if their canopies merged. In the sampled locations willows did not form continuous thickets.

To help distinguish the influences of bison and elk, each tall willow bush or clump was divided into two browsing height zones, a lower zone below 1 m accessible to all ungulates, and an upper zone from 1.5 m to 2 m easily accessible to elk but not bison. A pilot study showed that almost all bison browsing occurs below 1 m (authors' unpublished data). Stems between 1 m and 1.5 m are unlikely to be browsed by bison, but could have a small amount of bison browsing; therefore, measures in this middle height zone would be ambiguous as indicators of browsing by bison, and were not used.

In each height zone we measured four leaders, for a total of eight leaders per bush. Sampled leaders were representative of those most accessible to browsing ungulates, and leaders that were inaccessible to browsers due to dead stems or other obstructions were not included. For those few stems that had never been browsed, the height at which the stem grew beyond browsing obstructions was substituted for the most recent browse height. We sampled an additional 12 leaders in each height zone to estimate the browsing rate for the current summer (2010) and for the previous year (summer 2009 to spring 2010), so browsing rates were based on 16 leaders in each height zone. For each bush we also measured the height of three of the oldest browse-killed stems (Keigley 1997). Variables were averaged for each bush or clump for each height zone, with 95% confidence intervals (*t* distribution), and compared between the two height zones. Because this comparison was between upper and lower heights on the same plants, topographic site variables were ruled out as confounding factors. Browse rates and growth-since-browsing were also compared between willow sites at Lamar and those at Oxbow Creek; these sites were all within the winter range of elk and bison, and were similar in slope, elevation, and water availability.

Cottonwood Methods

Young cottonwood seedlings and saplings occurred in dense “stands” in discrete sites on alluvial bars along the Lamar River. These sites were relatively homogeneous in age and density, with hundreds of seedlings distributed in a long band on a gravel bar (Fig. 5.4). Many plants were short (<1 m) and hedged, with a bush growth form. We sampled all stands that were longer than 50 m and with most plants older than 3 years, based on the growth visible above the ground. Each stand was a separate study site and sampling unit. For each site, data collected included length, width, distance from river bank, and height above water.

A line transect was placed through the centroid along the long axis of each site, and every 5 m the plant nearest to the line was measured. For the shortest site, 75 m in length, the sampling interval was shortened to 2.5 m. If the nearest plant was covered with debris above the base of current annual growth, or had less than 3 years of growth visible, or appeared diseased or dying, the next closest plant was chosen. In addition, the tallest cottonwood bush in each 50 m segment (25 m in the smallest site) was measured, as an indication of the leading edge of growth. For each plant we measured the leader with the tallest spring-time height. The field data were used to calculate browsing rate, mean height, mean height of browse-killed stems, and mean growth-since-browsing for each of the seven sites. These quantities were compared using 95% confidence intervals (*t* distribution) to ascertain significant differences among sites, and between height and browse-killed stem height within the same site. The relationship between mean plant height and height above water was analyzed using simple linear regression, to assess the possible influence of water availability. In Site 6, where cottonwood saplings were taller with a single-stem growth form (Fig. 5.4b), the browse status and height for previous years were also recorded.

Indications of Ungulate Use

The amount of use the study sites received by bison, elk or other ungulates was evaluated based on counts of fecal piles, along with other evidence such as the presence of tracks, wallows and hair, and sightings of the animals. Fecal piles were counted in plots (belt transects) 2 m wide, extending for the length of the wet meadow or cottonwood site. For willows, plots were spaced 10 m apart to the edge of the wet meadow containing the willows. For cottonwood, there were two plots in the site and two on the adjacent bank, separated by 4 m. Fecal piles were categorized as from the current summer or a previous season, as determined by color, state of decomposition, and relationship to growing vegetation.

5.5. Results

Willow

Of 53 tall willow clumps found in wet meadows on the floor of the Lamar Valley, 18 were rejected because of extensive horning damage (almost all had some horning damage), and three were rejected because their few leaders were protected from browsing by dead branches. Some tall willows growing along the river bank near the east end of the valley were excluded by the decision to limit sampling to wet meadows. The sampled willows included 20 tall willow bushes or clumps in the largest wet meadow and 12 from five additional locations, for a total of 32 in the Lamar Valley (Fig. 5.3a). The largest clump was 8.6 m by 4.3 m, the smallest 1.7 m by 0.5 m (the widest extent of live branches). The Oxbow Creek site contained 14 tall willow clumps that met the sampling criteria (Fig. 5.3b). Unlike Lamar, none were rejected due to horning damage and all had full canopies with many leaders. Height ranged from 2.2 to 5.2 m in Lamar (mean 3.5, standard error 0.1), and from 2.3 to 4.2 m in Oxbow (mean 3.1, standard error 0.1). All tall willows and most short willows sampled were Geyer willow (*Salix geyeriana*); some short willows were Booth (*S. boothii*) or Bebb (*S. bebbiana*) willow species.

Measures of browsing intensity at low height in Lamar Valley were significantly different (*t* test, 95% confidence) from the upper height in Lamar, and also different from either height in Oxbow. These differences were very pronounced (Fig. 5.5). Differences in browsing intensity between upper and lower heights in Oxbow were small, but still statistically significant for growth and previous year browse rate.

In the Lamar Valley willow sites, short willows far outnumbered tall willows (196 short/ 32 tall), but in Oxbow there was a much smaller proportion of short willows (26 short/ 14 tall). For short willows, the summer browsing rate was 88% in Lamar and 0% in

Oxbow. Previous year browsing was 100% and 72%, respectively; growth-since-browsing was -3 cm and 7 cm.

Cottonwood

There were seven cottonwood sites that met the sampling criteria (at least 50 m long with most saplings older than 3 years) along the Lamar River from near the confluence with Soda Butte Creek to the beginning of Lamar Canyon (Table 5.1). These seedling patches ranged in length from 75 m to 250 m, and in width from 11 m to 52 m. All were in the active channel of the river, and drift accumulations indicated that four of the seven sites were flooded in the spring of 2010. Most plants were in the form of small bushes (Fig. 5.4a), an indication of intensive browsing (Keigley 1997), and the mean summer browsing rate was 54%. Plants were generally shorter than 1 m except in Site 6 (Fig. 5.4b), but even there the mean spring height was shorter than 1 m (Table 5.1, Fig. 5.6). Growth-since-browsing was strongly and inversely correlated with summer browsing rate, with both variables log transformed in a linear regression (r^2=0.92, p<0.001, n=7); height was also strongly correlated with summer browsing (r^2=0.69, p<0.02, n=7). Most of the top leaders were browsed in the summer of 2010 preventing direct measurement of current annual growth and productivity, but all of the sites were in a similar landscape position in the active river channel, and there was no significant relationship between mean spring height and height of the plants above water (Table 5.1; linear regression, r^2=0.03, p=0.70). Mean spring height was not significantly different (*t* test, 95% confidence) from the mean height of browse-killed stems, except in Sites 1 and 6 where the summer browse rate was low, and this difference was much greater in Site 6, with the lowest summer browse rate. Of the selected saplings in cottonwood Site 6, 19% were too damaged by horning to be measured for browsing, so the next closest sapling was used.

Ungulate Use

Bison fecal piles were abundant in sampling plots in the Lamar Valley (Table 5.2), along with wallows and many bison tracks, horned bushes, and clumps of bison hair; there were many bison in Lamar, sometimes browsing willows or cottonwoods (Fig. 5.2). In contrast, no elk pellet piles or tracks from the 2010 summer season were found in either the Lamar Valley or the Oxbow Creek study sites. All bison fecal piles counted in sample plots were found in Lamar, none in Oxbow. The difference in total number of scat piles counted for bison compared to other ungulates was very large in Lamar Valley (Table 5.2). In both Lamar and Oxbow some elk and bison scat piles from previous seasons were present in the area.

5.6. Discussion

Willows and cottonwoods in the Lamar Valley were browsed at a high rate, and much of this browsing occurred in the summer season, when herds of bison were present and elk were scarce. Most browsing occurred at low height, and browsing rates were much less at heights above the reach of bison (Fig. 5.5). The season, height, and rate of browsing demonstrate that browsing by bison in summer was common, and that bison were responsible for a large proportion of annual browsing of terminal leaders, enough to suggest a significant ecological effect. For both cottonwood and willow, high summer browsing rates were associated with severely restricted growth (Fig. 5.5, 5.6). For tall willows in the Lamar Valley, mean growth-since-browsing was negative (-3 cm) at heights below 1 m, showing that stems have not grown back to the heights at which they were previously browsed, a characteristic of bushes that are severely hedged by browsing (Keigley and Frisina 1998, Keigley et al. 2002). On the same bushes, growth-since-browsing was strongly positive (36 cm) at heights from 1.5 to 2 m, demonstrating that these same willows have been increasing in size at heights accessible to elk but not bison. Similarly for willows shorter than 1 m in the Lamar Valley sites, growth-since-browsing was -3 cm, indicating suppressed growth.

If elk were primarily responsible for browsing willows in the Lamar Valley, then the browsing rate would likely be similar in the lower part of a bush and the upper part, because elk can reach the entire height range. Also, the browsing rate should be very low in summer, because the study locations are in elk winter range, with few elk in summer. The summer browsing rate in Lamar was nearly zero in the upper height zone, but very high, 84%, at low height below 1 m (Fig. 5.5). The high summer browse rate is strong evidence that bison are eating most of the accessible leaders before the end of the summer. Browsing below 1 m was also very intensive in the previous year (summer 2009 to spring 2010), with 100% of sampled leaders browsed, as compared to 28% above 1.5 m. Short willows had similar browsing rates, 88% in the summer. The severely hedged condition of willows in the low height range (Fig. 5.3a), and the negative growth-since-browsing (Fig. 5.5), indicate that the high browsing rate measured in the summer of 2010 may represent the typical browsing intensity for recent years.

For cottonwood, measurements were compared across the seven cottonwood sites (Fig. 5.6). Four sites had summer browsing rates greater than 50%, and two were greater than 90%, with an average of 54%. Growth was suppressed in six of the seven sites as indicated by short average height (<1 m), hedged growth form, and low growth-since-browsing. Only Site 6, with summer browsing rate of 13%, had saplings close to 2 m in height (Table 5.1, Fig. 5.4). This site was farther out in the river channel than the other sites, and was shaded in winter by a tall adjacent slope, factors that may have reduced browsing and allowed cottonwood saplings to grow taller once pressure from elk was reduced.

There was no evidence of elk in the Lamar Valley in summer, either from pellet counts, field sightings, or other evidence, and the area is not considered part of elk summer range. Elk pellets from any season were rare; only 1 elk pellet pile was found in 12,620 m^2 of scat sampling plots (Table 5.2). Although detectability was poor in many of these plots, the low elk pellet density is consistent with a major reduction in elk use of the eastern portion of the northern range over the last decade, as reported by White et al. (2010, 2012). It was probably during this period of declining elk density that the tall willows in the Lamar Valley grew beyond the reach of elk to their present height; tall willows were not reported in the area previously (Kay 1990, Chadde and Kay 1996, Ripple and Beschta 2006, Beyer et al. 2007). This increased height of willows is evidence of a trophic cascade from wolves to plants; if the increase in bison density is a response to reduced elk density, then the bison increase and their resulting effect on plants would represent an additional pathway associated with this trophic cascade (Ripple et al. 2010).

No evidence of moose or deer was found in the Lamar Valley study sites. At Oxbow Creek, deer trails and bedding areas were present among willows, yet summer browsing was minimal, 0.5% percent. Given the clear evidence of deer in Oxbow Creek with little summer browsing, and the lack of any evidence of deer in the Lamar Valley where browsing rates were very high, it is reasonable to conclude that deer were not responsible for the summer browsing of willow and cottonwood observed in the Lamar Valley. Pronghorn were present in the Lamar Valley in summer, in much smaller numbers than bison (Table 5.2). Studies of the diet and habitat selection of pronghorn on the northern range and elsewhere have found little evidence of willow or cottonwood consumption (Singer and Norland 1994, Barmore 2003, Jacques et al. 2006, Boccadori et al. 2008). Low numbers and dietary preferences make it unlikely that pronghorn are having a significant effect on growth or browsing rates of browse plants.

Where plants are intensively browsed in summer, as in Lamar Valley, tall willows are constricted below the height at which they are accessible, creating a clump with a mushroom shape. The lower stems are continually clipped but the upper stems continue to lengthen (Fig. 5.2a, 5.3a). This shape, called "highlining," is seen in many of the tall willows in the Lamar Valley, but where bison are less numerous, as at Oxbow Creek (Fig. 5.3b), willows become full with new growth in summer and have a roughly hemispherical shape. In the Lamar Valley, the low height of this growth suppression suggests that bison, not elk, are now the primary browsers.

All tall willows had browse-killed stems with browse brooms (clusters of browse-killed twigs), an indication of past suppression of growth. In the Lamar Valley the mean height of these stems was 147 cm (SE=3.6), and in Oxbow 108 cm (SE=8.3). The fact that these plants are now growing well beyond this previous growth limit is further evidence that they have experienced a release from elk browsing (Keigley and Frisina 1998). They were previously suppressed by elk, but now are growing freely at those heights.

In six of the seven cottonwood sites, the spring height was very close to the height of browse-killed dead stems (Fig. 5.6). This strongly suggests cottonwood saplings at these sites are stunted by browsing, limited to about the same height as the old leaders killed by browsing. The exception is cottonwood Site 6, where live leaders were much taller than browse-killed stems, indicating that something has changed about the browsing and growth dynamics at this site (Fig. 5.4b). In the previous year (summer 2009 to spring 2010) in Site 6, stems shorter than 1 m were browsed at a rate of 45%, while those taller than 1 m, above the reach of bison, were not browsed at all, suggesting that recent browsing has been due to bison and not elk.

The results of this study make possible an evaluation of alternative explanations for the fact that willow and cottonwood growth in the Lamar Valley has been generally less than in some adjacent areas of the northern range, such as the upper Lamar River and Soda Butte Creek (Ripple and Beschta 2003, Beschta and Ripple 2010). One hypothesis could be that there has been no trophic cascade sufficient to release plants from elk browsing. The pronounced changes in height and cover of willow and cottonwood in areas peripheral to the Lamar Valley in conjunction with the recent decline in elk density make this “no-effect” explanation unlikely. An alternative hypothesis is that wolves have caused a release of vegetation by reducing elk browsing, but bison are having an increased effect on plants, counteracting the reduced effects of elk – a secondary trophic cascade (Ripple et al. 2010). The evidence from this research supports this second explanation, for three reasons: 1) plants grew larger and taller where they were beyond the reach of bison, demonstrating release from the effects of elk; 2) browsing rates were very high in summer, when elk were absent, therefore, elk could not have been responsible for most of the browsing of new leaders, because bison consumed them first; and 3) plant growth was suppressed by browsing where the summer browse rate was high, showing that browsing by bison has been affecting plant growth. This growth suppression, and the fact that browsing rates for the previous year were high, are evidence that the summer browsing rates observed in 2010 are indicative of a multi-year pattern. The comparison between the lower portion and the upper portion of the same willows shows that differences in site moisture or productivity were not significant factors, as does the similarity in landscape position of cottonwood sites.

The bison of Yellowstone today differ from their pre-settlement ancestors in two important ways. First, bison are prevented from moving freely or expanding their range outside the park (White et al. 2011). Second, bison in Yellowstone experience very low predation pressure, compared to what was likely in the past with hunting pressure from humans, and larger numbers of wolves focused on bison (Young and Goldman 1944, Carbyn 2003, Kay 2007). Even if predation was compensatory in ancient times and bison numbers were high, it is likely that predation pressure would have caused bison herds to move, perhaps long distances, as occurs with Canadian bison and wolves (Carbyn 1997). These differences – freedom to move and greater predation pressure from humans and wolves – make it unlikely that bison would have concentrated in the Lamar Valley in the past as they do today, even if they were present in the region in similar numbers.

The consequences of preventing bison movement may extend beyond the bison population to the ecology of the range, in summer as well as winter. The potential effects of bison and other large ungulates include suppression of woody plants and changes in plant communities (Meagher 1973, Coppedge and Shaw 1997, Baker 2003, Gates et al. 2010, Martin et al. 2011). Bison have the potential to limit recovery of willow and cottonwood in the Lamar Valley, and possibly elsewhere in the Yellowstone area. Lack of willow and cottonwood could slow or prevent colonization by beaver and other species, with cascading effects on plant communities, stream morphology, and biodiversity (Kay 1994, Smith and Tyers 2008, Baril 2009, Beschta and Ripple 2010, 2011). Bison, cottonwood, willow and beaver evolved together, but the effects of bison may be more pronounced in Yellowstone today, where bison occur at higher densities and with less movement than was likely when they and the people and other predators that hunted them roamed freely across the landscape.

5.7. Acknowledgements

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Table 5.1. Mean data values for seven cottonwood sites in the Lamar Valley.

Site	Browse Rate (%) Summer	Spring Height (cm)	Browse-killed Height (cm)	Growth Since Browse (cm)	Three Tallest Height (cm)	Height Above Water (cm)	Count
1	23	46	39	6.2	60	138	44
2	68	41	37	-1.4	78	109	44
3	92	26	23	-0.7	40	77	36
4	56	27	27	-0.9	37	73	55
5	27	56	51	6.2	121	75	30
6	13	94	49	35.4	199	74	32
7	100	40	43	-1.7	68	129	30
Grand Mean	54	47	38	6	86	96	39

Table 5.2. Lamar Valley ungulate scat counts, for plots covering 12,620 m^2. In Oxbow, no scat piles were found in sample plots, but elk and bison scat from previous seasons were present near the site.

Species	Total Fecal Piles	Summer 2010	Older	Density (100 m^{-2})
Bison	1302	1079	223	10.3
Elk	1	0	1	0.0
Pronghorn	23	23	0	0.2

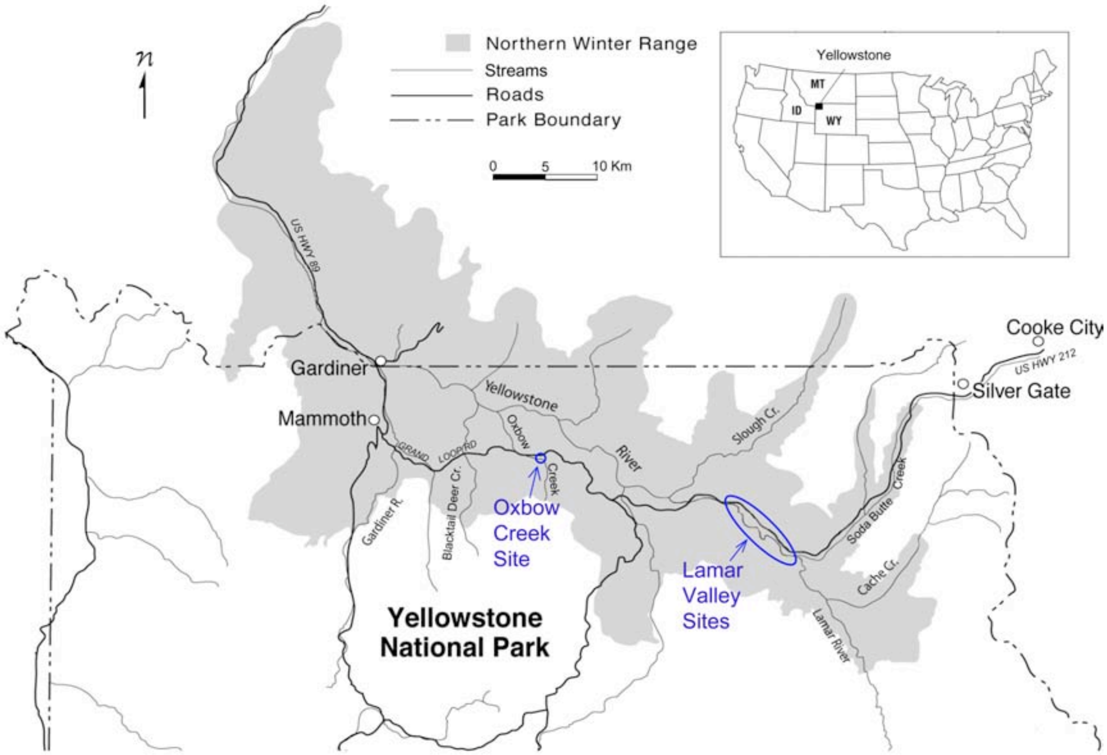

Figure 5.1. Map of northern Yellowstone National Park, showing the location of study sites at Lamar Valley and Oxbow Creek.

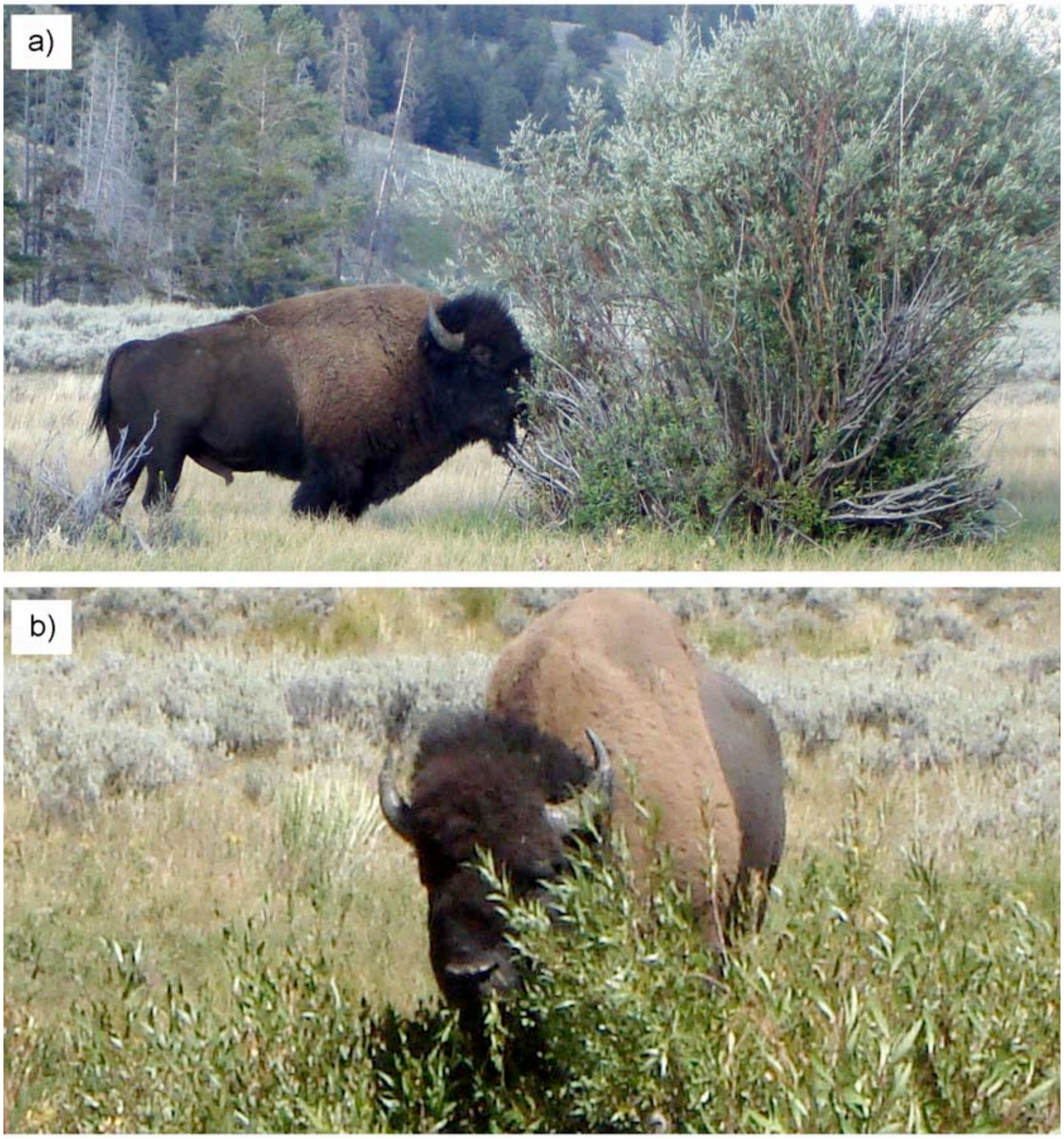

Figure 5.2. Summertime browsing by bison of (a) a willow clump in the Lamar Valley; (b) young cottonwood plants on the bank of the Lamar River. Photos from August 2010.

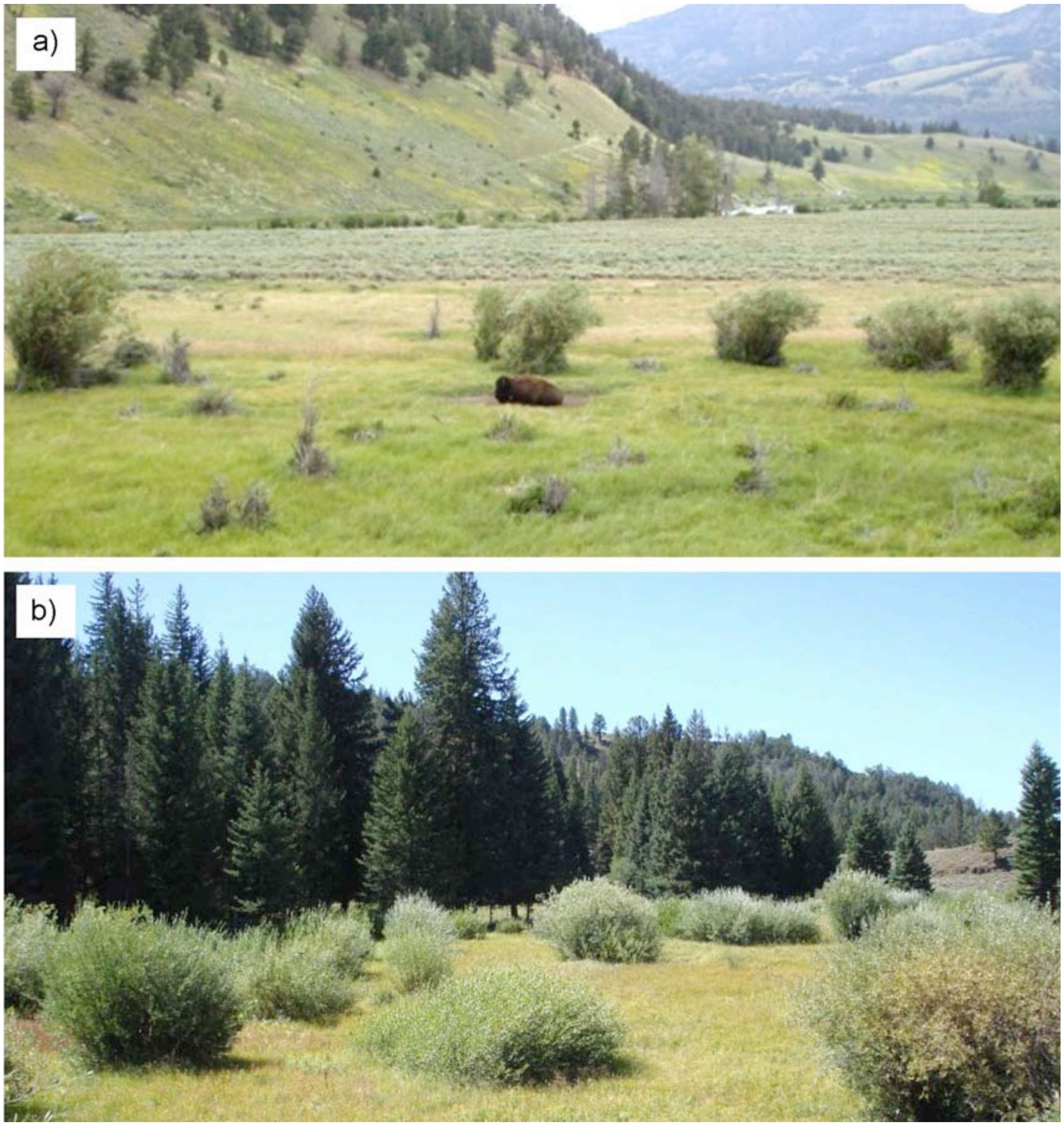

Figure 5.3. Tall willow sites on the Yellowstone northern ungulate range.
(a) In the Lamar Valley a bison rests in a wallow among tall willows. Willow growth is constricted by browsing below about 1 m, but expanding above that height, resulting in a mushroom shape. Most willows are short, with many dead branches (as in foreground). Tallest willows in the photo are approximately 5 m in height.
(b) On Oxbow Creek, willow growth at low height is not suppressed and willows have a full, hemispherical shape. Most are tall, few are short. Tallest willows in the photo are approximately 4 m in height. Photos from August 2010.

Figure 5.4. Cottonwood saplings at two sites in the Lamar Valley.
(a) Cottonwood Site 4, typical of sites in the Lamar Valley, with hundreds of saplings hedged and stunted by browsing.
(b) Cottonwood Site 6, the exception in Lamar Valley with lower browse rates and taller saplings. Inconvenient location away from foraging areas, shading by the adjacent slope in winter, and flooding in spring are possible factors reducing browsing in this site. All browsing in 2009-2010 was at heights below 1 m. Photos from September 2010.

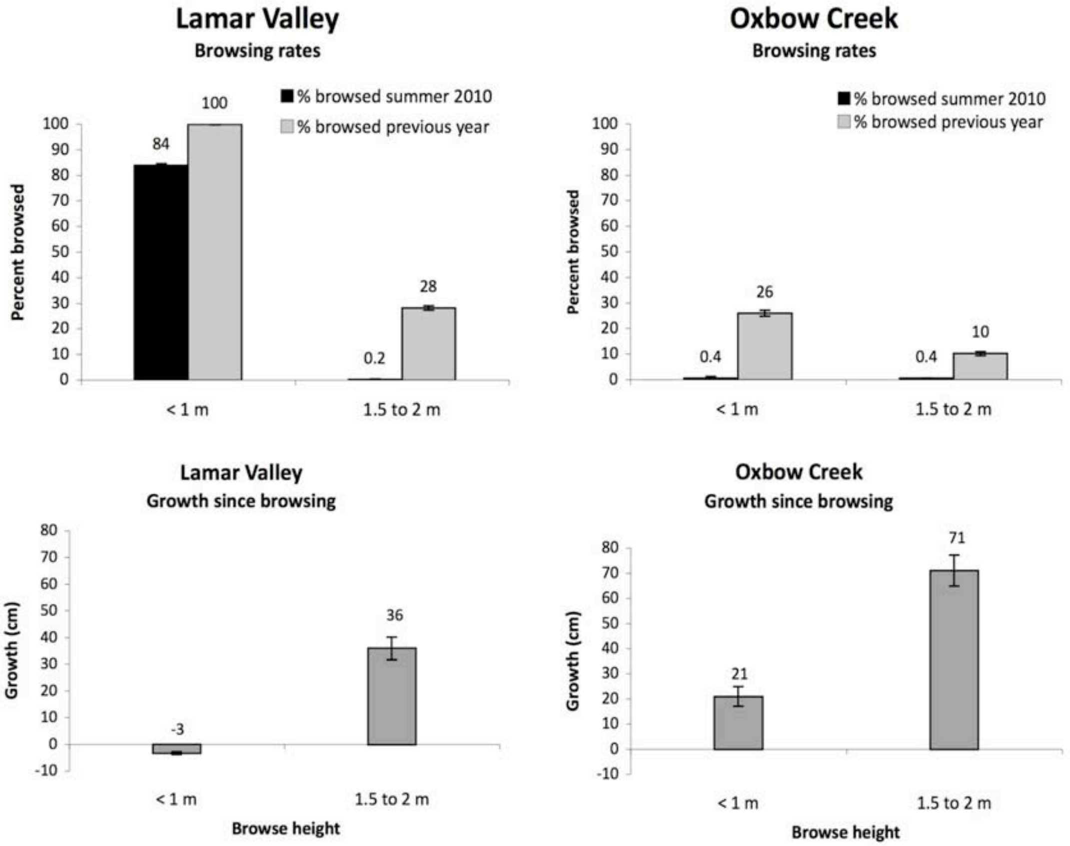

Figure 5.5. Willow browsing rate and growth-since-browsing (spring height – browse height = growth-since-browsing). Summarized data show browsing rate is very high in Lamar below 1 m, but low otherwise, and this difference is reflected in growth (bars show standard error). Summer browsing is near 0% except in Lamar Valley at low height.

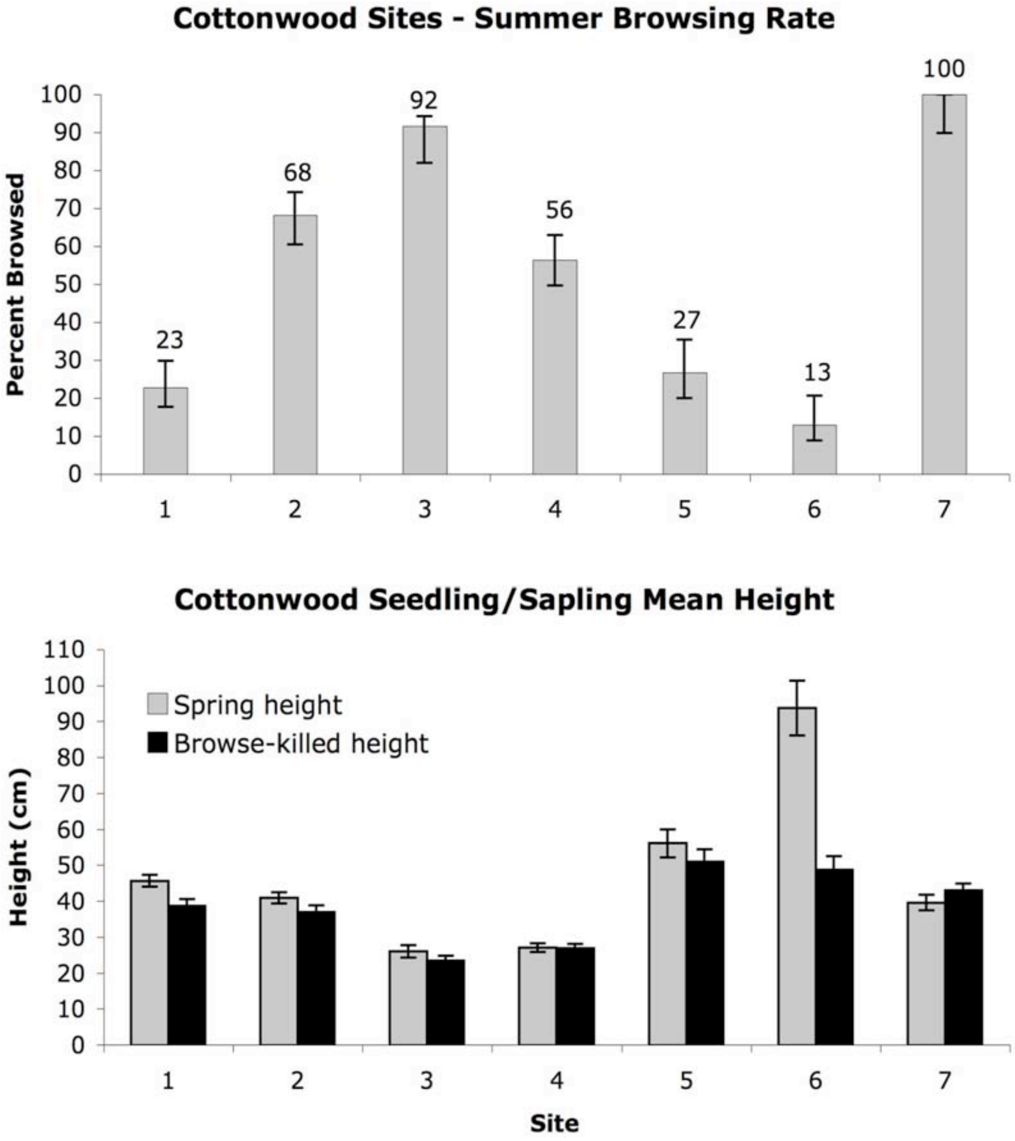

Figure 5.6. Seven cottonwood sites in the Lamar Valley in summer 2010 (bars show standard error).
a) Four of seven sites had summer browsing rates >50%, with two greater than 90%.
b) Mean height was strongly suppressed except in Site 6, where summer browse rate was very low. Mean height was similar to the height of browse-killed stems except in Site 6, so plants have grown little beyond the height at which they were previously hedged by browsing except where summer browse rate was low.

6. CONCLUSION

During the 1980s and 1990s prior to wolf reintroduction, controversy raged over the management, or lack of management, of the northern Yellowstone elk herd and cascading effects on plants and biodiversity (Singer 1996). The reintroduction of wolves in 1995-96 changed the Yellowstone ecosystem, through the reduction and redistribution of herbivory by elk. Aspen stands have begun to recover in northern Yellowstone after decades of suppression by intensive browsing that prevented growth of young aspen into saplings and trees. Elk population densities have been relatively low in the east sector of the Yellowstone northern ungulate winter range (northern range) since about 2005, corresponding with the approximate time of release from browsing of the tallest aspen saplings. In the central and west sectors of the northern range, elk densities have declined more slowly and about half of stands in those sectors were still suppressed with high rates of browsing in 2012. If the current trend of declining elk densities in most of the range stabilizes at or below current levels, reduced browsing rates and recovery of aspen are likely to continue, allowing aspen stands to persist and regenerate. Many stands have already produced tall saplings that are likely to survive to replace overstory trees.

A landscape-scale shift in elk distribution toward the northwest part of the northern ungulate winter range appeared to be the primary driver of aspen recovery in northern Yellowstone National Park (YNP). Elk densities were high in the park before wolves (White et al. 1998), and aspen recovery required a substantial reduction and redistribution of the elk herd. Direct mortality from predation was one cause of the large-scale change in elk distribution, but behavioral responses to risk of predation or human hunting may have contributed (Haggerty and Travis 2006, Proffitt et al. 2009, White et al. 2010, 2012). In the 1950s and 1960s, culling of elk in the park and hunting outside the park kept overall elk densities relatively low, yet elk continued to winter at locally high densities inside the park and aspen did not recover (Houston 1982, Barmore 2003). After wolves returned to the area, elk greatly reduced their use of the east sector of the winter range, and a similar change may be occurring in portions of the central and west sectors.

Trophic relationships involving wolves, elk and woody browse plants are part of a much larger food web (Estes et al. 2011, Eisenberg 2012, Seager et al. 2013). Elk are also affected by humans, bears, climate and possibly bison (Fig. 1). For example, predation by bears on elk calves has increased since the late 1990s (Barber-Meyer et al. 2008), and one contributing factor may be the decline in cutthroat trout due to invasive lake trout (Middleton 2012), evidence of wide-ranging trophic links in the Yellowstone food web. In addition to the effects of browsing by elk, plants are influenced by climate and site conditions, and also by the increasing bison herd. I investigated the effects of bison on woody browse plants (aspen, willow and cottonwood) and found significant herbivory in areas where bison were in high concentration. Despite local impacts from bison, aspen recovery was widespread in the east sector of the range where bison densities have been high in recent years, so bison have not caused a general suppression of aspen in that sector.

A trophic cascade from wolves to elk to plants could be mediated simply by an effect on overall elk population density if density were kept very low, but indirect effects including behavioral responses to predation risk may be involved particularly with moderate elk densities (White et al. 2003, Fortin et al. 2005). Discussion of predation risk responses in the Yellowstone system has generally focused on small-scale behavioral effects at the scale of individual stands and between stands, for example, the potential effects of fallen logs or complex terrain (Ripple and Beschta 2007, Kauffman et al. 2010, Winnie 2012). I found evidence for an influence on aspen height from the number of logs and the topographic position of a stand; however, with continued high elk densities in much of the northern range the more important predation risk responses so far may be those operating at large scales influencing the choice of winter range areas by elk. As overall elk numbers on the northern range declined, some areas continued to have high elk densities while others had much lower densities, resulting in a patchy and spatially variable trophic cascade to plants. Where elk densities are relatively low as in the east sector, small-scale factors such as predation risk, difficulty of access, proximity to preferred foraging areas and random chance may be causes of local variation in browsing intensity and aspen recruitment.

Changes cascading through the Yellowstone ecosystem following the return of wolves challenge the usual dichotomy between large-scale “density-meditated” or small-scale “behaviorally mediated” trophic cascades (Fortin et al. 2005, Ripple and Beschta 2007, Kauffman et al. 2010). This paradigm may be inadequate to describe recent changes in Yellowstone, where large-scale changes in elk density may have a behavioral component. In national parks in the Canadian Rockies, elk distribution at the landscape scale reflected differences in predation risk from both wolves and hunting (White et al. 2003, Hebblewhite et al. 2005), similar to elk distribution patterns occurring recently in the Yellowstone area (Haggerty and Travis 2006, Proffitt et al. 2009, Middleton et al. 2013). Indirect effects may operate at an intermediate scale as well, due to more dynamic elk movement and changes in grouping behavior in response to predation risk (Mao et al. 2005, Gude et al. 2006, Gower et al. 2009a, Gower et al. 2009b, Middleton et al. 2013), changes that could affect the distribution of elk impacts on aspen. Because direct and indirect effects operate simultaneously they may be difficult to separate, but future research into trophic cascades in Yellowstone may benefit from consideration of indirect effects of predation at multiple spatial scales (White et al. 2003).

My results are consistent with those of other studies suggesting that aspen stand regeneration is rare with high elk densities and predation risk effects are not sufficient to change this result as long as elk densities remain high (White et al. 1998, Seager et al. 2013); however, small-scale responses to predation risk may affect the threshold of elk density at which plant release begins to happen, and may cause a greater and more heterogeneous response in plants than would otherwise occur with similar elk density (White et al. 2003). Behavioral effects of predation have the potential to redistribute herbivory impacts, perhaps increasing herbivory in some places while decreasing it in others. While the behavior of elk in places or times with or without wolves can be readily studied, the link between behavioral effects and changes in plants is difficult to demonstrate. The potential for wolves to benefit plants could be studied by comparing elk densities and plant conditions in places with and without wolves, but most places without wolves have high elk densities so it may be difficult to find suitable systems to compare. Studies of the behavioral responses of elk to wolf proximity have demonstrated the fine-scale complexity of these interactions (Creel and Winnie 2005, Middleton 2012), but the ability of such studies to infer cascading effects to plants is very limited without a comparison to places where wolves are absent. The temporal scale of wolf absence is also important; changes that occurred when wolves returned to Yellowstone after a complete absence may not be apparent at the short temporal scale of wolf encounters where wolves are already established. One approach to measuring fine-scale predation risk might be to combine studies of the responses of elk to wolves with measurements of browsing intensity that could be correlated with elk movement data. These two approaches – studying animals or studying plants – have generally been used separately. An exception is the work of Eisenberg (2012); however, elk densities in that study were high, above the level at which aspen recruitment has generally been observed (White et al. 2003, Seager et al. 2013).

The effects of bison in the Yellowstone ecosystem are poorly understood and becoming more significant with bison numbers much higher than in most of the park's history (Plumb et al. 2009). Bison densities in recent years have been comparable to those of elk in much of the northern winter range. Bison have been recognized as a "keystone" species with profound effects on plant and animal communities (Knapp et al. 1999), and I found evidence of significant browsing by bison. The ecological effects of bison in the Yellowstone area may be an important and somewhat neglected area of research, and these effects must be taken into consideration in any studies of ungulate herbivory in Yellowstone.

These research results suggest that wolves have initiated a recovery of aspen in the Yellowstone ecosystem, and further cascading effects may be expected. As recovering aspen stands develop an understory of saplings and shrubs, biodiversity of both plants and animals may increase with cascading effects throughout the food web (Beschta and Ripple 2012, Ripple and Beschta 2012). Other factors such as fire, floods and beavers can also affect recovery of woody browse plants, but only if browsing intensity is low enough that new growth stimulated by these agents of disturbance can survive to maturity. Wolves appear to have reduced browsing by elk, tipping the balance in favor of these plant species.

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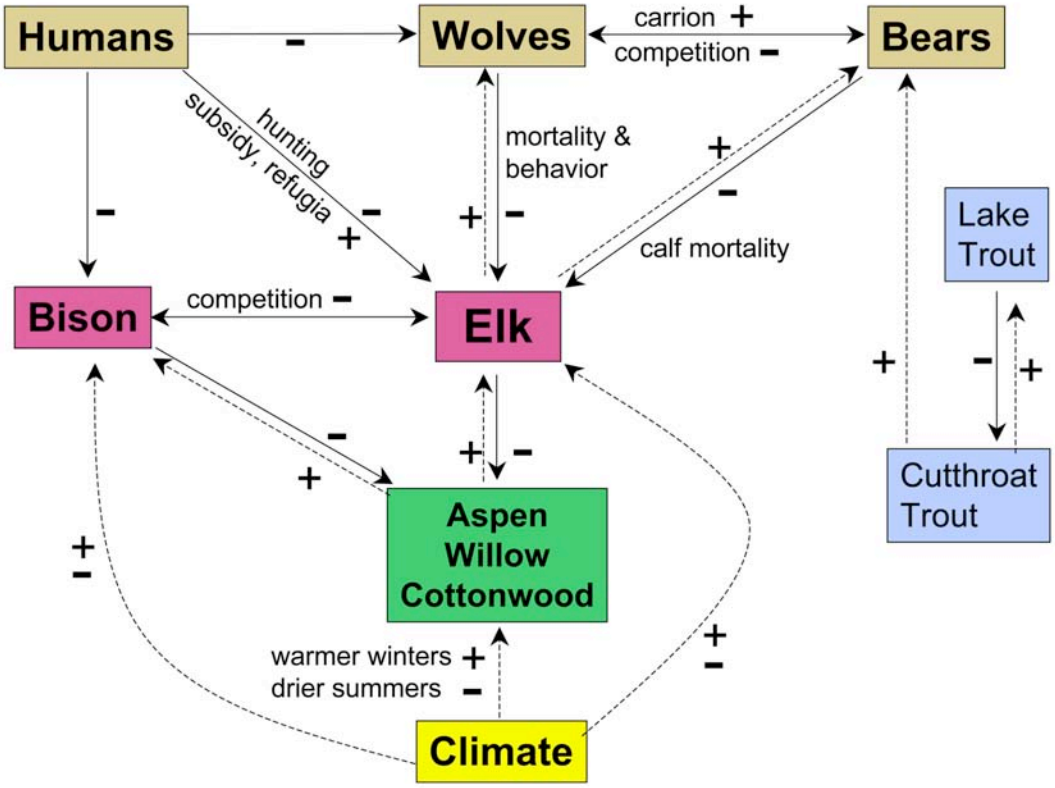

Figure 6.1. Some trophic relationships affecting elk and woody browse plants in the Yellowstone ecosystem. Dotted lines represent "bottom-up" factors, such as primary production and the influence of climate. Climate affects ungulates indirectly through plants, but also directly as snowpack affects movements and access to forage. Wolves and bears compete directly for carcasses and elk calves, and wolves may kill bear cubs, but wolves also provide carcasses for bears. Humans are the primary predators of bison, killing them when they leave the park.

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APPENDIX – ASPEN SAMPLING LOCATIONS

Table A.1. Aspen sampling locations in northern Yellowstone in 2012; height in cm. Columns include range sector; UTM location, projection NAD83, zone 12N; height and browsing rate in plots; height of 5 tallest in stand.

	Sector	UTM north	UTM east	Height spring 2012	%Browsed 2012	Height 5 tallest 2012
1	west	4976812	521011	32	61	91
2	west	4979075	519621	59	50	115
3	west	4979575	519144	59	80	75
4	central	4974947	532117	36	68	77
5	central	4975633	531705	24	94	43
6	central	4976287	531501	37	85	59
7	central	4976716	531308	38	100	38
8	central	4976940	530726	27	77	44
9	west	4977627	525888	24	80	46
10	east	4968261	565952	149	17	280
11	east	4972657	552919	49	85	71
12	east	4972489	552448	35	78	55
13	east	4972356	552578	52	52	125
14	east	4972420	553987	53	74	279
15	central	4976164	536033	88	11	229
16	central	4974635	536036	54	41	148
17	central	4974562	535877	61	48	200
18	central	4974859	535470	51	60	128
19	central	4974348	534828	77	34	126
20	central	4974344	533430	37	61	93
21	central	4977825	538076	50	62	89
22	central	4975084	543146	53	67	215
23	west	4981411	522416	21	100	24
24	west	4980974	522431	40	82	113
25	central	4978481	542791	42	69	88
26	central	4979721	536771	48	76	241
27	central	4979848	536491	96	61	228
28	east	4973231	560971	76	21	110
29	east	4972152	561090	80	19	184
30	east	4969745	562723	105	52	277
31	east	4970466	561722	48	53	199
32	west	4985827	518965	26	91	27
33	west	4986385	519218	22	93	28
34	west	4984438	520470	22	100	54
35	west	4984389	520827	31	84	59
36	west	4984376	520480	25	82	37
37	east	4973824	569586	84	21	112
38	east	4971890	568184	101	30	193
39	east	4971670	569450	70	42	183
40	west	4983749	526542	33	83	96
41	west	4984237	527574	127	24	286
42	central	4979230	544932	43	100	98
43	central	4979277	545614	137	16	381
44	central	4980426	532534	90	29	167
45	west	4978736	530669	38	68	75
46	west	4979995	529962	70	72	124

	Sector	UTM north	UTM east	Height spring 2012	%Browsed 2012	Height 5 tallest 2012
47	west	4980217	529801	50	40	117
48	west	4980253	530048	46	60	120
49	west	4980273	530474	66	55	197
50	east	4975064	558261	78	59	223
51	east	4974057	556940	92	30	255
52	east	4970617	567149	106	12	226
53	east	4980945	562331	81	0	211
54	east	4978350	559143	148	5	354
55	east	4978189	558969	138	0	273
56	east	4977442	553462	54	68	141
57	east	4977260	553466	125	30	302
58	east	4976786	553363	220	7	480
59	east	4976462	553192	92	39	340
60	central	4980585	538874	65	60	162
61	central	4981560	537551	32	29	78
62	central	4980244	537642	51	87	96
63	west	4979710	528508	59	31	198
64	west	4980626	527310	77	20	161
65	west	4980823	527121	71	47	147
66	central	4982445	529326	53	55	72
67	west	4981624	527769	88	8	232
68	east	4964981	567714	52	30	188
69	east	4964689	566987	75	16	161
70	east	4965383	566563	87	36	185
71	east	4966228	565985	74	46	175
72	east	4967075	563902	11	73	44
73	east	4977224	549687	99	40	167
74	east	4976195	550194	66	36	275
75	east	4975394	550785	48	76	65
76	east	4975745	549242	73	55	402
77	east	4975376	549122	21	67	257
78	east	4972438	556515	46	56	346
79	east	4970691	555972	165	6	267
80	east	4970078	555480	81	20	153
81	east	4970892	558919	75	35	252
82	east	4970623	559040	177	0	306
83	central	4985015	533243	53	77	94
84	central	4985882	533771	67	69	136
85	central	4981733	545142	39	88	76
86	central	4981556	541682	81	56	267
87	west	4976278	517509	52	50	168

Table A.2. Aspen sampling locations in Shoshone National Forest in 2011, height in cm. Columns include range sector; UTM location, projection NAD83, zone 12N; height and browsing rate in plots; height of 5 tallest in stand.

	Area	UTM north	UTM east	Height spring 2011	%Browsed 2011	Height 5 tallest 2011
1	Sun	4950878	610021	79	0	213
2	Sun	4950544	610618	67	13	178
3	Sun	4956808	621102	113	46	289
4	Sun	4956464	620745	25	62	115
5	Sun	4956528	620815	52	29	190
6	Sun	4956679	621048	79	53	167
7	Sun	4952429	611506	106	32	331
8	Sun	4956758	621336	56	69	144
9	Sun	4956876	621675	35	76	159
10	Sun	4956939	621746	74	43	184
11	Sun	4954852	615987	52	67	486
12	Sun	4954962	615852	27	79	79
13	Sun	4954800	611316	37	87	111
14	Sun	4955047	611224	32	43	75
15	Sun	4955729	619489	24	48	77
16	Sun	4957085	622101	55	70	139
17	Sun	4955272	623083	44	81	97
18	Sun	4954930	622667	48	82	132
19	Sun	4954459	621929	91	41	297
20	Sun	4957777	620202	48	72	327
21	Sun	4958183	620006	62	81	217
22	Sun	4958272	619910	103	35	277
23	Sun	4958002	620310	78	59	147
24	Sun	4958475	620501	55	77	247
25	Sun	4958568	620178	150	19	422
26	Sun	4958497	620180	104	71	296
27	Sun	4954714	622387	34	47	111
28	Sun	4958385	620565	29	84	92
29	Sun	4958233	620414	50	78	172
30	Sun	4957947	620907	43	93	107
31	Sun	4958026	621014	45	71	136
32	Sun	4958036	620555	54	69	202
33	Sun	4958178	620437	51	81	157
34	Sun	4954655	615553	62	6	221
35	Sun	4954521	615169	34	0	193
36	Cran	4966967	606262	29	55	67
37	Cran	4967208	604995	47	29	180
38	Cran	4965992	604808	92	38	339
39	Cran	4966103	604821	178	33	409
40	Cran	4966461	604883	39	28	81
41	Cran	4966348	605277	117	25	439
42	Cran	4966401	605452	270	0	478
43	Cran	4966978	603162	85	55	413