

AN ABSTRACT OF THE DISSERTATION OF

Joshua S. Halofsky for the degree of Doctor of Philosophy in Forest Resources presented on April 19, 2007.

Title: Evidence of a Trophic Cascade among Wolves, Elk, and Aspen in Yellowstone National Park, USA.

Abstract approved:

William J. Ripple

According to general top-down trophic theory, in the presence of carnivores, herbivore behavior and/or densities could change and result in an overall decrease in herbivory on plant communities. In this dissertation, I examined the potential relationship between gray wolf (*Canis lupus*) presence and absence on elk (*Cervus elaphus*) herbivory of aspen (*Populus tremuloides*). Based on aspen tree cores and an age-diameter relationship, I approximated aspen origination dates both within and outside two elk exclosures to study long-term patterns of aspen recruitment in the Gallatin elk winter range of northwestern Yellowstone National Park, USA. From aspen data, I concluded that while a host of interacting biophysical factors may influence aspen recruitment and growth, the observed pattern of aspen decline is most correlated with elk herbivory, coincident with the presence and absence of wolves.

Outside of the elk winter range, but still within the northwestern portion of the park, I studied growth patterns of clonal upland aspen thickets since wolf reintroduction. Growth patterns were compared in an area burned in the 1988 fires to an adjacent area that was unburned. From the results, I proposed that in addition to any wolf-mediated changes in elk densities, a recoupling of fire with increased elk predation risk in the presence of wolves may improve upland clonal aspen recruitment.

To examine the potential for a trophic cascade from the perspective of elk, I measured vigilance behavior in female elk throughout the park during both winter and summer seasons. After vigilance behavior was recorded, I noted the distance to, and type of, objects that could have impeded observed female elk escape from predators. From my model selection procedure, I concluded elk foraging behavior appeared to vary with physical features in the landscape. This variation in foraging behavior with risk of predation provides a potential mechanism to explain the patchy release of preferred woody browse species within the Park. Therefore, in addition to density-mediated effects, the results are consistent with a behaviorally-mediated top-down trophic cascade between wolves, elk, and aspen.

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Evidence of a Trophic Cascade among Wolves, Elk, and Aspen in
Yellowstone National Park, USA

by
Joshua S. Halofsky

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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.

Joshua S. Halofsky, Author

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CONTRIBUTION OF AUTHORS

Dr. William J. Ripple assisted in the design, writing, and interpretation of Chapters 2 through 4. Dr. Robert L. Beschta assisted in the design, writing and interpretation of Chapter 3.

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DEDICATION

To Marty, Sandy, Ada, and especially Jessica. Without your presence and support, my sanity and balance in life would be sorely lacking.

CHAPTER 1 – INTRODUCTION

Trophic cascade theory focuses on the influence of top carnivores on successively lower trophic levels. Early research on the topic was directed toward density-dependent trophic cascades, whereby predators directly influenced prey densities, which in turn impacted consumption of plants by prey species (Estes et al. 1978; Carpenter et al. 1985). The influence of predators on prey, however, need not be limited to density dependence. In a series of experiments involving spiders, grasshoppers, and herbaceous plants, Schmitz et al. (1997) found that changes in grasshopper behavior in spider presence caused plant biomass responses statistically similar to measured changes in plant biomass under density-dependent scenarios (spider predation). Thus, the relative importance of density-mediated trophic cascades over behaviorally mediated trophic cascades was questioned. Studies in other systems (Godin & Smith 1988; Lima 1988; Kotler et al. 1991; Krause & Godin 1996; Peacor & Werner 2001) have also documented changes in prey behavior and foraging patterns in the presence and absence of predators. Taken together, in a three level species trophic cascade, trophic theory would predict an increase in plant biomass due to a decline in herbivore densities and/or changes in herbivore behavior. Without the top carnivore trophic level, trophic cascade theory further predicts an increase in herbivore densities and/or changes in behavior resulting in a loss of plant biomass.

Despite the development of trophic cascade theory, studies of terrestrial trophic cascades involving large predators and prey are rare (Shurin et al. 2002). Large carnivores have been removed from much of the landscape while instances of their

reintroduction are uncommon. The extirpation of gray wolves (*Canis lupus*) from Yellowstone National Park, USA, by 1930 and their reintroduction in the winters of 1995 and 1996 facilitated the present trophic cascade study involving carnivore absence and presence at a broad geographic scale and long temporal scale. Through this study, I was able to clarify if observed plant responses conformed to trophic theory under a two- and three-level species trophic cascade.

My research on trophic cascades in Yellowstone National Park began by examining both the historic and current origination and growth of aspen (*Populus tremuloides*) in the Gallatin elk winter range, located in the northwest corner of the park. In Chapter 2, I described patterns of aspen origination before wolf extirpation (pre-1930s), during a wolf-free period (1930s to early 1990s), and after wolf reintroduction (mid-1990s to present). I also measured aspen in two elk exclosures erected in 1945 in the same winter range to investigate aspen origination and growth without elk (*Cervus elaphus*) browsing. Such an approach enabled me to determine the possibility for a trophic cascade at the temporal scale of aspen growth and mortality, a temporal constraint that has generally limited the study of terrestrial trophic cascades involving large vertebrate predators and herbivores.

In Chapter 3, I examined variations in browsing history and growth patterns of upland aspen stems following wolf reintroduction. I compared growth patterns in two adjacent areas with potentially similar browsing levels but with different disturbance histories. One area was burned in the 1988 Yellowstone fires, while the adjacent area was unburned. Although studies have reported how fire and browsing have

individually influenced aspen origination and growth, few studies have looked at both factors simultaneously. In the study, I proposed that a recoupling between fire effects and increased elk predation risk following wolf reintroduction might improve aspen recruitment. This study also appears to be the first report of tall, high-density upland aspen thickets in the park in several decades.

While measurements of plant origination and growth can provide patterns consistent with expectations of a trophic cascade, in Chapter 4 I directly investigated trophic cascade theory by studying the relationship between female elk foraging behavior and elk predation risk from predators. Female elk predation risk was determined by observing elk vigilance behavior and then assessing the animal's surroundings to determine if certain features in the landscape contributed to female elk vigilance levels. This study therefore explores a process to explain the patchy distribution of woody plant release observed in the park.

Individually, each chapter examines a different aspect of trophic cascades. Collectively, the chapters illustrate the possible role of top carnivores in structuring complex ecosystems through changes in behavior in addition to any changes in densities. Chapter 5 provides general conclusions from the research and potential directions for future research.

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CHAPTER 2 - LINKAGES BETWEEN WOLF PRESENCE AND ASPEN
RECRUITMENT IN THE GALLATIN ELK WINTER RANGE OF
SOUTHWESTERN MONTANA, USA

Abstract

The decline of aspen (*Populus tremuloides*) in the Greater Yellowstone Ecosystem, USA, has been attributed to conifer encroachment, climatic influences, ungulate herbivory, and more recently, a lack of gray wolves (*Canis lupus*) via trophic cascades. We focused on a trophic cascades hypothesis while considering other potential reasons for aspen decline. We conducted the study in the Gallatin elk winter range of Yellowstone National Park, where aspen (*Populus tremuloides*) have not previously been studied. In the summer of 2004, we obtained tree cores and diameter at breast height (DBH) measurements of aspen trees to create an aspen age-diameter relationship. We approximated aspen origination dates, defined as the year the aspen sprouted, from the age-diameter relationship to examine the potential relationship between wolf presence, elk (*Cervus elaphus*) herbivory, and aspen recruitment into mature trees. We compared aspen recruitment and growth to historical climate, current conifer encroachment, and fire information. We compared aspen data collected in the winter range with aspen data collected within two elk exclosures, both erected in 1945 and within the same elk winter range. Within the elk exclosures, aspen successfully recruited since fence construction in the 1940s. Outside the exclosures, aspen recruitment into mature stems began to decline in the 1920s (during wolf extirpation), completely ceased after the 1950s, and has only been observed since the 1990s (post wolf reintroduction). Within the scope of the study, we found little

association between aspen decline and climate, conifer encroachment, or fire suppression. While a host of interacting biophysical factors may influence aspen recruitment and growth, the correlative results between aspen recruitment and historical elk browsing activities, coincident with the presence and absence of wolves, are consistent with a top-down trophic cascade.

Introduction

The ability of a predator to influence lower trophic levels beyond a predator's immediate prey base is known as a trophic cascade (Estes et al. 2001). Controversy over the capacity of a predator to influence lower trophic levels has been present since Hairston et al. (1960) disputed the notion that herbivores are generally limited by plant biomass (bottom-up forces). Rather, they argued the global level of plant biomass existed because herbivores were limited by predators. Trophic cascades theory thus argues top-down forces have greater influence on lower trophic levels than bottom-up forces have on higher trophic levels. Support for a top-down argument is frequently found in aquatic environments, leading to questions over the prevalence and strength of trophic cascades in terrestrial environments (Strong 1992; Polis & Strong 1996; Schmitz et al. 2000; Halaj & Wise 2001; Shurin et al. 2002; Borer et al. 2005). Additional factors such as predator and prey body size, species diversity, plant nutrition, and plant chemical defenses have all been suggested to contribute to the strength and direction of a trophic cascade (Strong 1992; Hairston & Hairston 1993; Polis 1999; Chase 2000; Polis et al. 2000; Shurin et al. 2002; Chase 2003). These

factors allude to the spatially and temporally dynamic nature of trophic cascades and imply the strength of top-down and bottom-up forces will vary from system to system as well as through time. The strength of top-down and bottom-up forces also will depend on whether a community trophic cascade, or a subset of the community known as a species-level trophic cascade, is examined.

Meta-analyses of trophic cascades have noted a dearth of long-term terrestrial trophic cascades studies linking large vertebrate predators and vertebrate prey (Shurin et al. 2002; Borer et al. 2005). Lack of terrestrial trophic cascades research involving large vertebrates can be attributed to the decades required to study trophic interactions at the scale of longer-lived terrestrial animals and tree species (rather than the few days to few years that may be needed to study aquatic and terrestrial invertebrate cascades). However, the removal of a terrestrial predator decades ago now affords investigators the opportunity to begin to fill this gap in the literature. Specifically, with the extirpation of the gray wolf (*Canis lupus*) by 1930 from Yellowstone National Park (YNP), an apex carnivore was removed from an ecosystem for more than six decades. Examining the period before and after wolf extirpation facilitates the study of top-down and bottom-up influences on trophic cascades at the temporal scale of elk (*Cervus elaphus*) herbivory and tree regeneration. The relatively long life (100-150+ yrs) and high palatability of quaking aspen (*Populus tremuloides*) make this species suitable to study within such a context.

The lack of regeneration of quaking aspen in the Greater Yellowstone Ecosystem has been documented for decades (Waren 1926; Grimm 1939; Barmore

1965; Houston 1982) and continues to be of concern to scientists and natural resource managers (Romme et al. 1995; YNP 1997; Meagher & Houston 1998; NRC 2002). Aspen decline has been variously attributed to conifer encroachment, natural stand dynamics, climate fluctuations, climate change, and ungulate browsing (Houston 1973; Loope & Gruell 1973; Romme et al. 1995; YNP 1997; Meagher & Houston 1998; Singer et al. 1998). It is also possible that large carnivore presence influences both ungulate population size and behavior, and in doing so, affect aspen population dynamics (White et al. 1998; Ripple et al. 2001; Mao 2003; Hebblewhite et al. 2005, Fortin et al. 2005; Binkley et al. 2006).

To understand future aspen dynamics, a first and necessary step is to comprehend present and historic aspen dynamics and the associated forces that may contribute to aspen origination. Our study was conducted in the Gallatin elk winter range, an area where to our knowledge aspen have not previously been studied. The winter range also contains two elk exclosures erected in 1945, which allows the comparison of areas that experienced no ungulate browsing pressure to an area accessible to ungulates but not human hunters inside the park. Our study objectives were to:

1. Examine aspen recruitment during several establishment periods: an intact species-level trophic cascade involving wolf-elk-aspen (pre-1930s and post 1995); a truncated species-level trophic cascade of elk-aspen (1930s-1995); and an aspen-only system inside the exclosures (post 1945).

2. Consider alternative hypotheses (conifer encroachment, climate trends and herbivory) in explaining the pattern of historic and current aspen recruitment during the various establishment periods.

Study Area

The Gallatin is the main wintering area of the Gallatin elk herd (Lovaas 1970). Based on incomplete data on early winter elk counts collected between 1929 through 1995 (n = 40) by the state of Montana, elk numbers have varied between 1214 and 3028 individuals, with an average of 1746 elk (SD = 440.1, ~ 9 elk/km²). Following wolf reintroduction, from 1996 through the year 2003, elk numbers have averaged 1048 animals (SD = 209, ~5 elk /km²).

Elevation varies from 2400 to 3000 m. Winter precipitation normally occurs as snow. Annual valley snowfall is approximately 250 cm, with over 750-1000 cm of annual snowfall at higher elevations. Heavy, deep snows in the fall and winter force the elk herd to move to lower elevations that include both the Daly Creek and Black Butte watersheds, core winter range areas for the Gallatin elk herd (Lovaas 1970). Both Daly Creek and Black Butte watersheds lie in the northwest corner of Yellowstone National Park. In our study of the core elk winter range, we examined all aspen stands within the Daly Creek and the northern half of the Black Butte watersheds, encompassing an area of approximately 35 km² (Figure 2.1).

The coniferous vegetation of the Gallatin is comprised of pure stands of lodgepole pine (*Pinus contorta*) or mixed stands of lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*), and Engelmann spruce (*Picea engelmanni*). Willow (*Salix*

spp.) is the most prevalent hardwood in the Gallatin valley bottom, and aspen is the dominant hardwood at higher elevations. Both willow and aspen are minor forest components in comparison to the coniferous species. On open hillslopes, sagebrush (*Artemisia* spp.), rabbitbrushes (*Chrysothamnus* spp.), Idaho fescue grass (*Festuca idahoensis*), wheatgrasses (*Agropyron* spp.), and bluegrasses (*Poa* spp.) are commonly found. Due to their higher nutritional content, preferred elk forage in the winter range includes herbaceous vegetation, willow, and aspen. Elk typically browse coniferous species in the winter range once they have depleted more nutritious forage.

European Americans first settled the Gallatin basin in 1863 (Lovaas 1970) although Native American use of the area was present before this time. While wildlife protection was more successful beginning in the 1880s, market hunting of elk and wolves in the 1860s and 1870s was wide-spread and could have continued until the early part of the twentieth century. “Abundant signs” of Native Americans were observed in the region as late as 1863 (Lovaas 1970), and Native American presence may also have influenced animal abundance. Today, hunting is permitted outside the park in the adjacent Gallatin National Forest.

Methods

During the summer of 2004, we enumerated and visited all aspen stands we located within the study area (35 km²) using 1:24000 scale aerial photography acquired in 1999 and field reconnaissance. We defined a stand as a minimum of three aspen stems greater than breast height, with each stem in the stand less than 30 m

away from any other stem in the stand. In small stands (< 9 aspen trees), we measured the diameter at breast height (DBH) of every tree. In larger stands (≥ 9 aspen trees) we measured all stems < 20 cm DBH and a haphazard selection of nine stems representing a range of diameters ≥ 20 cm DBH. In addition, we obtained increment cores from aspen trees representing a range of diameters to estimate tree age.

To explore potential bias, we compared the age distribution (see age-structure methods below) of all trees in stands that had < 9 total aspen trees and were therefore completely sampled (69% of all stands sampled) to the age distribution of all stands with ≥ 9 total stems. Results of the Kolmogorov-Smirnov two-sample goodness-of-fit test indicated the age distribution of our sampled population (stands with ≥ 9 aspen trees) was not significantly different from the distribution of ages in stands where all aspen trees were measured ($k_s = 0.25$, p -value = 0.75). We therefore assumed there was no bias in our sampling protocol and pooled our data.

We established a 2x20 m belt transect in every third aspen stand to examine current aspen reproduction levels, running this transect from the stand edge toward the stand centroid, and randomly selecting the direction of the belt transect with a random number table. Within each transect, we collected aspen sprout information, defining aspen sprouts as immature aspen less than breast height. We recorded the total number, height, and evidence of previous years browsing (yes/no) for all aspen sprouts within each transect. We determined the previous year browsing through visual inspection of aspen sprouts. Both aspen basal area and current conifer encroachment was quantified by collecting aspen and conifer basal area information from the

approximate stand centroid using a basal area gauge with a basal area factor of five. We regressed aspen sprout density on conifer basal area to ascertain the relationship between the two variables. We noted the presence or absence of fire from fire scars on Douglas-fir and from historic documents.

Within the same elk winter range, we collected additional data on aspen within two fenced elk exclosures which were erected in 1945. Crown Butte exclosure is approximately 2.0 ha and 0.3 km from the park boundary (Figure 2.1). The Porcupine exclosure is approximately 1.9 ha and 11 km north of the park boundary. Both exclosures were erected to “determine the effect of grazing by big game on winter ranges.” In exclosures, we collected DBH measurements on all aspen stems greater than 1 cm in DBH and extracted additional increment cores from a variety of tree sizes ≥ 5 cm. Trees cored at breast height were also cored 0.2 m from the tree base to derive an estimate of time required to grow to breast height.

All tree cores were stored, air-dried, mounted, and sanded following procedures outlined by Stokes and Smiley (1968). We used a dissecting microscope and standard dendrochronological procedures (Stokes & Smiley 1968) to count the rings on each core. Due to ring complacency, cross-dating was unsuccessful. From the aspen tree ring counts and corresponding DBH measurements, we quantified an aspen age-diameter relationship from 59 complete cores. Five years were added to each age based on the difference in tree age calculated from seven 0.2 m and 1.5 m cores (Mean = 5 yrs, SD = 1) located within the exclosures. The final age-diameter equation was: $\text{Age} = 2004 - (2.50 \text{ DBH} + 0.02 \text{ DBH}^2 + 5)$ ($r^2 = 0.9$). We used this

regression equation to approximate aspen origination years for all DBH measurements.

To examine climate trends, we averaged two Palmer Drought severity indices (PDSI) (Cook et al. 2004) downloaded from the International Tree Ring Databank website (grid points 84 and 100 from <http://www.ncdc.noaa.gov/paleo/treering.html>; accessed March 01, 2007). This long-term record is based on climatically sensitive tree-ring chronologies. Negative values are indicative of drought conditions (moderate = -2, severe = -3, extreme = -4), whereas positive values are associated with above average precipitation.

Results

Aspen Stands

We collected a total of 476 DBH measurements from the 73 enumerated aspen stands in the winter range, 353 DBH measurements within Crown Butte enclosure, and 653 DBH measurements within Porcupine enclosure (Figure 2.2). Outside of the enclosures, aspen recruitment began declining during wolf extirpation (1920s), completely ceased in the 1950s, and has only begun to occur again since wolf reintroduction in the 1990s (Figure 2.3), illustrating a large gap in tree recruitment. In contrast, the number of aspen originating within the enclosures began to increase after the fences were constructed, and aspen have continued to establish inside the enclosures through the present (Figure 2.4).

Conifer Encroachment

We found a total of 262 aspen sprouts within the 23 transects situated in aspen stands, with a mean sprout density of 2837 per ha (Range: 0 – 12,500 stems/ha). Within the 23 stands, mean conifer basal area was 14.7 m²/ha (Range: 0 – 42 m²/ha), and mean live aspen basal area was 21.3 m²/ha (Range: 0 – 54 m²/ha). We found no association ($F_{1, 21} = 1.52$, $R^2 = 0.07$) between the current proportion of conifer basal area in a stand and current aspen sprout densities.

Fire

No fire scars were observed on any Douglas-fir trees we observed in the study area. In his history of the Gallatin elk winter range, Lovaas (1970) did not document any historic fires. We therefore concluded there was a low likelihood of high intensity and severity fires, typically associated with a flush of aspen recruitment, in the study area during the 20th century.

Climate

Annual PDSI values indicated similar periods of above- and below-average wetness before and after wolf extirpation (Figure 2.5). Before wolf-extirpation (pre-1930s), the total number of positive and negative annual PDSI values more than one standard deviation from mean PDSI was 11 and nine respectively. Following wolf extirpation and before wolf-reintroduction, there were 11 positive and 12 negative PDSI values more than one standard deviation away from the mean annual PDSI value. Between the time of wolf reintroduction through 2003, there have been two positive and four negative PDSI values more than one standard deviation away from

the mean annual PDSI value. Thus, no apparent climate trend was observed during the different periods of analysis.

Herbivory

Of the 262 aspen sprouts measured in the winter range, 95% had been browsed between 2003 and the 2004 measurements and had a mean height of 26.3 cm (Lower and Upper 95% CL = 24.3, 28.4). Within the Crown Butte and Porcupine exclosures, 94 and 99% of the aspen respectively originated after the exclosures were erected in 1945 (Figures 2.2 and 2.4).

All stems ($n = 14$) originating in the 1990s were found along forest edges adjacent to scree. On average, these stems were browsed 3.9 times between 1998 and 2003. The percentage of stems browsed consistently declined from 100% browsed in 1998 to ~7% browsed in 2003 (Figure 2.6a). In 1998, mean \pm SE stem height was 98.8 ± 14.5 cm (Figure 2.6b). By the end of 2003, the last full year each stem was exposed to herbivory, mean \pm SE stem height was 229.9 ± 18.6 cm and only one stem had been browsed (Figure 2.6). No stems were browsed after reaching 200 cm in height.

Discussion

Our data provides indirect support for top-down trophic cascades as a mechanism controlling aspen populations in the Greater Yellowstone Ecosystem. To best examine the different reasons for aspen decline, we will address each factor

individually, including conifer encroachment, fire suppression, climate, herbivory, and trophic cascades.

Conifer Encroachment

It has been shown that, as stands change from aspen- to conifer-dominated, aspen recruitment will often decline (Jones & DeByle 1985). Thus, aspen stands with greater conifer basal area could have less current aspen recruitment than those aspen stands with lower conifer basal area. However, our results do not support such an assertion. With a mean sprout density of 2,837 aspen per hectare in the current study, aspen growth into large stems appears to be more problematic than the number of regenerating aspen sprouts. However, if conifer basal area continues to increase, it is likely future aspen regeneration in the study area will be negatively impacted.

Fire

If fire suppression is the main factor causing aspen decline, few aspen should recruit without fire. While historic fire records for the study area are limited, both the successful recruitment of aspen inside the exclosures and the recent aspen recruiting adjacent to scree illustrate fire is not a necessary requirement for aspen to recruit in this area. Lastly, although studies have documented vigorous aspen sprouting occurring immediately after fire (Jones & DeByle 1985), under heavy browsing, sprout numbers rapidly return to pre-fire levels (Romme et al. 1995; Bartos & Mueggler 1981). Hessel and Graumlich (2002) found that under high browsing levels, the positive relationship between fire severity and aspen recruitment was lost. Bartos (1994) and White et al. (1998) have questioned whether the addition of fire under high

browsing levels actually hastens the demise of aspen stands. Therefore, even if a fire had occurred in the Gallatin within the approximate 40-50 year age gap (1950's-1990s) due to high elk densities, the fire effect on aspen recruitment would not have necessarily been positive.

Climate

Climate can influence forage production and the ability of plants to successfully regenerate. Researchers have therefore suggested the decline in aspen is attributable to a drier climate (Houston 1982; Singer et al. 1994; Romme et al. 1995; YNP 1997, Singer et al. 1998). If the overall regional climate influence is toward drying, then a decrease in aspen over the entire winter range is expected. However, three lines of evidence suggest climate is insufficient in and of itself to explain aspen decline:

- 1) Aspen have successfully recruited inside the elk exclosures since their construction in 1945. With the exclosures in the same elk winter range as the rest of the study, it is unlikely that those plants would respond differently to climate than would aspen stands outside of the fenced areas.
- 2) According to the PDSI record for the region (Figure 2.5), the period since the 1940s has included both years of above- and below-average wetness. Only aspen within the exclosures consistently recruited from the late 1940s to the present, regardless of general climate conditions.

- 3) Aspen sprout densities averaged 2837 per ha (Lower CL = 1571, Upper CL = 4102). Such densities indicate aspen are successfully establishing within the study area. The paucity of aspen between one and 16 cm DBH outside of the exclosures indicate aspen recruitment into mature trees is lacking.

Other researchers have similarly found weak support for associations between climate and aspen, willow, and cottonwood growth throughout the Rocky Mountains (Baker et al. 1997; White et al. 1998; Ripple & Larsen, 2000; Hessler & Graumlich 2002; Barmore 2003; Beschta 2003, 2005; Ripple & Beschta 2004).

Herbivory

If contemporary levels of herbivory were significantly influencing aspen growth, recruitment of aspen trees should be minimal within the elk winter range and extensive within the elk exclosures. This pattern is supported by the data (Figures 2.3 and 2.4). Currently, the only multi-aged aspen stands successfully recruiting in the entire winter range study area lie inside the elk exclosures and adjacent to scree outside of the exclosures. It is only inside both fences that the distribution of aspen origination ages follows the expected J-shaped distribution (i.e. few old trees and an increasing number of younger trees) of a healthy reproducing plant population, illustrating the abundance of small stemmed individuals. The unimodal distribution of aspen origination outside the exclosures, as evinced by a recruitment gap (Figure 2.3), is indicative of a declining aspen population.

Romme et al. (1995) and Ripple et al. (2001) reported mean aspen sprout heights between 25 and 43 cm in other portions of the park, while Bartos (1994) reported a mean aspen sprout height of 50 cm 12 yrs after a fire in western Wyoming. All authors attributed the low aspen sprout heights to herbivory. With mean aspen sprout heights in our study similar to those reported by other authors working in the Greater Yellowstone Ecosystem, it is probable that high levels of chronic herbivory is also influencing aspen sprout heights in the Gallatin elk winter range.

Looking over a longer time period, heavy grazing by elk was reported in Daly Creek watershed in 1920, 1921, and 1923, and in both Black Butte and Daly Creek watersheds in 1924 (White 1924). A US Forest Service report encompassing the winters of 1934/1935 and 1935/1936 in the Gallatin notes, “in many places, the elk have eaten the willow and aspen so closely that they have driven the beaver out” (Stock et al. 1937). Another US Forest Service report from the winter of 1935-1936 estimates that, during critical winter periods, 80% of the elk diet consisted of important browse plants, such as aspen and willow (Stock 1936). The Conservation Committee of Bozeman noted in 1937 that elk had browsed much of the willow and aspen, while also stripping conifer needles and twigs as high as the animals could reach (Bozeman Daily Chronicle 1937). The pattern of decline in aspen recruitment beginning in the 1920s in the current study (Figure 2.3) is consistent with historic testimonies.

In the 1940s, the Conservation Committee of Bozeman noted the “almost complete absence of aspen reproduction within (Buffalo Horn, Elk Horn and

Porcupine drainages),” areas north of the current study, but within the same elk winter range (Upper Gallatin Conservation Committee 1946 as cited by Lovaas 1970). They further noted the “nearly normal” vegetation within an exclosure and the “extremely short” vegetation surrounding the exclosure. In our study, outside of the elk exclosures, few measured stems originated in the 1940s (Figure 2.3).

In the 1950s, a report from a technician in the Fish and Game Department noted “the elk range (in the Upper Gallatin) definitely shows deterioration in the loss and size of vegetation . . . the forage was licked clean in the Black and Crown Butte areas during the past two falls and winters” (Bozeman Daily Chronicle 1953). In our study, almost no measured aspen outside of the exclosures originated in the 1950s (Figure 2.3).

The decline of aspen beginning in the late 1920s due to elk browsing (as reported in historical documents), the lack of aspen recruitment for more than half a century based on our results (Figure 2.3), and the ability of aspen to successfully recruit in the last half century almost entirely only within the exclosures (Figure 2.4), all lend strong evidence for the influence of herbivory on aspen recruitment in the Gallatin elk winter range. However, since we located aspen stems originating in the 1990s and a decline in browsing on these stems beginning in 1998, we could conclude recent shifts in ungulate herbivory patterns have occurred. We might therefore ask: 1) why was the increase in herbivory in the Gallatin only noted beginning in the 1920s; 2) why did we only locate new stems outside of the exclosures beginning in the 1990s; and 3) why were all new stems outside of the exclosures adjacent to scree slopes?

Trophic Cascades

Similar patterns of age gaps and suppressed woody growth have been noted in other studies. Terborgh et al. (2001, 2006) attributed the lack of small-stemmed individuals in Venezuela to increased herbivory. They concluded herbivory increased following predator removal, a top-down phenomenon. On Isle Royale, Michigan, McLaren and Peterson (1994) observed that as wolf numbers declined, moose numbers increased, resulting in a suppression of balsam fir. According to historic documents and our tree origination data (Figure 2.3), an increase in aspen browsing in the Gallatin began in the 1920s, a time when wolves were being extirpated from the park.

Other studies in YNP have shown similar patterns of tree species decline following wolf extirpation. Within the northern range of YNP, Ripple and Larsen (2000) observed a decline in aspen recruitment from the 1930s through 1995 in the park's northern range. As with aspen, Beschta (2003, 2005) documented a decline in cottonwood (*Populus* spp.) beginning in the 1920s within YNP. He also did not find a correlation between cottonwood decline and climate. Thus, two browse species in different winter ranges and growing under different conditions (riparian cottonwood versus upland aspen) concurrently declined during the time of wolf extirpation.

The only recruitment we found outside of the exclosures originated in the 1990s (Figures 2.3 and 2.6). The decline in percent of stems browsed on the recruiting individuals began in 1998, coinciding with the presence of, and denning by, the Chief Joseph wolf pack in Daly Creek beginning in the winter of 1996-1997 (Smith 1998).

We therefore have evidence of recruitment when wolves were historically present, a gap in aspen recruitment following wolf extirpation coinciding with reports of increased herbivory, and the start of aspen recruitment only since wolf reintroduction. These patterns are consistent with the trophic cascades hypothesis.

Theoretical Implications

In ecosystems driven by bottom-up processes, plants dictate herbivore numbers. Bottom-up theory predicts herbivores have a minimal impact on vegetation, and the stability of a system is largely independent of predators (Terborgh 2005). Consequently, predators have a compensatory effect, meaning predators only kill prey that would have died due to other causes if not predation. Bottom-up theory further predicts a positive relationship between plant biomass and herbivore density. In contrast, the Green World Hypothesis and general top-down theory predict that in a two-level trophic system, herbivores directly impact vegetation by reducing plant biomass (Ray et al. 2005). Thus, as herbivore numbers increase, plant biomass should decrease, indicating an inverse relationship between trophic levels. With a carnivore trophic level added, top-down theory predicts that predators force herbivore numbers down, which in turn increases plant biomass. Top-down theory therefore supports the concept that predators, either alone or in conjunction with other predator species, can have an additive effect on prey mortality. Examination of aspen within the Gallatin elk winter range of YNP yielded little evidence of successful aspen recruitment outside of the elk exclosures in the absence of wolves. Thus, we observed a negative plant response to predator removal outside the exclosures, and a positive plant

response under limited herbivory (inside the exclosures), consistent with top-down theory.

Trophic theory as originally stated in the Green World Hypothesis (Hairston et al. 1960) was based on density-mediated effects of predators on prey. However, recent evidence suggests that behaviorally-mediated trophic cascades may be equal to or greater than density-mediated effects (Schmitz et al. 2004). While the recruiting aspen adjacent to scree may have been aided by a decline in elk densities since wolf reintroduction, a 94% browse rate and a mean height of 26.3 cm on the aspen sprouts in the study area illustrate elk densities are still sufficient to browse nearly all aspen sprouts in a given year. Therefore, in addition to any density-mediated effect on elk due to wolf predation, the presence of recruiting aspen stems only adjacent to scree may represent a change in elk behavior.

Evidence is mounting in the form of vigilance studies that elk predation risk from predators has increased since wolf reintroduction (Laundré et al. 2001; Childress & Lung 2003), while other studies have illustrated changes in habitat preference by elk due to wolf presence (Mao et al. 2005; Fortin et al. 2005; Gude et al. 2006). Ripple and Beschta (2004) list “gravelly/rocky surfaces” as a potential terrain factor that might increase elk predation risk and therefore could be areas elk avoid when browsing. Such gravelly surfaces also would include the scree slopes adjacent to the 14 recruiting aspen sprouts in the current study. Although our results are in agreement with the expected outcome from changes in elk behavior, whether such behavioral

shifts would result in woody plant release throughout the entire study area remains uncertain.

While Schmitz (2000) tended to find the strongest top-down effect in terrestrial trophic cascades when plant damage, rather than plant biomass, was measured, the current study illustrates that in carnivore absence, herbivores negatively affect aspen biomass. Specifically, we documented several decades of a gap in aspen recruitment. Therefore, aspen numbers, as well as biomass, have declined in the Gallatin.

With the small number of recruiting stems found outside of the exclosures, it is too soon to know if they portend the successful recruitment of future aspen, or if they are more of an exception to the general rule of aspen decline. Consequently, within the scope of our study, if elk herbivory patterns do not change, aspen species loss and a conversion of available resources will likely occur, potentially resulting in an alternative stable state.

Although Native Americans probably influenced both historical wolf and elk populations, we were unable to quantify their impact. While wolves in and of themselves might not have the ability to indirectly increase the recruitment of woody browse species, with the full suite of top carnivores in YNP and no wolves for approximately 70 years, little aspen, willow, or cottonwood recruitment has been documented (NRC 2002). However, 60-70 years of documented willow and cottonwood suppression has begun to reverse itself only since the late 1990s, coincident with wolf reintroduction in the winters of 1995 and 1996 (Ripple & Beschta 2003, 2004; Beyer 2006).

Conclusion

Terrestrial trophic cascades studies involving large vertebrate mammals are rare. Humans have greatly altered animal migration routes and the structure and composition of vegetation on the earth through habitat modifications, and also through the reduction and elimination of top predators. Because most terrestrial vertebrate systems are therefore not fully intact, the information gleaned from a time when the system was more complete becomes valuable. The correlative evidence presented in our study supports the positive top-down influence of wolf presence on aspen via additive predation pressure and a negative top-down influence on aspen when wolves are absent. Therefore, the presence of wolves may be integral to the long-term recruitment of this woody browse species within the study area.

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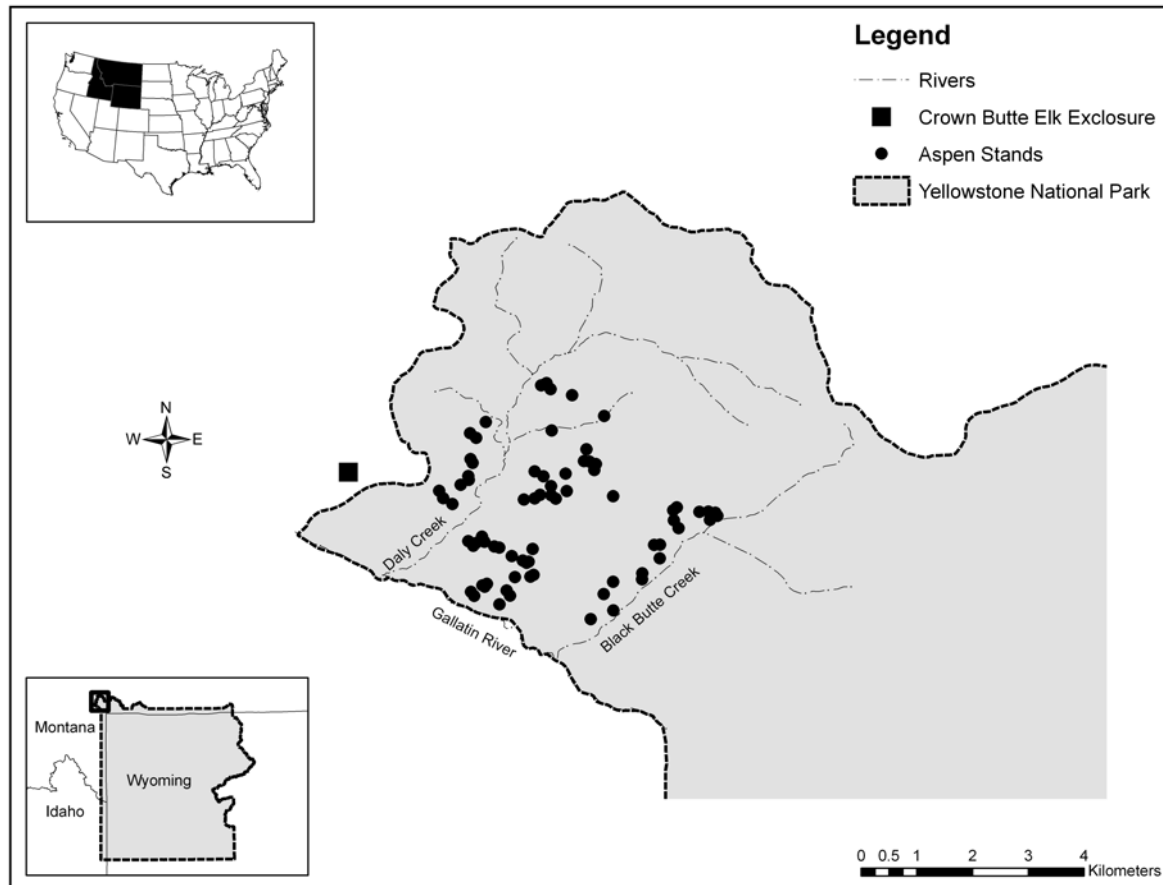


Figure 2.1. Study location. All data were collected within the Gallatin elk winter range, southwestern Montana. Porcupine exclosure is approximately 11 km north of the study area.

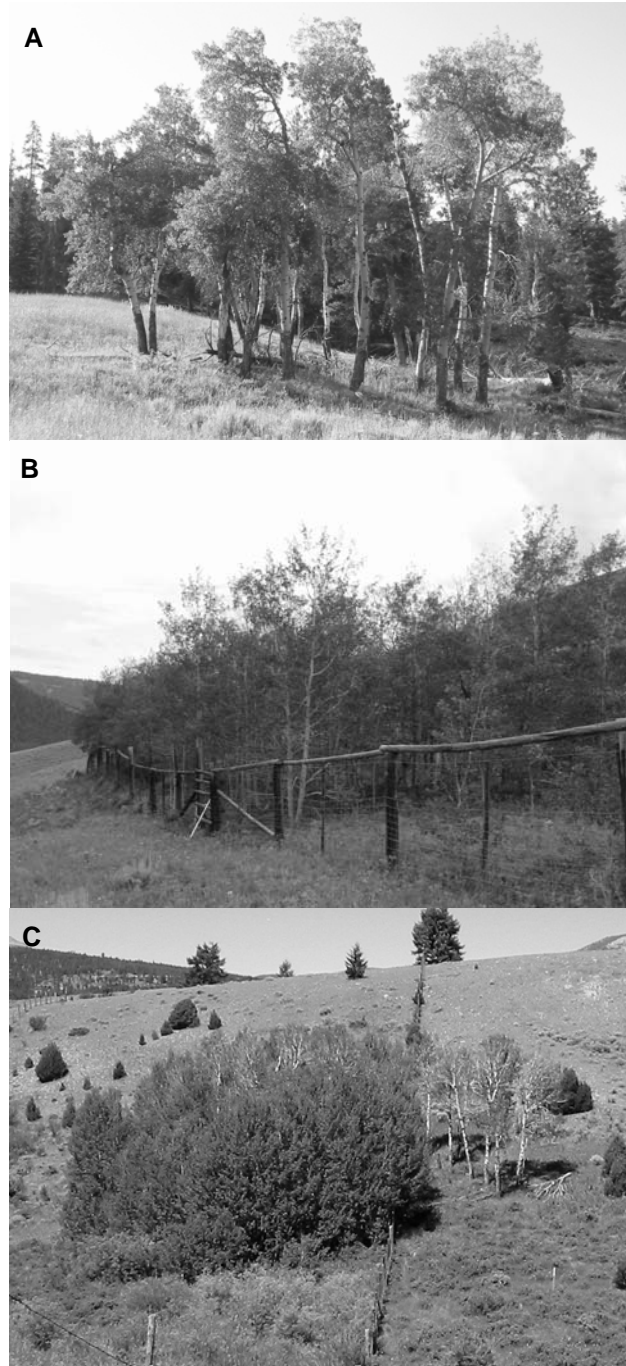


Figure 2.2. Photographs of aspen inside and outside elk enclosures. (A) A typical winter range stand, (B) Crown Butte enclosure, and (C) Porcupine enclosure. Note the lack of aspen recruitment in the typical winter range stand and the lack of aspen recruitment outside (left) of Crown Butte enclosure and outside (right) of Porcupine enclosure.

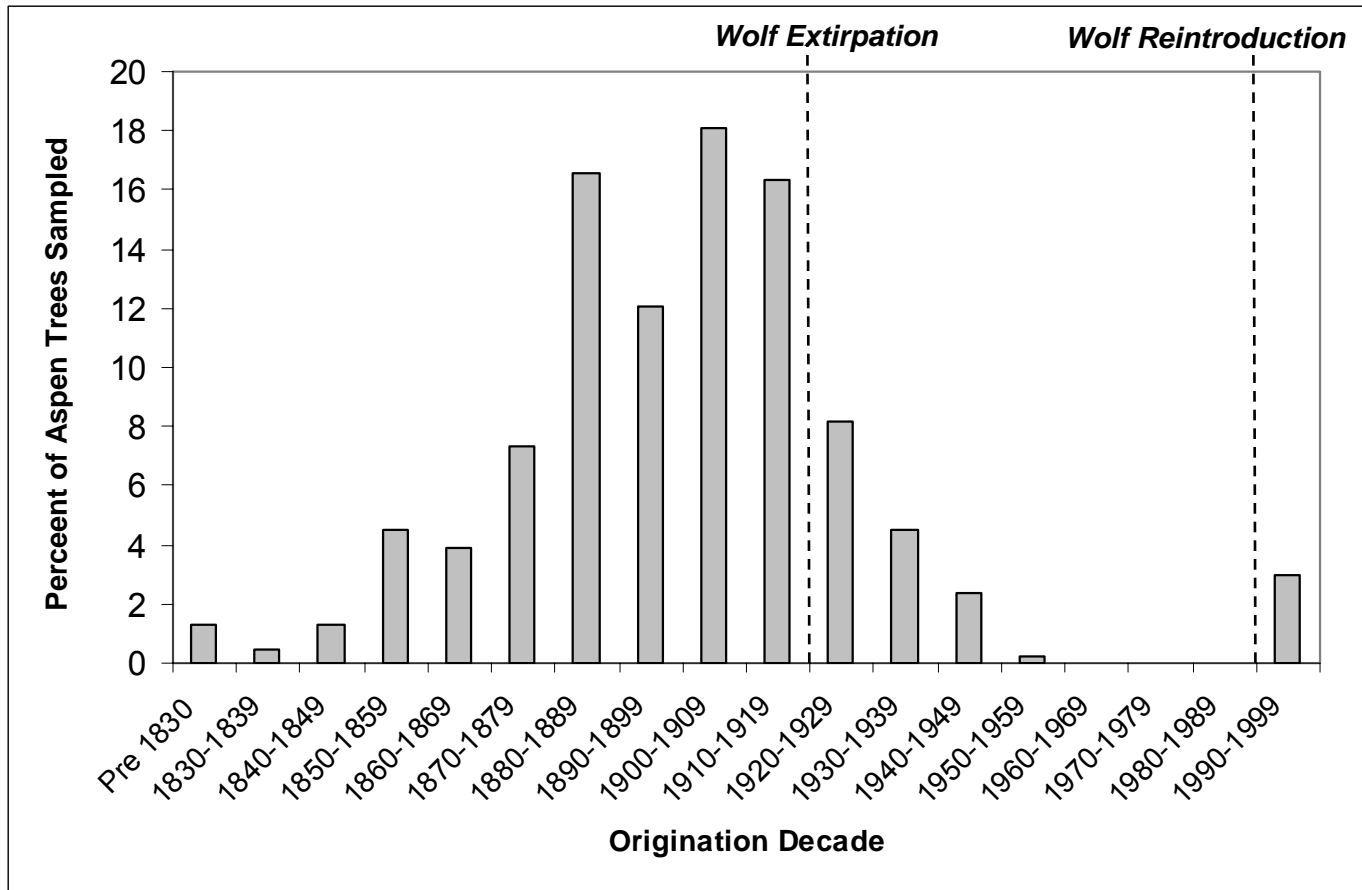


Figure 2.3. Winter range aspen origination (n = 476). While declining in the 1920s, 1930s, and 1940s, essentially no aspen trees were found originating between the 1950s and 1980s during a time of wolf absence. Recent recruitment in the 1990s is coincident with wolf reintroduction.

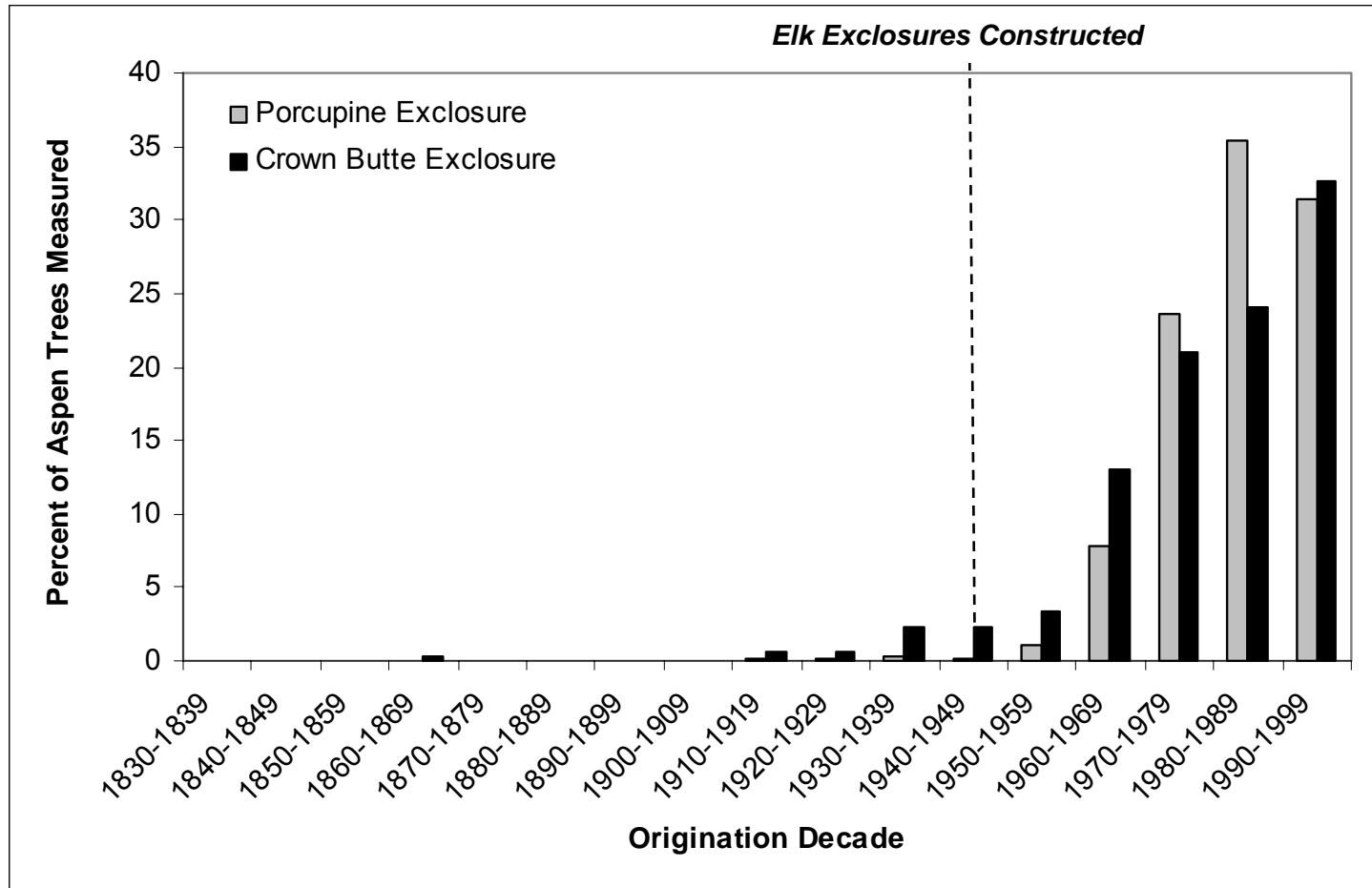


Figure 2.4. Aspen origination inside Crown Butte (n = 353) and Porcupine (n = 653) exclosures. Aspen have consistently recruited inside the fences since their erection in the 1945.

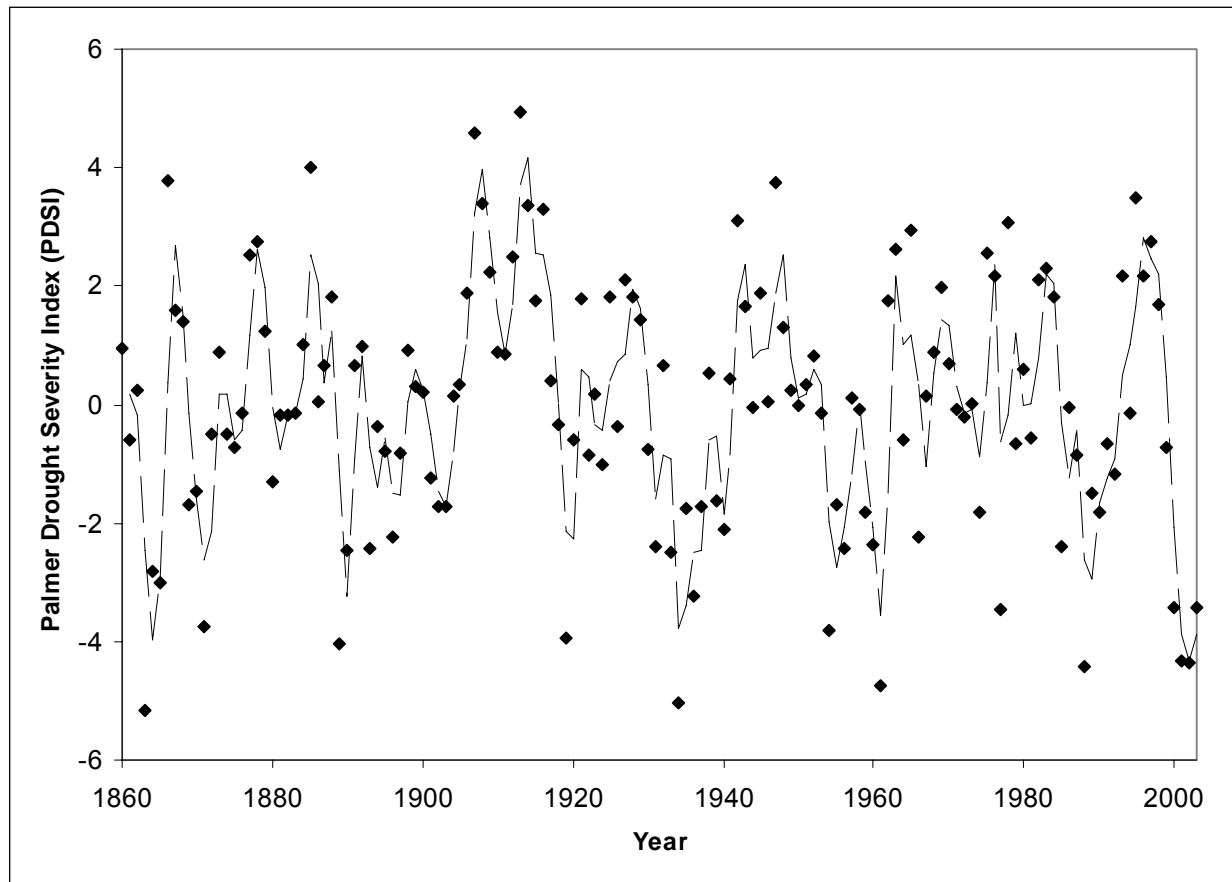


Figure 2.5. Palmer drought severity index (PDSI) values through time with a fitted moving average line. The more negative the PDSI value, the dryer the year. The more positive a PDSI value, the wetter the year. A PDSI value of zero indicates an average year.

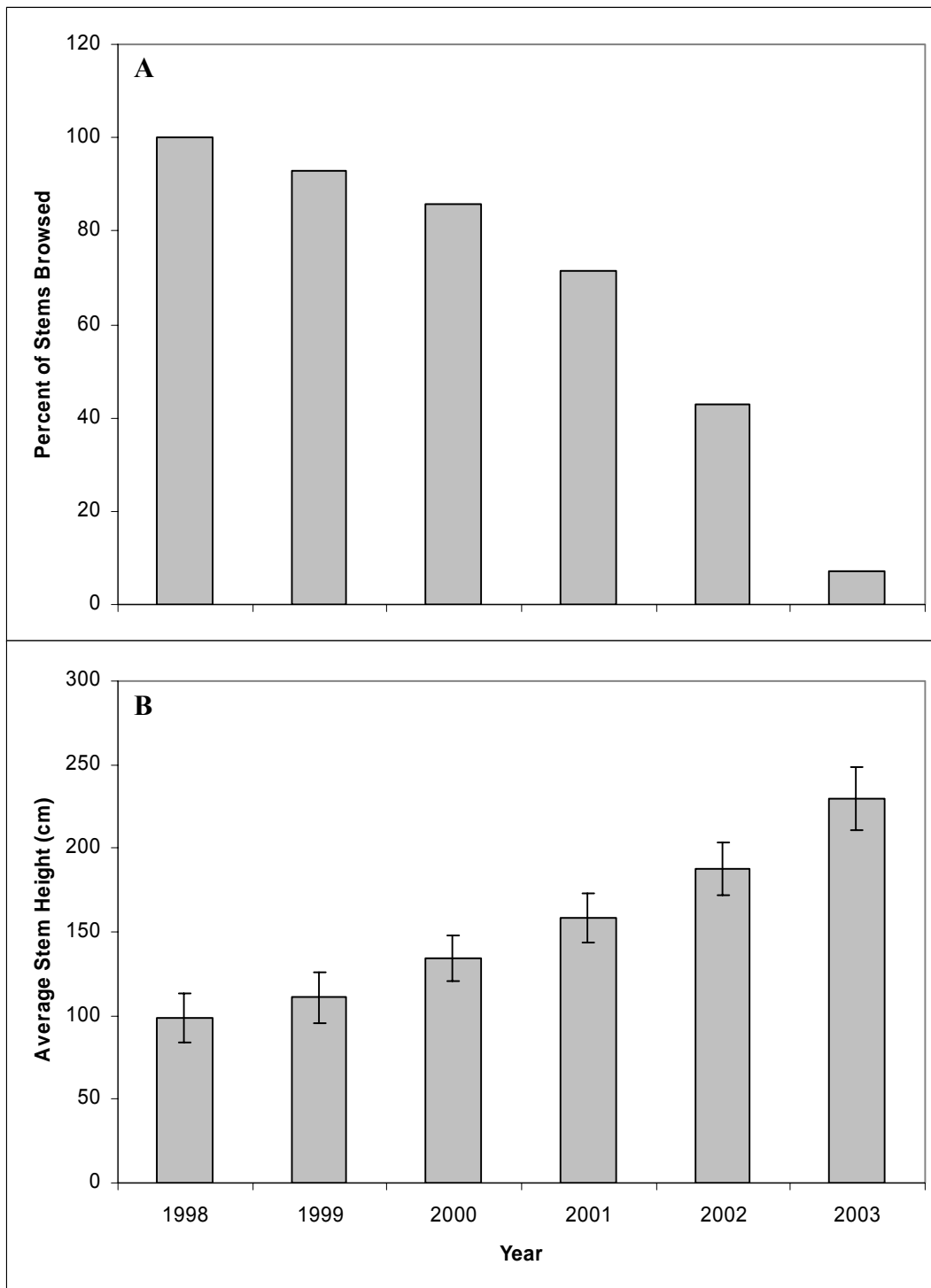


Figure 2.6. Aspen recruitment originating in the 1990s ($n = 14$). A) The percentage of the stems browsed in a given year. B) Average height and standard error bars for recruiting aspen stems.

CHAPTER 3 - REESTABLISHING LINKAGES BETWEEN FIRE AND ASPEN RECRUITMENT AFTER WOLF REINTRODUCTION

Abstract

We report on the recent growth of dense, tall upland aspen (*Populus tremuloides*) thickets in northwestern Yellowstone National Park, USA, following wolf (*Canis lupus*) reintroduction in the winters of 1995 and 1996. We assessed aspen growth patterns since wolf reintroduction by comparing post-fire aspen growth patterns in an area burned in the 1988 fires to aspen growth patterns in an adjacent unburned area. Within a 2x6 m belt transect placed within every aspen thicket, we measured aspen densities and recorded annual browsing and height information on the three tallest aspen stems during November 2005. We found greater aspen stem densities ($p < 0.01$) and taller aspen ($p < 0.01$) in the burned area when compared to the unburned area. Although still within the reach of elk (*Cervus elaphus*), a decline in the percentage of stems browsed in the burned area began in 1997 with no measured stems browsed after the 2001 growing season. In contrast, the percentage of stems browsed in the unburned area began declining in 2002, although 41% of stems were browsed in 2004. We conclude that the combined effect of fire and a subsequent decrease in herbivory following wolf reintroduction facilitated aspen growth. We postulate that in addition to any changes in elk density in recent years, a recoupling of fire with increased predation risk in the presence of wolves may improve aspen recruitment.

Introduction

Intense, chronic herbivory by wild or domestic ungulates can prevent aspen (*Populus tremuloides*) from growing above an upper browse level. For ungulates such as elk (*Cervus elaphus*), this height is approximately 200 cm (Keigley et al. 2002). Where such herbivory occurs and overstory trees die of disease or other causes, the likelihood of aspen persisting into the future becomes low. Thus, in areas of the Rocky Mountains frequented by ungulates, long-term browsing may represent a major factor contributing to the local decline of aspen and associated plant species (Bartos et al. 1994; Romme et al. 1995; Baker et al. 1997; White et al. 1998; Ripple & Larsen 2001).

Although aspen stem densities can greatly increase following fire, Bartos et al. (1994) found post-fire stem densities returned to pre-fire levels within 12 years due to high levels of wild-ungulate herbivory in western Wyoming. Similarly, Romme et al. (1995) documented overall suppression and mortality of post-fire aspen stems largely as a consequence of wild-ungulate herbivory in the northern range of Yellowstone National Park. In effect, intense, chronic herbivory “uncoupled” the normally expected increase in aspen height and densities (Hessl & Graumlich 2005).

While Bartos et al. (1994) and Romme et al. (1995) reported a decline in post-fire growth of new aspen stems as a consequence of herbivory, these studies were conducted in wolf-free (*Canis lupus*) environments. In Canada, White et al. (2003) found the relationship between aspen, disturbance, and elk herbivory varied with risk

of predation from human hunters and/or wolves (a behaviorally-mediated effect). Specifically, they observed a positive relationship between predation risk and aspen densities illustrating that a numerical decline in elk (a density-mediated effect) was not the only factor contributing to aspen growth in their study area. After seven decades of wolf absence in Yellowstone National Park, changes in elk behavior have been documented following the reintroduction of wolves (Laundré et al. 2001; Childress & Lung 2002) demonstrating variation in elk predation risk with wolf absence or presence. Because of their potential to influence other animals, wolves have been identified as a strongly interacting species (Soulé et al. 2005).

The objective of this study was to assess differences in patterns of aspen growth between a paired burned and unburned area following wolf reintroduction. Before their reintroduction, wolves had been absent in the park since prior to 1930. To our knowledge, the occurrence of upland aspen recruitment outside of exclosures and fine-scale browsing refugia has not been reported within Yellowstone National Park for several decades.

Study Area

Our research was located on the northwest edge of the park, approximately 15 km north of West Yellowstone. The study area is dominated by gentle, undulating topography (mean elevation of study area = 2083 m, standard deviation [SD] = 8; mean slope = 7 %, SD = 5) and lodgepole pine (*Pinus contorta*) forests. Douglas-fir (*Pseudotsuga menziesii*) was present in low numbers. Our study area was ~3 km² in

size and consisted of mostly pure aspen stands with minimal conifer presence inside any stand. Aspen understories were primarily composed of grasses and forbs.

Hunting occurs adjacent to the park boundary and two elk feedgrounds located on private land within ~8 km of the study area were open since at least the 1970s until approximately 1995 (Pils, personal communication). While the study area is used year round by elk, greatest use occurs in the spring/early summer and late fall/early winter (Pils, personal communication). Winter use of the area by elk declines during years of deep snowpack.

The study encompassed two areas defined by overstory mortality of aspen trees (aspen boles >5 cm in diameter at breast height) resulting from the 1988 Yellowstone fires: 1) an unburned area with an aspen overstory present and 2) a burned area characterized by a near absence of overstory aspen trees. Both areas were initially identified from a burn-severity map for the 1988 Yellowstone fires but were further adjusted from field observations of charcoal and residual overstory tree presence. To minimize potential edge effects due to changes in fire severity, a 250 m buffer was positioned between the two areas, and a 100 m buffer was placed between the unburned area and the park boundary. We used the generic term “stem” to describe any aspen originating after the 1988 fires. We defined high-density aspen thickets as containing ≥ 120 aspen stems/100 m². Due to a lack of high-density thickets in our unburned area, we measured low-density thickets in that area, defined as locations with ≥ 20 aspen stems/100 m². No thicket was within 15 m of any other thicket.

Methods

Within the study area, all thickets were located, classified as burned or unburned, and measured. For each aspen thicket, we oriented a 2x6 m belt transect from a thicket's edge toward the thicket centroid. For circular thickets, we randomly determined where transects began. Elliptical thickets were defined as the major axis being at least twice as long as the minor axis based on measurements with a laser range finder. For elliptical thickets, we randomly placed our belt transect in the middle third of the thicket, perpendicular to the major axis.

We measured plant architecture, an approach that examines plant growth form to determine annual browsing and height history (Keigley et al. 2003), on the terminal leader of the three tallest aspen stems within each transect. For the three stems, we recorded annual occurrence/absence of browsing and stem height for a minimum of six and a maximum of ten previous years. We also extracted an increment core ~20 cm above the base of each measured aspen for determining stem age. Following Stokes and Smiley (1968), aspen cores were air-dried, mounted, and sanded to aid in counting growth rings using a dissecting binocular microscope.

Because elk may browse thicket edges but not thicket interiors depending on predation risk (White et al. 2003), we measured the tallest stem in each meter of transect to determine if stems closer to thicket edges were shorter than stems further from thicket edges. We tallied the total number of stems within each belt transect to calculate stem density. In addition to annual height growth and browsing patterns, we used the plant architecture information to determine if the last year aspen stems were

browsed was within the normal reach of elk (< 200 cm). Since the contiguous area of this study comprised ~ 3 km², we assumed climate and browsing opportunities were similar between the two areas.

We used two-sample *t*-tests with unequal variances to determine if differences in aspen densities and growth patterns were present between the two areas. Before conducting *t*-tests, stem densities, 2004 stem heights, and the height when each stem was last browsed were log-transformed to better meet the assumptions of normality. We also conducted a regression to determine if there was significant relationship of stem height with distance along transects.

Results and Discussion

We located 21 aspen thickets in the unburned area and an additional 23 aspen thickets in the burned area. All measured aspen originated after the 1988 fires. Aspen densities were more than three times greater in the burned area (*t*-statistic = 9.8_{20,22}; *p*-value < 0.01) compared to the unburned area (Table 3.1 and Figure 3.1). Aspen densities in the burned area were similar to trends reported in the aspen literature (Debyle & Winokur 1985; Bartos et al. 1994; Romme et al. 1995; Bailey & Whitham 2002) and in part likely related to a release from apical dominance following the removal of overstory trees by fire (Frey et al. 2003). While differences in stem heights between areas have been present since at least 1995 (Figure 3.2), stem heights for the burned area have greatly increased in recent years. In 2004, unbrowsed aspen stems in the burned area had more annual growth (*t*-statistic = 8.1_{16,22}; *p*-value = < 0.01) than

unbrowsed stems in the unburned area (Table 3.1). Increased growth in the burned area was likely due to less overstory presence, greater carbohydrate reserves, and less shade than those stems in the unburned area (Table 3.1).

There were no differences in stem heights along our transects within the burned and unburned areas (unburned: $F_{5,85} = 0.21$, $R^2 = 0.05$; burned: $F_{5,128} = 1.76$, $R^2 = 0.08$) indicating elk were not preferentially browsing stems closer to thicket edges. Twenty-seven of 66 stems (41%) in the unburned area were browsed in 2004 whereas 2001 was the last year any of the measured stems in the burned area were browsed (Figure 3.2). Aspen were last browsed between 29 and 158 cm in height in the unburned area and between 102 and 133 cm in the burned area illustrating a decline in aspen browsing when stems were within the reach of elk.

Herbivory levels in the unburned area were $\geq 73\%$ between 1995 and 2002 (Figure 3.2a). In contrast, browsing levels on aspen stems in the burned area declined from nearly 100% in 1995 to zero in 2002. Based on optimal foraging theory (Lima & Dill 1990), in a predator-poor environment, herbivores should spend more time in areas with greater energy gain and minimal search effort (burned area). Such an expectation is consistent with the $\sim 100\%$ stems browsed in 1995 and 1996 in the burned area (Figure 3.2). However, the percentage of stems browsed in the burned area following 1996 declined even though all measured stems were within the reach of elk (Table 3.1) and browsing opportunities were equivalent between burned and unburned areas.

If reduced predator detection and maneuverability through tall high-density thickets can increase ungulates risk from predation (Lima 1992; Ripple & Beschta 2004), this could result in thicket avoidance by elk creating a potential feedback mechanism that enables these aspen to grow taller. In areas with a high risk of predation, White et al. (2003) noted an inverse relationship between predation risk and the number of elk pellets in high-density thickets. They suggested high-density thickets might increase aspen fitness in predator-rich environments whereas the same thickets could be detrimentally impacted in herbivore-rich situations. Their suggestion is consistent with our observation of suppressed aspen growth in high density stands in 1995 and 1996, an herbivore-rich situation, followed by a decline in browsing following wolf reintroduction (increased predator richness and predation risk). The occurrence of a predation risk effect is also consistent with observations by Halofsky (2007, Chapter 4) who found greater female elk vigilance near escape impediments such as down woody debris, a common feature in burned forests. Lastly, while not common in the park, cougars (*Felis concolor*) are present and do prey on elk. As an ambush predator, tall, high-density thickets could provide stalking and hiding cover for mountain lions (Kunkel et al. 1999).

From the perspective of aspen, there could be safety in numbers in an herbivore-rich system. With a relatively high density of stems, perhaps there is a greater likelihood some stems would escape herbivory. Yet the converse can also be argued. Assuming browsing opportunities in both areas were similar, it would have been more energetically efficient to browse in the burned area thus enabling the

dispersed stems in the unburned area to escape repeated herbivory. However, our results suggest elk were browsing both areas at high levels in 1995 and 1996 after which they preferentially browsed the unburned area following wolf reintroduction (Figure 3.2a).

In Yellowstone's northern range, Romme et al. (1995) concluded elk browsed aspen sprouts regardless of aspen densities and fire severities both two and three years after the 1988 fires. Bartos et al. (1994) reported an average aspen stem height of 50 cm 12 years after a prescribed fire across fire severities in Wyoming and attributed the lack of tall aspen stems primarily to elk herbivory. They further suggested that fire, in combination with high levels of herbivory, could hasten the loss of aspen stands. Both Bartos et al. (1994) and Romme et al. (1995) studied aspen in wolf-free environments. In contrast, White et al. (2003) observed high-density aspen thickets after disturbance in areas of low elk use and high hunter/wolf predation risk. Based on 95% territory estimates, the current study area has been part of a wolf pack territory for every year between 1995 and 2004 except for 1997 and 1999 (Phillips & Smith 1997; Smith 1998; Smith et al. 1999; 2000; 2001; Smith & Guernsey 2002; Smith et al. 2003; 2004; 2005). While suppression of young aspen from herbivory has been reported where wolves were absent (Bartos et al. 1994; Romme et al. 1995) the current study and White et al. (2003) found a patchy occurrence of tall and dense thickets of aspen after disturbance in the presence of wolves.

Studies of elk behavior in the park have documented increased vigilance levels since wolf reintroduction (Laundré et al. 2001; Childress & Lung 2002), changes in

elk movement patterns in wolf presence (Fortin et al. 2005; Hebblewhite et al. 2005; Mao 2005), and changes in elk reproductive physiology (Creel et al. 2007) all of which could potentially cause a change in woody plant browsing. With documented changes in elk behavior since wolf reintroduction, in the presence of wolves we postulate fire can influence upland aspen in two distinct ways: 1) increasing densities and growth rates of aspen reproduction; and 2) increasing predation risk for ungulates through thicket effects and potential increases in down woody debris. Therefore, the combined effects of fire and predation are likely to facilitate successful clonal aspen recruitment.

Conclusion

The presence of tall high-density aspen thickets is currently rare in Yellowstone National Park. Our data indicate an inter-relationship between fire and reduced herbivory on thicket density and growth coincident with wolf reintroduction. Therefore, the coupling of predation risk with fire may aid upland clonal aspen recruitment. Although changes in herbivory may have in part resulted from density-mediated effects, our results are consistent with expected changes also associated with a behaviorally-mediated trophic cascade.

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Table 3.1. Aspen characteristics between the burned and unburned areas. * indicate both the mean and the 95% confidence limits (CL) for the mean were back-transformed from log space. ^ψThe height at which stems were last browsed was used to determine if measured aspen stems stopped being browsed within the reach of elk (< 200 cm).

Variable	Unburned Area	Burned Area	<i>t</i> -statistic	<i>p</i> -Value
	Mean (95% CL)	Mean (95% CL)		
Density of stems originating after the 1988 fires (per ha)*	8118 (6616, 9960)	28344 (23931, 33571)	9.8 _{20,22}	<0.01
Height (cm) when stems were last browsed* ^ψ	71 (63, 80)	114 (105, 124)	-6.9 _{20,22}	<0.01
Stem height in 2004 (cm)*	88 (77, 101)	330 (294, 370)	15.6 _{20,22}	<0.01
Annual growth of unbrowsed stems in 2004 (cm)	20 (15, 26)	47 (42, 52)	8.1 _{16,22}	<0.01

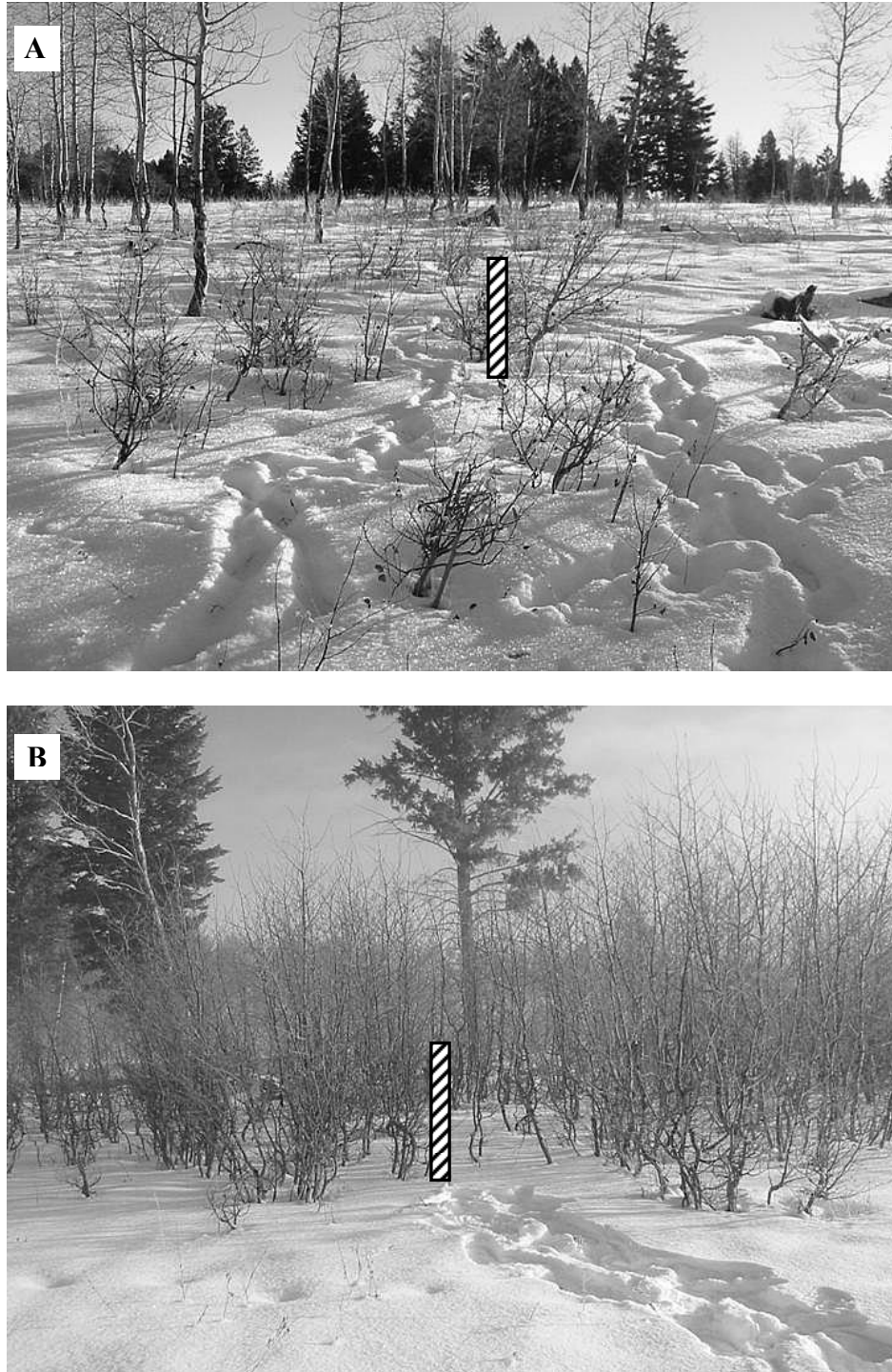


Figure 3.1. Aspen thickets in Yellowstone National Park: (A) A short low-density thicket in the unburned area and (B) a tall high-density thicket in the burned area. The bar in each picture is approximately 1 meter.

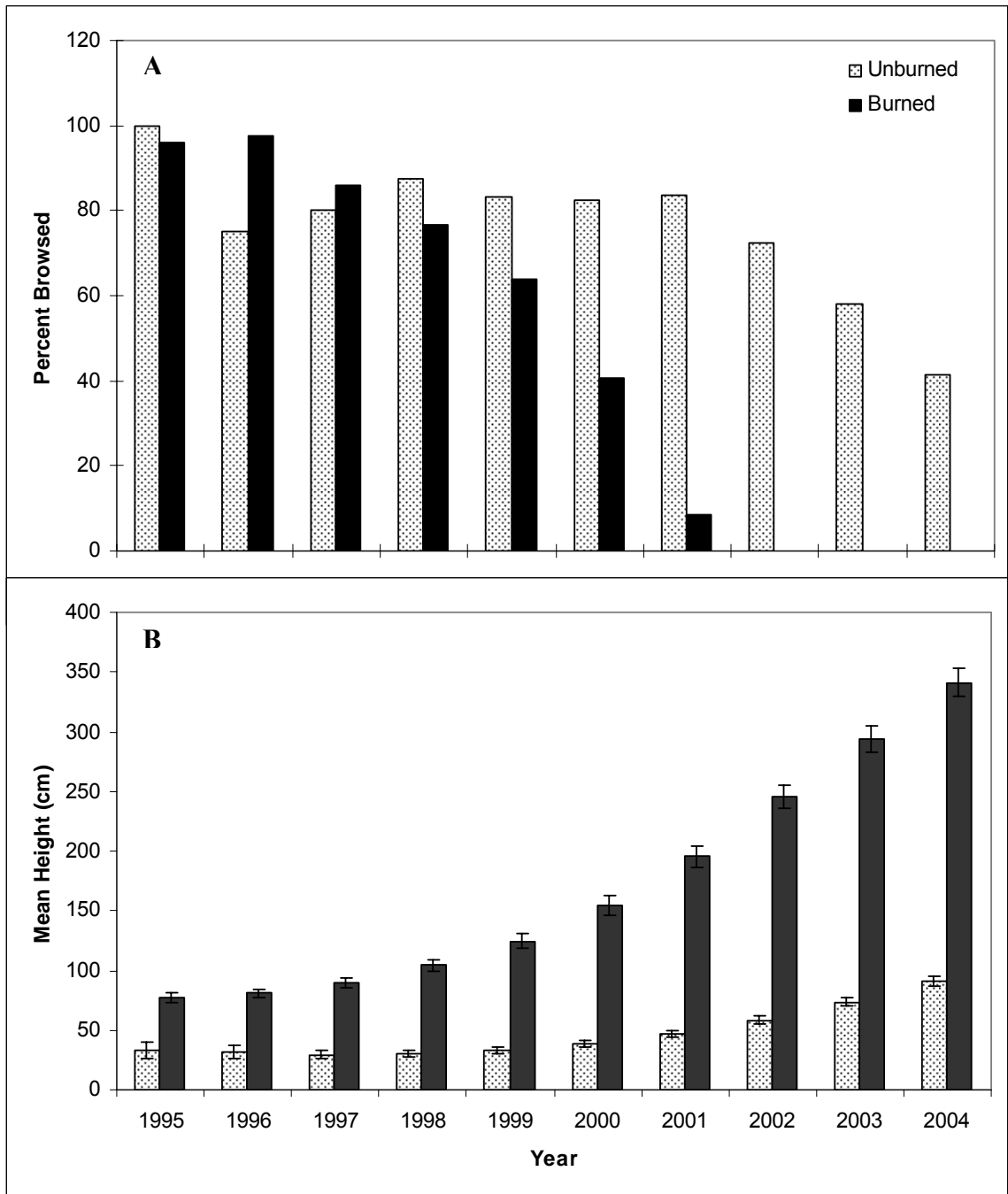


Figure 3.2. Attributes of aspen in burned and unburned areas of Yellowstone National Park: (A) Percentage of measured aspen stems browsed in each area and (B) mean annual height with standard errors in each area. November 2005 height data was excluded because those stems had not been exposed to a full year of browsing at the time of measurement.

CHAPTER 4 - MODELING FINE-SCALE PREDATION RISK ON ELK IN YELLOWSTONE NATIONAL PARK, WYOMING, USA.

Abstract

To determine if a relationship exists between predation risk perceived by elk (*Cervus elaphus*) while browsing and elk position within the landscape, we observed a total of 56 female elk during two summers and 29 female elk during one winter. At a fine spatial (0-187 m) and temporal scale (145-300 s), results from our model selection indicated summer vigilance levels were greater for females with calves than for females without calves, with vigilance levels greater for all females at closer escape impediment distances. Winter results also suggested greater female vigilance levels at closer escape impediment distances, but further indicated an increase in vigilance levels with closer conifer edge distances. Placed within the context of other studies, the results were consistent with a behaviorally mediated trophic cascade and provide a potential mechanism to explain the variability in observed woody plant release from browsing in Yellowstone National Park, Wyoming, USA.

Introduction

An animal's landscape can be described by surrounding vegetation, topography, and climate. Another lens through which an animal's landscape can be viewed and defined is by varying levels of predation risk, also known as the landscape of fear (Laundré et al. 2001). Peaks and valleys in a landscape of fear can be related to relatively greater and lesser risks from predation. Such a landscape can be explicitly measured and defined through an animal's behavior, and also by the

animal's location within the landscape at any given moment. Risk from predation can therefore vary temporally over minutes, days, seasons, and years, and spatially with proximity to refugia. An outcome from behavioral decisions related to predation risk will also partially dictate the duration, frequency, and location of food acquisition. Therefore, outcomes of behavioral decisions related to predation risk could in part dictate present and future prey fitness, as well as modify plant communities (Brown et al. 1999; Schmitz et al. 2004; Ray et al. 2005).

According to foraging theory, prey should balance resource acquisition (food, shelter, and mates) and safety, demands that can conflict with one another (Sih 1980; Lima & Dill 1990; Brown et al. 1999). Whether prey decide to seek food in a risky patch over a safe patch depends on many factors including: the physical state of the forager (starving or satiated); the potential energy gain from the food source; direct and indirect indicators of predation risk such as frequency with which prey encounters a predator; time since last predator encounter; and forager and predator species size (Berger & Cunningham 1988; Brown 1999).

Prey have various methods of decreasing their individual predation risk. Although not always observed (Laundré et al. 2001), an anti-predator strategy often described in ungulate literature relates to group size. While predator detectability of prey might increase with prey herd size (Hebblewhite & Pletscher 2002), several anti-predator advantages of larger group sizes potentially exist including the decreasing probability that any single individual will be killed (dilution effect), and the possibility of more "eyes" to scan the environment for predators (many eyes effect) (Dehn 1990;

Geist 2002). Hence, the amount of scanning done by a given individual could decrease with increasing group size. With decreased scanning time, the amount of time spent on other activities, such as foraging, can increase for an individual.

While behavioral predator-prey studies involving large predators are limited in Yellowstone National Park (YNP), Wyoming, USA, the reintroduction of gray wolves (*Canis lupus*) into the park in the winters of 1995 and 1996 offered researchers an opportunity to study behavioral changes in this species' primary Park prey: elk (*Cervus elaphus*). When an ungulate is killed by a wolf, studies have observed the occurrence of kills to be greater in certain landscape locations than others. In YNP, Bergman et al. (2006) found greater elk vulnerability to wolf predation when elk were closer to edges, defined as changes to the forest structure that could impede animal movement, suggesting speed, maneuverability, and escape potential decreased around these structural elements of the landscape. Gula (2004) in Poland and Kunkel and Pletscher (2001) in Glacier National Park, Montana, USA, observed greater wolf kill success near riparian areas and in ravines, with the latter study further detecting greater wolf kill success near ice. Geist (2002) noted running elk tended to avoid impediments, such as slash, deep snow, and swampy grounds.

Vigilance represents a frequent behavioral measure of elk response to predation risk (Hunter & Skinner 1998), a behavior described by an alert posture where the animal is erect with its head above shoulder height (Geist 2002). To date, research on elk within YNP has documented increased average female elk vigilance levels following wolf reintroduction, greater female elk vigilance levels in high wolf-

encounter regions, and lower female elk vigilance in low wolf-encounter regions (Laundré et al. 2001, Childress & Lung 2003). Other post-wolf reintroduction studies have observed seasonal changes in habitat preference by elk (Mao et al. 2005) and changes in habitat preference by elk dependent upon wolf presence or absence (Wolff & Van Horn 2003; Creel et al. 2005; Fortin et al. 2005; Gude et al. 2006).

Concurrent with post-wolf reintroduction studies on elk behavior, plant research in the Park has tested the theory of trophic cascades, defined as the indirect effects of carnivores on plants. According to trophic cascades theory, elk densities should decrease, and/or elk foraging behavior should change as a consequence of increased predation risk with wolf reintroduction, thereby allowing browse plant species preferred by elk to grow taller. Correlative evidence has documented decreases in aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and willow (*Salix* spp.) regeneration following wolf extirpation in 1926 (Larsen & Ripple 2003; Ripple & Beschta 2004; Beschta 2005), and a patchy release in cottonwood and willow following wolf reintroduction (Beyer 2006; Ripple & Beschta 2006), in some areas of the Park. Yet these data and conclusions are vegetation-based, without any direct elk behavior observations other than population estimates and telemetry inferences.

Collectively, recent research in the Park broadly indicates that: 1) elk vigilance behavior and movement patterns have changed since wolf reintroduction; and 2) certain woody browse species preferred by elk are beginning to release in some locations within elk winter ranges throughout the Park for the first time in several

decades. The overall research goal is to improve our understanding of elk vigilance behavior and fine-scale foraging patterns as they relate to ongoing patterns of woody plant release. The specific question we addressed was: does elk vigilance while foraging vary across the landscape?

Methods

Field methods

We observed elk vigilance in YNP through binoculars (8 x 23 m) from roads in the park. We studied summering female elk observed along the paved road corridor between West Yellowstone and Madison Junction, and from Madison Junction to Mammoth Hot Springs, and wintering female elk observed along the road corridor from Tower Junction to Buffalo Ranch in the Lamar Valley. Elk vigilance was defined as the proportion of time an elk had its head above shoulder height as compared to browsing and grooming. Because not all elk were observed for the same length of time, we calculated the ratio of the amount of time an elk was vigilant to the total observation time thereby standardizing all observations for comparative purposes. We observed female elk from 1 August to 10 August 2005, and from 7 June to 15 June 2006, between 0530-2100 hours. Winter elk observations were made between 15 November and 26 November 2005 from 900-1630 hours.

Once we located an elk herd, a focal female elk was haphazardly chosen based on herd position and if she was in a bout of feeding (Childress & Lung 2003). We defined an elk herd as any elk that was separated by less than 100 m from any other

elk (Childress & Lung 1003). We defined a feeding bout as an active feeding period for an individual and only female elk in the midst of a feeding bout were selected for observation.

To reduce the likelihood of observing the same individual more than once, we only observed one to three focal individuals in each herd, and only revisited herds at a particular location if they contained more than 10 individuals (Childress & Lung 2003). Like Fortin et al. (2004), each focal observation ended after five minutes or if the animal lay down. Because we were interested in the distance between the observed animal and fine-scale features in the landscape, observations also ceased if the animal moved more than six steps. For summer observations, the female social status of each focal elk was further noted as either females with calves or females without calves. Because 2006 summer observations were conducted during the birthing season when newborn calves are often hiding, it is likely some mothers were misclassified as females without calves. Due to large winter herd sizes, we were unable to measure female social status during winter observations. For all herds, we recorded the group size, or total number of animals in a herd. All observations were recorded using a tape recorder and later transcribed.

Any observation less than 120 seconds long was discarded. We also discarded observations if the behavior was compromised due to road noise, the presence of the observer, or the presence of other Park visitors. All elk had to be greater than 75 m from the primary road (mean summer road distance \pm SE = 216 \pm 23 m, mean winter road distance \pm SE = 535 \pm 58 m). To lessen the impact an observer might have on

elk behavior, we initiated observations only after the observer was situated for five minutes.

We recorded the position of each observation point with a global positioning system receiver, noting the distance and azimuth from the observation point to the focal elk with a laser range finder and compass. Once the herd was no longer present, we moved to the location of the focal elk based on azimuth and distance from observation point and recorded fine-scale spatial information in each of four 90° quadrants defined by the cardinal directions. Within each quadrant, we noted escape impediment type (boulders or downed woody debris > 15 cm in diameter at breast height), distance to each escape impediment, distance to conifer edge, and distance to primary road. All distance measurements were made with a laser range finder that had a maximum search radius of 999 m. We also recorded visibility within a quadrant, defining visibility as the distance to an object or landform that blocked more than ¼ of the potential view within the quadrant. Visibility evaluation was based on the assumption that an elk is approximately 2 m tall.

Data Analyses

Because both the response variable (elk vigilance) and the majority of measured landscape variables were continuous, we developed multiple regression models and conducted model selection using Akaike's Information Criteria (AIC) (Burnham & Anderson 2002). We used AIC_c to account for potential bias when the sample size is small relative to the number of parameters in the candidate models (Burnham & Anderson 2002).

We generated a set of *a priori* hypotheses (Table 4.1) to guide the development of biologically reasonable one-, two- and three- factor regression models explaining elk vigilance. As elk vigilance is a proportion between 0 and 1, we applied a logit transformation ($\log[Y/1-Y]$) to our response variable (Ramsey & Schafer 2002). We found high correlations ($r > 0.90$) between the distance to nearest escape impediment and average distance to nearest two and three escape impediments. Because explanatory variables with correlations > 0.90 can inflate the amount of variation explained if placed in the same model (Burnham & Anderson 2002), we included only the distance to nearest escape impediment, rather than the average distance to the nearest two and three escape impediments, as an explanatory variable in all further analyses.

All candidate models were created from some combination of the following explanatory variables: distance to nearest structural impediment to escape (Impediment), distance to nearest visibility impediment (Visibility), distance to nearest conifer edge (Conifer Edge), Group Size, and female with or without a calf (Social Status) (Table 4.2). To better meet the assumptions of regression, we log-transformed Visibility, Impediment, and Conifer Edge (Ramsey & Schafer 2002). As we collected data over two summers, the summer analysis was blocked by year. Winter data were analyzed separately from summer data because observations were conducted in different portions of the Park and factors associated with elk behavior could differ seasonally. Seven winter observations were beyond the search radius of our laser

range finder for impediment distance and were therefore discarded from the AIC_c analysis.

We ran the AIC_c analyses using the PROC MIXED function with maximum likelihood estimation methods in SAS v9.1 (SAS Institute, Cary, NC, USA), ranking the 21 summer and 13 winter candidate models from lowest to highest AIC_c values. The difference in AIC_c values between the model with the lowest AIC_c value and each successive model, known as Δ_i , was used to help determine the best set of candidate models. Δ_i values between 0-2 indicate strong support for the model being the best approximate model, Δ_i between 4-7 indicate moderate support for the model being the best approximate model, and Δ_i greater than 10 indicate weak support for that particular model (Burnham & Anderson 2002). We also generated Akaike's weights (ω_i) to further help determine the strength of evidence for each model, given a specific set of candidate models (Burnham & Anderson 2002). Akaike's weights are normalized to be a set of positive weights that sum to 1. We examined negative 2 log-likelihood values when choosing the set of best models. Negative 2 log-likelihood values reflect the overall fit of each model, where smaller values indicate a better fit. We calculated 95% confidence intervals to evaluate additional strength of support for various models. We also applied Welch's Two Sample *t*-tests with unequal variances to determine if differences at the 0.05 level were present in our explanatory variables by social status, year, or season.

Previous research on willow recruitment and elk browsing (Ripple & Beschta 2006) noted less browsing on willow ≤ 30 m of escape impediments. As *post-hoc*

analyses, we therefore examined the relationships between vigilance levels ≤ 30 m to the nearest escape impediment to vigilance levels beyond 30 m of the nearest impediment using Welch's Two Sample t -tests with unequal variances. All analyses were conducted with logit-transformed vigilance and log-transformed impediment distances to better meet the assumptions of t -tests.

Results

Summer Elk Vigilance

We collected a total of 56 summer elk observations ($n = 26$ in summer 2005, and 30 in summer 2006). On average, elk were observed for 260 s ($SE \pm 8$). Results from Welch's Two sample t -test revealed no differences (p -value ≥ 0.1) in observation length, Impediment, Conifer Edge, and Group Size between years or by social status. We therefore pooled the summer landscape explanatory variables from both years by social status (Table 4.3) to examine general observation trends. Female elk with calves spent an average $\pm SE$ of $22 \pm 5\%$ of their time being vigilant, while females without calves spent an average of $9 \pm 2\%$ of their time being vigilant.

Evidence from the AIC_c analyses strongly suggested Impediment was the most important variable measured in explaining summer elk vigilance (Table 4.4). When ranked by AIC_c score from lowest to highest value, all models with this explanatory variable were selected before any other model. Its importance was further supported by an examination of Akaike weights (Table 4.4). The combined Akaike weight, or importance value, of all models with the variable Impediment was

0.99 out of a possible total weight of 1.00, indicating 99% of the weight in favor of any of the 21 candidate models was for the six models containing this variable. In addition, results from our analyses suggested that of the other explanatory variables measured, Social Status helped explain additional variation in vigilance (importance value = 0.81). The top two candidate models included both the additive and interaction model with Impediment and Social Status. In the additive model, the 95% confidence interval for Social Status did not overlap zero (parameter estimate = -1.38 , SE = 0.36) and the back-transform 95% confidence interval for Impediment did not overlap one (parameter estimate = -0.62 , SE = 0.11) providing additional support for the selection of the top candidate model. Models including Group Size, Visibility, and Conifer Edge had relatively low ΔAIC_c , Akaike weight, and importance values. The non-hypothesized variable Road Distance had no relationship with summer vigilance levels ($F_{1,53} = 0.00$, $R^2 = 0.00$)

We created a graph of predicted elk vigilance using parameter estimates from the additive model: Impediment + Social Status (Figure 4.1). Predicted vigilance levels for females with calves were greater than predicted vigilance levels for females without calves (Figure 4.1). Predicted vigilance decreased with log-transformed escape impediment distance regardless of social status. The relationship between predicted vigilance and Impediment was not linear with predicted vigilance levels initially decreasing rapidly with increasing escape impediment distances before flattening.

Winter Elk Vigilance

We observed 22 elk during the 2005 winter (Table 4.3). Mean \pm SE winter observation length was 284 ± 7 s. On average, female wintering elk spent $10 \pm 3\%$ of their time being vigilant. Results from our comparison between combined summer explanatory variables to winter explanatory variables indicated wintering female elk were not further from impediments ($t_{56,22} = 1.13$, p -value = 0.26) or conifer edges ($t_{56,22} = -0.52$, p -value = 0.61), but had larger group sizes ($t_{56,22} = -6.67$, p -value < 0.001) (Table 4.3). The non-hypothesized variable Distance to Road had no relationship with winter vigilance levels ($F_{1,17} = 0.04$, $R^2 = 0.00$)

Although the top candidate models were within four ΔAIC_c units of the null model (Table 4.5), the Akaike weight of the null was small relative to the top three candidate models. The model with the greatest Akaike weight, Impediment + Conifer Edge, was slightly stronger than either explanatory variable by itself. While back-transformed 95% confidence intervals for the variables in this additive model slightly overlapped one (Impediment parameter estimate = -0.30; SE = 0.16; Conifer Edge parameter estimate = -0.42; SE = 0.21), the overlap was likely a result of increased variance in estimates with the inclusion of more parameters. However, since both the single variable model Conifer Edge (parameter estimate = -0.54; SE = 0.21) and the single variable model Impediment (parameter estimate = -0.40; SE = 0.17) had back-transformed 95% confidence intervals that did not overlap one, the pattern of the results support that both Impediment (importance value = 0.61) and Conifer Edge (importance value = 0.59) likely influence winter vigilance behavior, but that our

overall power was slightly low. Group Size (importance value = 0.18) was only selected first in models that also contained Impediment or Conifer Edge.

Impediments and Predation Risk –Post-hoc analyses

Summering female elk were more vigilant when ≤ 30 m to the nearest escape impediment (p -value ≤ 0.02) (Figure 4.2a). However, we found no difference in vigilance levels between summer and winter female elk ≤ 30 m ($t_{27,14} = 0.09$, p -value = 0.93) or for summer and winter female elk > 30 m from the nearest structural impediment to escape ($t_{29,8} = -0.52$, p -value = 0.61, Figure 4.2b). We then compared vigilance levels between all female elk without consideration of season (Figure 4.2c). Regardless of social status and season, female elk were more vigilant ≤ 30 m of the nearest impediment than they were beyond 30 m ($t_{41,37} = 4.40$, p -value < 0.001) (Figure 4.2c).

Discussion

Summer Observation

We found structural escape impediments in the landscape influence summering female elk vigilance at a very fine spatial (1-187 m) and temporal scale (145-300 s). It is therefore possible that measured escape impediments might be fine-scale analogues of broader-scaled hard edges such as ravines, riparian areas, ice, and burned forest edges, where greater numbers of wolf-killed ungulates have been found (Bergman et al. 2006; Gula 2004; Kunkel & Pletscher 2001) and where elk maneuverability could be hampered.

Like other vigilance studies conducted in the Park (Laundré et al. 2001; Childress & Lung 2003; Wolff & Van Horn 2003), we also observed greater vigilance by females with calves as compared to females without calves. In fact, our vigilance levels by social status were very similar to those reported by Childress and Lung (2003). While excluded from all analyses, on several occasions ($n = 4$), we opportunistically observed constant vigilance by a mother when a calf was actively suckling. Such observations, along with our observed greater vigilance by females with calves, are consistent with predation risk theory. From a risk perspective, since females with calves must not only assess their surroundings for themselves, but also for their calves, we would anticipate greater vigilance from mothers. In addition, it is likely a suckling calf underneath the mother increases calf exposure to predators while also causing the mother to be less able to maneuver if surprised by a predator.

Winter Observations

Consistent with the summer data, distance to nearest impediment helped explain winter female elk vigilance (Table 4.5). Thus, results from different Park locations, seasons, and herds suggest a similar mechanism, Impediment, influencing elk vigilance. Unlike the summer models, Conifer Edge also was also associated with female winter elk vigilance. The data indicated an increase in vigilance levels with closer conifer edge distances.

Greater elk vigilance near conifer edges is consistent with Mao et al. (2005), who found elk winter range use shifted to more open habitat following wolf reintroduction. In a winter study, Bergman et al. (2006) found wolves preferred to

move along hard edges, with elk vulnerability to wolf predation greatest along meadow/conifer and riparian hard edges. Frair et al. (2005) found elk in Canada were more likely to relocate when within 50 m of human created linear clearings; they suggested that elk predation risk was greater near linear features due to either wolf travel preferences or to the association of the clearings with people.

Creel et al. (2005) and Fortin et al. (2005) observed a shift to conifer forest by elk in the presence of wolves. Such findings do not necessarily contradict our results of greater vigilance near conifer edges. Because conifer forests can afford elk protection from some predators while open areas will typically contain more biomass available for consumption (Anderson et al. 2005), the transition zone between ecotypes and the associated wolf movement along hard edges could cause elk to temporarily be more vulnerable to predation and therefore be more vigilant. Levels of vigilance near conifer edges also could vary depending on the structural complexity of the forest, wolf presence, and/or current anti-predator strategy employed by elk.

Impediments and Predation Risk – A post-hoc analysis

Because models with Impediment were top candidate models for both summer and winter observations, we further investigated the relationship between vigilance levels and Impediment. We found female elk tended to be more vigilant within 30 m of an impediment despite the differences in location, group size, and potential predation risk between winter and summer data. As suggested by the AIC_c results and *post-hoc* analyses, Impediment appears to be biologically important with respect to vigilance and thus to elk predation risk. While elk were responding to Impediment,

due to the high correlation between Impediment and the average distance to the nearest two and three impediments, it is possible elk were responding to a cluster of structural features rather than just to the distance of the nearest single impediment.

As noted previously, Ripple and Beschta (2006) found locations of tall willow growth in northern YNP tended to be ≤ 30 m of the nearest impediment and tall willows had lower browsing intensities relative to shorter willows. Taken together, their observation of greatest willow heights ≤ 30 m from an impediment and our study of greatest female vigilance levels ≤ 30 m of the nearest escape impediment suggest the observed patchy distribution of woody plant release in YNP may be at least partially due to differences in elk browsing behavior mediated by predation risk. Therefore, in addition to any density-mediated effect, the cumulative evidence is consistent with a behaviorally-mediated trophic cascade between carnivore predators, elk, and woody browse species. As predation risk has also been observed over broad scales whereby elk select habitat based on the frequency of wolf-ungulate encounter (predation risk) and distance to safe habitat in YNP, we propose predation risk could be considered as an additional factor by which plant communities are structured across multiple scales.

Study Limitation

Although our vigilance responses were similar to those reported in other wolf-elk behavior studies, with most of the known elk behavioral research in the Park centering on wolf effects, knowledge of additive or compensatory vigilance behavior from elk in the presence of sympatric predators in this area, such as grizzly bear

(*Ursus arctos*), cougars (*Felis concolor*), and coyotes (*Canis latrans*) that feed on calves during the spring and summer (Houston 1978; Gese & Grothe 1995; Mattson 1997), is limited. We were therefore unable to quantify any effects that specific predators may have had on vigilance levels observed in this study.

Conclusion

The results of this study document non-lethal predator effects on prey in both winter and summer ranges of YNP, illustrating variation in behavior while foraging. Specifically, elk appeared to respond to proximity of structural escape impediments while foraging through increased vigilance at all times of the year. Although vigilance levels cannot be attributed to any specific predator, these results complement studies on factors associated with locations of documented willow recruitment and are consistent with a behaviorally-mediated trophic cascade. Thus, at fine spatial and temporal scales, female elk appear to forage optimally, balancing forage gain against predation risk.

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Table 4.1. List of *a priori* hypotheses used to generate candidate models.

Hypothesis	Vigilance Is Greater
1	As visibility decreases
2	As the number of escape impediments increases
3	As the distance to impediments decreases
4	As distance to the nearest conifer edge decreases
5	As group size decreases
6	For females with calves as compared to females without calves (social status)

Table 4.2. List of summer candidate models. Winter candidate models are identical except summer models with social status are not included in the winter analysis.

Null Model

- 1) Intercept Only

Vigilance Models

One Factor Models

- 2) Visibility
- 3) Social Status
- 4) Impediment
- 5) Group Size
- 6) Conifer Edge

Two Factor Models

- 7) Visibility + Social Status
- 8) Visibility + Impediment
- 9) Visibility + Group Size
- 10) Visibility + Conifer Edge
- 11) Social Status + Impediment
- 12) Social Status+ Group Size
- 13) Social Status + Conifer Edge
- 14) Impediment + Group Size
- 15) Impediment + Conifer Edge
- 16) Group Size + Conifer Edge

Three Factor Models

- 17) Visibility * Social Status + Visibility + Social Status
- 18) Visibility * Impediment + Visibility + Impediment
- 19) Social Status * Impediment + Social Status + Impediment
- 20) Social Status * Conifer Edge + Social Status + Conifer Edge
- 21) Impediment * Conifer Edge + Impediment + Conifer Edge

Table 4.3. Summary statistics of explanatory variables (mean \pm se, and range) included in AICc analyses.

Observations	n	Impediment (m)	Visibility (m)	Conifer Edge (m)	Group Size
Summer					
Female with calf	17	32 \pm 6.3; 1 - 79	74 \pm 13; 8 - 187	116 \pm 20; 17 - 260	9 \pm 1; 1 - 23
Female without calf	39	45 \pm 6; 1 - 169	96 \pm 6; 11 - 182	157 \pm 19; 40 - 763	9 \pm 1; 1 - 23
All females	56	41 \pm 5; 1 - 169	90 \pm 6; 8 - 187	144 \pm 14; 17 - 763	9 \pm 1; 1 - 23
Winter					
All females	22	29 \pm 6; 0.5 - 104	30 \pm 8; 12 - 119	250 \pm 50; 6 - 850	30 \pm 3; 9 - 59

Table 4.4. Results of AICc analysis for models explaining summer female elk vigilance. The number of parameters estimated in the model (K), the negative 2 log-likelihood (-2LogL), the AICc, the difference in AICc values between any given model and the model with the lowest AICc (Δ_i), and the Akaike's weight (ω_i) are listed for each candidate model.

Model	k	-2LogL	AIC_c	Δ_i	ω_i
Impediment + Social Status	5	176.6	187.9	0	0.63
Impediment * Social Status + Impediment + Social Status	6	176.6	190.4	2.51	0.18
Impediment	4	183.9	192.7	4.81	0.06
Impediment + Group Size	5	181.5	192.7	4.82	0.06
Impediment + Conifer Edge	5	182.3	193.5	5.68	0.04
Impediment + Visibility	5	183.8	195.0	7.16	0.02
Impediment * Conifer Edge + Impediment + Conifer Edge	6	182.2	195.9	8.08	0.01
Impediment * Visibility + Impediment + Visibility	6	183.8	197.5	9.67	0
Visibility + Social Status	4	196.2	205.0	17.15	0
Social Status + Group Size	4	196.3	205.1	17.22	0
Social Status	4	200.8	207.2	19.36	0
Social Status * Visibility + Social Status + Visibility	5	196.2	207.4	19.53	0
Social Status + Conifer Edge	4	200.7	209.5	21.62	0
Social Status * Conifer Edge + Social Status + Conifer Edge	5	200.6	211.8	23.92	0
Visibility	4	2030	211.8	23.98	0
Visibility + Group Size	5	200.7	212.0	24.1	0
Visibility + Conifer Edge	5	201.2	212.5	24.59	0
Group Size	4	206.9	215.7	27.84	0
Group Size + Conifer Edge	5	206	217.2	29.35	0
<i>Null Model</i>	3	212	218.5	30.6	0
Conifer Edge	4	210.6	219.4	31.52	0

Table 4.5. Results of AICc analysis for models explaining winter female elk vigilance. The number of parameters estimated in the model (K), the negative 2 log-likelihood (-2LogL), the AICc, the difference in AICc values between any given model and the model with the lowest AICc (Δ_i), and the Akaike's weight (ω_i) are listed for each candidate model.

Model	k	-2LogL	AIC_c	Δ_i	ω_i
Impediment + Conifer Edge	4	65.9	76.2	0	0.24
Conifer Edge	3	69.3	76.6	0.41	0.20
Impediment	3	69.7	77	0.78	0.16
Impediment + Group Size	4	67.9	78.2	2.00	0.09
Conifer Edge + Group Size	4	68.7	79	2.82	0.06
Impediment + Visibility	4	69	79.3	3.10	0.05
<i>Null Model</i>	2	74.9	79.5	3.27	0.05
Impediment * Conifer Edge + Impediment + Conifer Edge	5	65.8	79.6	3.34	0.05
Conifer Edge + Visibility	4	69.3	79.6	3.40	0.04
Group Size	3	73.9	81.2	4.99	0.02
Visibility	3	74.6	82	5.73	0.01
Impediment * Visibility + Impediment + Visibility	5	69	82.7	6.50	0.01
Visibility + Group Size	4	73	83.3	7.31	0.001

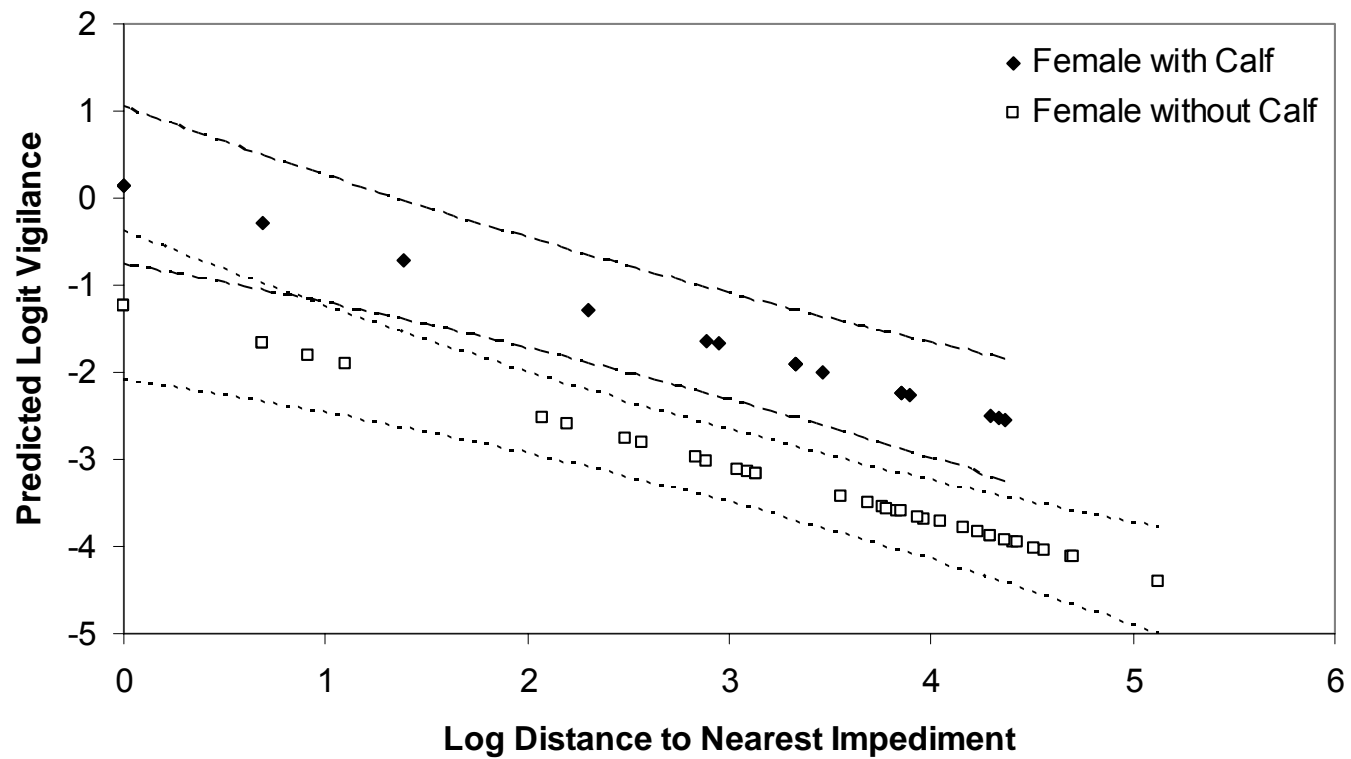


Figure 4.1. Predicted summer elk vigilance based on the best approximate model of summer elk vigilance without an interaction. The equation for the best approximate model with standard errors in parentheses is: $1.51 (0.68) - 1.38 * \text{social status} (0.36) - 0.62 * \log \text{ impediment} (0.11)$. 95% confidence interval for social status is -2.09, -0.66. The back-transformed confidence interval for log impediment is 0.43, 0.38. Dashed lines represent 95% confidence bounds. A graph of the interaction between Impediment and Social Status was similar in appearance and interpretation.

Figure 4.2. Variations in the percent of time female elk were vigilant (mean \pm SE) within and beyond 30 m to the nearest impediment to escape. Females \leq 30 m to the nearest impediment were always more vigilant (p-value \leq 0.02) than females $>$ 30 m to the nearest impediment. Significance was determined from Welch's Two Sample t-tests with unequal variances on the logit-vigilance data. Social status data (with/without calves) were unavailable for winter elk.

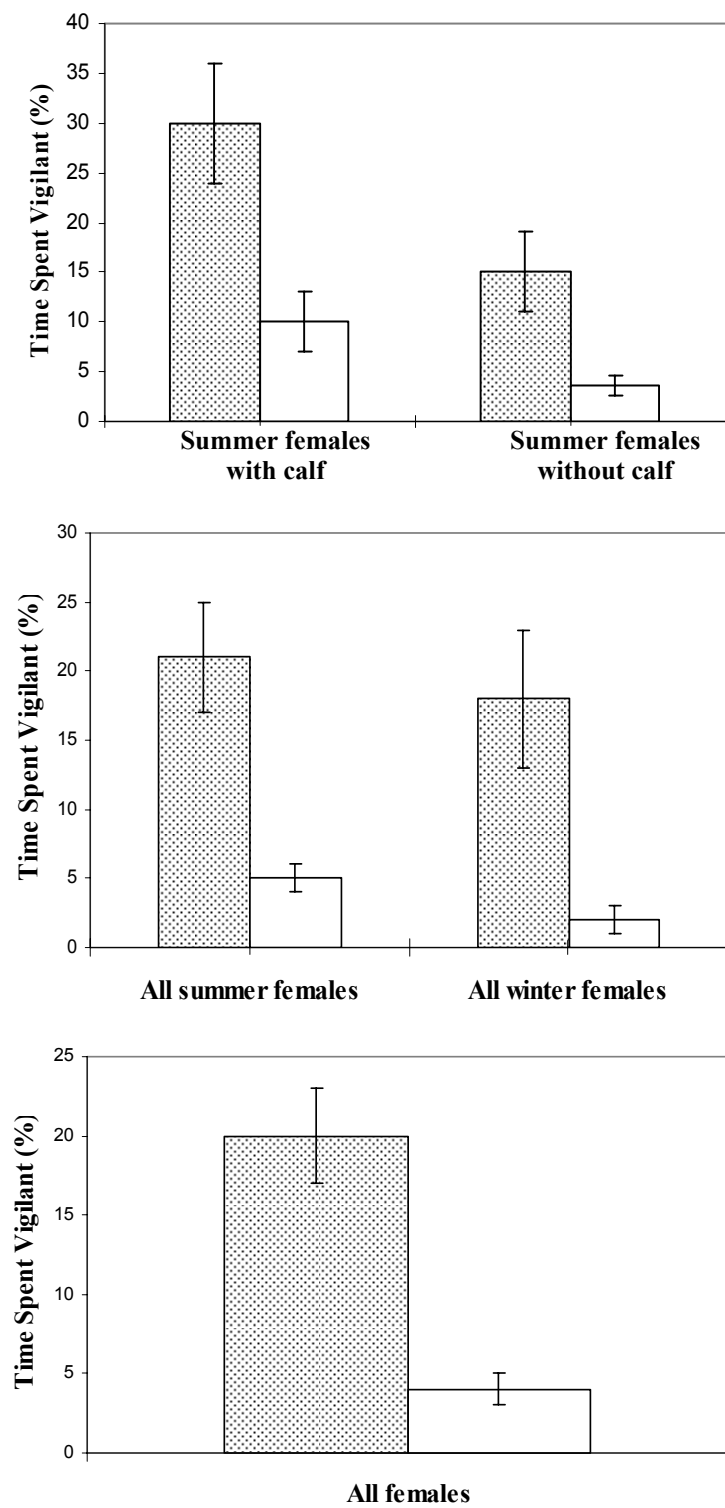


Figure 4.2

CHAPTER 5 - CONCLUSION

Trophic cascades can be defined as the indirect effects of carnivores on plants resulting from changes to intermediate trophic levels such as herbivores. However, such a definition does not specify whether changes to intermediate trophic levels result from direct mortality (i.e. density-dependence) or from behavioral changes to intermediate trophic levels arising from anti-predator behavior. Although the processes creating the outcome, behavioral and/or density-mediated effects, differ, expected patterns of a trophic cascade can be identical (Schmitz 2004).

While it is difficult to disentangle density-mediated from behaviorally-mediated effects, aspen (*Populus tremuloides*) recruitment adjacent to scree and in a burned portion of the park in this study collectively suggested elk (*Cervus elaphus*) browsing in certain locations declined during a time when browsing in the rest of each respective landscape continued. Such divergent patterns in browsing and aspen recruitment were only observed following wolf (*Canis lupus*) reintroduction. Therefore, I suggested changes in elk browsing behavior have occurred since wolf-reintroduction.

Conclusions from Chapters 2 and 3 are based on plant origination and growth patterns. Plants provide a longer record of historical conditions than would be available based on many animal communities. However, studies of plant origination and growth can only be used to infer historic and current processes at higher trophic levels. Because of this limitation, I examined the potential for a behaviorally-mediated trophic cascade from the perspective of elk, the primary prey of gray wolves

in Yellowstone National Park. Specifically, I wanted to determine if elk were more vigilant, and therefore had a greater risk of predation near impediments thought to hamper elk movement. The result of greater vigilance for female elk near escape impediments is consistent with the locations and patterns of aspen growth documented in Chapters 2 and 3. Furthermore, the observed similarities in elk behavior in both summer and winter ranges illustrate the prevalence of vigilance anti-predator behavior throughout much of the park. Chapter 4 therefore provides an additional line of evidence of predators structuring ecosystems via anti-predator behavior at fine spatial and temporal scales.

It is difficult to ascertain how the interaction between wolves, elk, and aspen in Yellowstone National Park will change in the future, particularly with predicted changes in climate. Such an uncertainty suggests an avenue of future research whereby different climate scenarios are modeled to examine the effects of future climate patterns, disturbance frequencies, and disturbance intensities on aspen recruitment, and on both carnivore and intermediate trophic level range expansions and contractions. Future research should also involve collecting more elk behavior data and associated impediment information both within and beyond the park to further investigate the role of escape impediments in elk vigilance behavior. Another potentially fruitful study would be to create a predation risk map. This map would be developed through the classification of aerial photographs of the park and be based on distance to escape impediments. Investigations of vegetation responses and elk

vigilance studies based on such a “fearscape” map could provide an independent assessment of a behaviorally-mediated trophic cascade.

While a fearscape map might provide insight into the role of behavior in shaping a trophic cascade, it is likely that the landscape of fear is dynamic rather than static. Changes in risk behavior could vary with factors such as winter severity, plant productivity, carnivore and prey densities, and energy needs of predators and prey. These potential influences on risk behavior demonstrate that different approaches to studying this topic are likely necessary.

Because elk behavior might change with various biotic and abiotic processes, the strength and direction of top-down and bottom-up effects will likely vary both spatially and temporally. Yet this dissertation provides evidence of a top-down trophic cascade under current conditions. Moreover, this work provides support for behaviorally-mediated wolf effects on elk in addition to any density-mediated effects. Therefore, this study illustrates both complexities and future research opportunities between wolves, elk, and aspen in Yellowstone National Park.

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