LONG-TERM RESPONSE OF WILLOW TO BEAVER REINTRODUCTION AND MOOSE BROWSING IN THE SOUTHERN ABSAROKA-BEARTOOTH WILDERNESS

by

Rachael Helen Dines

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Animal and Range Science

MONTANA STATE UNIVERSITY
Bozeman, Montana

December 2022

DEDICATION

I dedicate this thesis to my grandmother, Carol Peterson (a.k.a. “Cookie”), whose unending love, support, and enthusiasm inspires me in everything I do. You are the one who introduced me to the great outdoors, and you’ve been with me every step of the way as I learn about what life has to offer. I am so grateful for your influence on my life. If it weren’t for you, I wouldn’t be where I am today. Thank you.

ACKNOWLEDGEMENTS

Thank you to Dr. Dan Tyers, my co-advisor, for starting this project in 1985 and keeping the project going for 37 years, and for the field support and guidance. And thank you to the many people who contributed to data collection over the years. Thanks to my advisor, Dr. Bok Sowell for the hours he invested in helping me through my M.S. program. I have learned a lot from you! Thank you to my committee members Dr. Doug Smith and Dr. Laruen Walker for their help. Thank you to project contributors, including the Forest Service, Montana Fish Wildlife and Parks, Yellowstone National Park, Montana State University, the Montana Agricultural Experiment Station. And thank you for the private donations from Dick and Mary Ohman, Gerry Bennett, and Carol Peterson. Thank you to Dr. Craig Olwert for his advice on statistics. And last but certainly not least, thank you to my mom, dad, and the rest of my wonderful family who provided much needed love and support throughout this journey.

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF FIGURES CONTINUED

ABSTRACT

Willow is an important component in the southern Absaroka Beartooth Wilderness (ABW) riparian areas because it provides critical beaver habitat and is an essential food source for moose populations. Forest Service managers have monitored long-term trends in willow condition and herbivore populations in the southern ABW. Beavers were extirpated in the mid-1900's and then reintroduced beginning in 1986. Moose numbers increased in the early 1900's and willow over-browsing followed until the population declined after habitat loss from the 1988 Yellowstone fires. The objective of this study was to examine willow condition in response to changes in beaver and moose populations in the southern ABW.

I used annual stream-side surveys to record the number and location of beaver colonies from 1986 to 2021 and aerial imagery to describe changes in willow canopy cover. I used a binomial regression to evaluate the relationship between willow canopy cover and beaver colony density and longevity to estimate if long-term beaver presence increased willow canopy cover. I used linear regression to analyze indices of moose relative abundance, willow plots recording height and browsing, and a long-term browsing exclosure to evaluate the effect of moose population trends on willow height.

Beaver have remained at carrying capacity over the last 20 years, and average willow canopy cover increased from 16% in 1981 to 37% in 2019. The probability of willow occurrence increased the longer beaver occupied an area and with colony density (colonies/km). Moose relative abundance declined from 1987 to 2021, while average willow height increased from 113cm in 1988 to 190cm in 2021 and browsing decreased from 53% in 1989 to 3% in 2021. Browsing was an important factor limiting willow height. Moose abundance had a positive linear relationship with average browsing pressure and negative linear relationship with average willow height. This study shows that the southern ABW was able to recover from historic over-browsing and beaver extirpation. The long-term effects of beaver reintroduction and reduced moose numbers in a historically degraded environment enhanced willow, indicating that under the right circumstances, willow communities have the potential to recover from a previously degraded state.

CHAPTER ONE

LITERATURE REVIEW

Willow Ecology

Willow (*Salix* spp.) is a woody plant species found, in shrub-form, in the intermountain west along waterways and in riparian meadows. It often grows in dense stands associated with a high water table. Throughout its range it is widely distributed but proportionally limited. Even though it is comparatively uncommon, it is recognized as an environmentally critical component of this landscape with many species at different trophic levels affected by its location and condition (Naiman & Decamps 1997; Naiman et al. 1993).

The ecosystem services offered by willow are well recognized in the mountainous regions of the American west, including the 89,000 km^2 Greater Yellowstone Ecosystem (GYE), which is one of the last remaining intact ecosystems in the northern temperate zone. Because of the importance of willow in this environment, researchers and agency managers in the GYE use willow stature and abundance as indicators of riparian system health and the status of ecological processes at a landscape-level. For example, monitoring willow condition is a focus on the Northern Yellowstone Winter Range (NYWR), a 1526 km^2 wildlife rich area in the northern tier of the GYE characterized by relatively mild winter conditions and low elevation grasslands (Coughenour & Singer 1996; Tyers 1981; Baril 2009; Naiman & Decamps 1997; Yellowstone National Park 1997). In this region, willow and other deciduous species comprise less than 5% of the area but provide critical habitat for wildlife (Smith et al. 2020; Skagen et al. 1998).

The ecological benefits of willow in the GYE and across its range involve providing important habitat for species that utilize woody plants for food (Baril 2009; Beschta & Ripple 2018). Native herbivores such as elk (*Cervus canadensis*), bison (*Bison bison*), deer (*Odocoileus* spp.), moose (*Alces alces*), and beaver (*Castor canadensis*) forage on willow, especially in the winter (Singer et al. 1994; Zeigenfuss et al. 2002; Baker et al. 2005). Willow stands also provide habitat for neotropical migrant birds species, as well as reptiles, amphibians, and mammals (Naiman & Decamps 1997; Naiman et al. 1993). Where willow overhangs stream banks, they reduce the water temperature, which is advantageous for fish populations. They also serve an important role in stabilizing stream banks and reducing erosion (Polvi et al. 2014). Willow can reproduce sexually via seed dispersal or asexually through adventitious roots or buried stems. Asexual reproduction is facilitated through disturbances like flooding or when beaver harvest stems and they take root where deposited (McColley et al. 2011; Kay & Chadde 1992; Johnston et al. 2011; Marshall et al. 2014). Given their resiliency and ability to recover after disturbances, willows are often the dominant and ecologically critical overstory in riparian areas.

Willow distribution is determined by abiotic and biotic factors. Willows are phreatophytes, which means their survival is predicated on access to groundwater. For example, Johnston et. al. (2011) found that the water table depth and accessibility can influence willow growth. Water availability can change dramatically in dynamic riverine systems and influence willow growth and establishment. Available moisture in riparian areas can be driven by climatic variables but can also by the amount of standing water and associated groundwater, such as water impoundments created by beaver dams (Johnston et al. 2011; Marshall et al. 2014; Wolf et al. 2007; Bilyeu et al. 2008).

In addition to groundwater access, other limitations to willow distribution and height include geomorphology, elevation, and climate (Marshall et al. 2014; Cooper et al. 2006). For example, some species of willow require more moisture and warmer temperatures, while others can tolerate colder temperatures that are characteristic of higher elevations. Eastwood willow (*Salix eastwoodiae*) has a greater tolerance for the high elevations and cold temperatures in subalpine regions, while Geyer willow (*Salix geyeriana*) is typically found in montane wetlands at lower elevations (Heinze 1992). While all willow is subject to changes in height based on environmental stressors, studies that investigate willow height and growth typically focus on tall willow species like Geyer because they display greater height fluctuations when suppressed by browsing or reduced access to water (Painter & Tercek 2020; Bilyeu et al. 2008).

When abiotic factors for site conditions allow willow to persist, herbivory is the limiting factor for willow establishment and growth (Johnston et al. 2011; Marshall et al. 2014). Willow is a common and critical browse for native ungulates. Leaves are utilized in the summer and stems throughout the winter (Baker et al. 2005; Kay & Chadde 1992; Singer et al. 1994). Moderate browsing can promote stem production but repeated over-browsing can suppress growth and stature (Johnston et al. 2007; Baker et al. 2005; Meiman et al. 2009). The consequences of over-browsing have been well-documented on the NYWR, where high numbers of elk were hypothesized to cause willow to decline (Beyer et al. 2007; Singer et al. 1994).

The distribution of specific willow species is important because of the variation in biomass, accessibility, and palatability (Burkholder 2012). Differences in biomass among species is related to twig production but is also tied to the phenotypic expression of plant height. Willow is a particularly favorable browse for herbivores in winter when other vegetation is buried under snow, so taller willow experiences more herbivory pressure in winter environments (Visscher et al. 2006; Nordengren et al. 2003). For example, Wolf willow only reaches heights of 1 to 2 meters, while Geyer's willow can grow as tall as 7 meters (Heinze 1992). Therefore, taller willow species are more susceptible to browsing in extreme winter environments (Tyers 2003).

Current Willow Research on the NYWR

The importance of willows as browse species for ungulates has generated extensive research on the effects of ungulate populations on willow abundance and stature. Much of this research addresses the ecological relationships among predators, herbivores, and willow in the GYE, specifically on the NYWR. The NYWR is year-round habitat for many species, but it is especially noteworthy as winter range for native ungulates such as elk, bison, deer, and moose (National Research Council 2002; Tyers 1981). The extent of the NYWR is defined by the rugged mountains of the Absaroka Beartooth Wilderness (ABW) to the north and high plateaus in Yellowstone National Park (YNP) to the south. The ABW is about 4050 km^2 of designated Wilderness. The southern drainages of this region are deeply incised glaciated valleys separated by prominent ridges. Winter conditions are much harsher than the adjacent NYWR, which limits access to ungulates except moose (*Alces alces shirasi*). Lower elevation grasslands and river corridors on the NYWR can sustain large numbers of elk and bison throughout the winter, providing an ideal environment for researchers to observe willow response to varying levels of browsing intensity (Houston 1982; Tyers 1981; Yellowstone National Park 1997). The findings of decades of research on the NYWR have been used to interpret the relationships among willow condition, ungulate populations, and predator effects throughout the intermountain west, leading to management decisions about ungulate winter range carrying capacity and landscape level ecological processes. Insights on willow ecology gained through these studies are often referenced to interpret willow response to browsing on other ungulate winter ranges in the GYE and throughout the intermountain west.

The condition of willow on the NYWR has fluctuated in both height and abundance historically. Prior to the extirpation of wolves and a human-caused decline in the grizzly bear population in the early to mid-1900's, willow on the NYWR was abundant and robust (Tyers 1981). This is because ungulate numbers were previously moderated by predation from wolves, bears, and other predators. However, the condition of willow and other deciduous vegetation indicated herbivory suppression after the predator population declined (Beschta & Ripple 2016; Ripple et al. 2013). With fewer natural predators to regulate ungulate numbers, willow browsing increased. YNP responded with an active reduction program that culled the elk herd from the 1920's to the 1960's. From 1923 to 1968, 26,400 elk were removed from the NYWR (Yellowstone National Park 1997). Bison and pronghorn were also reduced in numbers during this period.

This program was abandoned in favor of a "natural regulation" management strategy, in which winter severity and availability of food resources was seen as the best mechanism to regulate ungulate numbers in the absence of predators (White et al. 2013; Yellowstone National Park 1997; Tyers 1981). This new strategy was implemented in YNP by the 1970's, partly in response to the 1963 Leopold Report that challenged the traditional practices of culling to control elk populations (Leopold et al. 1963; Yellowstone National Park 1997). With the implementation of the natural regulation strategy, an increase in elk numbers followed, with renewed evidence and concern related to over-browsing of aspen and willow (Coughenour & Singer 1996).

Within the last several decades, researchers have documented an increase in willow and aspen height in YNP, especially on the NYWR, which some attributed to a reduction in elk numbers following wolf reintroduction in 1995-96 (Beschta & Ripple 2010; Ripple & Beschta 2006, 2003; White et al. 2013). These researchers introduced the concept of a top-down trophic cascade effect. It hypothesizes that the reintroduction of wolves caused elk numbers to decline resulting in a recovery of woody vegetation. To quantify the effects of the trophic cascade theory, Ripple and Beschta (2006) compared photos of NYWR riparian communities from 1998 and 2004 to demonstrate an increase in willow height directly correlated with a decrease in ungulate numbers. Subsequent investigations have added evidence to support the presence of a top-down trophic cascade effect on the NYWR (Smith et al. 2020; Ripple & Beschta 2012).

Beaver Ecology

Beaver are riparian rodents that rely on water and deciduous woody vegetation for survival. Adaptations such as webbed feet and large, flat tails enable them to thrive in riparian environments. An adult beaver weighs an average of 18 to 22 kg, making them the largest rodents in North America (Müller-Schwarze 2011; Baker & Hill 2003). They are generalists but primarily feed year-round on the bark of deciduous woody plants and supplement their diet with herbaceous species during the growing season (Smith 1997).

On the NYWR and the adjacent ABW, the food source and building material for beaver is predominantly willow (Ritter 2018; Scrafford et al. 2018). In this region, beaver successfully occupy areas where willow availability, water depth, and topography are appropriate for creating structures, including dams to impound water and lodges for security (Wright et al. 2002; Smith & Tyers 2008, 2012).

Beavers are known as ecosystem engineers because of their ability to alter their habitat by impounding and redirecting water. Water provides beaver security from predators and allows them to float woody material they cut on the bank to safe locations for feeding or to sites where they are constructing dams and lodges (Ritter et al. 2019; Warren 1926; Smith & Tyers 2008). Consequently, they build dams to create deeper water and more flooded areas. They also create canals to extend waterways beyond the stream margin and into adjacent foraging areas to facilitate more secure harvesting efforts. This activity raises the water table which benefits willow growth, enhancing their supply of food and building material (Levine & Meyer 2019; Baker & Hill 2003; Kay 1994).

Beavers can also improve willow condition and enhance growth through harvesting. Cutting willow stimulates new stem growth at a faster rate, which can allow beaver to harvest twigs in the same areas repeatedly, even over multiple years (McColley et al. 2011; Scrafford et al. 2018; Ritter et al. 2019). Therefore, beaver that occupy riparian habitat dominated by willow can potentially inhabit the area for decades. Furthermore, beaver can enhance willow canopy cover by stashing harvested willow twigs. Branches and twigs that are partially buried during dam and lodge construction or food caching can sprout and grow into new plants (Levine & Meyer 2019).

Previous research in the GYE has suggested that beaver can play a large role in the recovery of willow in riparian areas. Scrafford (2018) found that willow canopy cover had increased by 16% from 1981 to 2011 with the reintroduction of beaver in the southern ABW just north of YNP. Others suggest that areas with ungulate over-browsing and willow stand degradation may have experienced dramatic hydrologic changes that prevent beaver-willow habitats from establishment (Wolf et al. 2007). Developing a site-by-site understanding of the relationship between beaver and willow and the potential for a stable riparian system requires long-term monitoring of beaver and ungulate populations and willow condition.

Beaver History in the Northern GYE

Beaver populations can be stable or cyclic, depending on their primary food source. Because of the different growth form and response to cutting, beaver populations utilizing willow stands are more stable and those associated with aspen experience a "boom or bust" cycle. However, large scale population oscillations have also occurred in the GYE and on the NYWR because of landscape-level environmental changes and anthropogenic factors. In YNP, trapping was encouraged through the 1870's but was curtailed in 1883 (Smith & Tyers 2008, 2012). Despite this, an abundant population of beaver was reported in the Tower Junction region of the NYWR in the 1920's (Warren 1926). However, beaver populations notably declined on the NYWR after the 1920's and were reported at near extinction through the mid-1990's (Jonas 1955; Smith 1997; Smith & Tyers 2012). This decline has been attributed to a 50% reduction in willow and a 3-fold decrease in aspen cover through the 1900’s (Chadde & Kay 1991; Houston 1982; Soulé et al. 2003). The decline of deciduous vegetation was ascribed to a warmer and drier climate, fire suppression, loss of beaver, and browsing by a large elk population wintering in the area (Yellowstone National Park 1997). As a result of wolf extirpation and YNP’s natural regulation policy, elk populations were as high as about 20,000 on the NYWR before wolf reintroduction in 1995 (Houston 1982; NRC 2002; Yellowstone National Park 1997). The suppression of tall willow communities across the NYWR has been attributed to large elk numbers during this era, which negatively affected the availability of food and building materials for beaver (Chadde & Kay 1991).

Beaver populations have similarly fluctuated in areas adjacent to YNP, such as in the southern ABW. These changes are most notably correlated with trapping. Osborn Russell mentioned trapping beaver in Slough Creek and Hellroaring drainages north of YNP in 1837, but it is assumed that populations were relatively stable until the mid-1900’s (Smith & Tyers 2008). Trapping occurred again but with greater intensity in the decades following and beaver populations in the southern ABW directly north of YNP were likely extirpated (Haines 1955; Smith & Tyers 2012). In addition to trapping, the decline in the beaver population in the mid-1900’s may be attributed to a regression in willow condition because of over-browsing from moose. The moose population in the area in the mid-1900’s was increasing and suspected of reducing willow height, thus compromising beaver habitat (Tyers 2003).

In 1985, the U.S. Forest Service surveyed all suitable beaver habitat in the southern ABW for activity (Dan Tyers personal communication). No evidence of current occupancy was found but abandoned lodges and dams were abundant. In response, a reintroduction effort was proposed. The Wilderness Act and National Environmental Policy Act provided direction for reintroducing a species into designated wilderness. This included soliciting input from the public and invested professionals on the efficacy of the project (Smith & Tyers 2008). Although comments were ostensibly favorable, some expressed concern because of the existing degraded nature of the willow stands from moose over-browsing (Smith & Tyers 2008; Tyers 2003). It was argued that the reintroduced beaver would die or relocate because of inadequate foraging habitat (Smith & Tyers 2008). Other reviewers postulated that rather than enhancing riparian areas, beaver would cause additional damage to already depleted willow stands by cutting stems for food and structures (Smith & Tyers 2008). The inability of beaver to reestablish on the NYWR where willow stands were dramatically suppressed by elk browsing was used to support this concern. Moreover, it was easy to imagine that willow harvesting by beaver in these NYWR areas would only cause additional damage to the riparian system. In response, as a precautionary measure, the United States Forest Service (USFS) agreed to monitor changes in the riparian areas targeted for reintroduction by tracking willow condition trends, the number and location of active colonies following beaver release, and the moose population (Smith & Tyers 2008). This initiated a beaver reintroduction effort into the southern ABW and a long-term monitoring program to track the effects.

Forty-six beavers were released in the southern ABW between 1986 and 1999. This was accomplished by live-trapping nuisance beaver from surrounding agricultural and residential areas and transporting them with pack stock into remote wilderness areas (Smith & Tyers 2008, 2012). Monitoring indicated that the resulting beaver population attempted to colonize all available meadows, but with varying levels of success. Monitoring efforts revealed that beaver in this area reached carrying capacity by 2001 and willow canopy cover in a subset of the study area increased 16% by 2011 (Scrafford et al. 2018).

Moose Ecology

Moose are only found in the northern hemisphere where they occupy boreal forests, post-disturbance shrub fields, and riparian areas. Their distribution is predominantly limited by food and cover to the north, and climate to the south (Ballenberghe & Ballard 1997; Bowyer et al. 1997). In the southernmost regions of their distribution, including Montana and Wyoming, moose are vulnerable to overheating, so they actively seek locations with shade and opportunities to cool down in the summer (Ballenberghe & Ballard 1997). In winter, they are commonly found in the cover of conifer forests and areas with abundant woody browse.

The distribution of sympatric cervids, including moose, in the GYE is largely determined by adaptations to climate and vegetation. Moose can tolerate colder temperatures, deeper snow, and have adapted to a diet with a larger composition of lignin found in woody plants, which other herbivores have difficulty digesting (Ballenberghe & Ballard 1997). Given these adaptations, moose are most often found at higher elevations than other ungulates like elk and deer, especially during the winter (Stephenson et al. 2006; Ballenberghe & Ballard 1997; Tyers 2008).

Moose are browsers, which means they primarily consume trees and shrubs. Due to their large body size, they require large amounts of forage and are therefore limited in density and distribution by the availability of food (Renecker & Hudson 1992; Stephenson et al. 2006). To compensate for this, moose gravitate to dense patches of vegetation such as willow. Renecker and Hudson (1992) and Cederlund and Okamara (1988) hypothesized that moose developed these foraging strategies involving use of concentrated patches of forage to compensate for harsh winters and deep snow that makes traveling more energy intensive. Using patches of food, they can minimize travel while maximizing calorie intake (Pyke et al. 1977; Cederlund & Okarma 1988; Renecker & Hudson 1992). Therefore, utilizing patches of willow and other woody browse is important for moose winter survival.

To assess moose habitat use, especially long-term impacts on primary foods such as willow stands, monitoring moose numbers and distribution is necessary (Tyers 2003). However, population analysis is difficult for moose because it is the least social of the North American deer, and they frequently occupy habitats with poor observability (Tyers 2006; Schladweiler & Stevens 1973; Houston 1982). Moose population levels are typically assessed in 3 ways: total area counts, sample estimates, and indices (Hinton et al. 2022; Timmerman & Buss 1997). Comprehensive aerial surveys on a grid pattern are the best method for counting moose, but they are only successful with open canopies where moose are very observable, such as northern taiga regions (Gasaway et al. 1986). This method was tried with limited success in the southern ABW and the NYWR (Tyers 2003).

Timmerman and Buss (1997) promoted several information sources to assess moose population status. Moose population assessments are most useful when trend-through time data are available, so single surveys are rarely sufficient. Therefore, developing moose population indices usually involves consistent long-term repetitive sampling efforts in favorable moose habitat that is accessible to observers (Tyers 2003; Timmerman & Buss 1997). For example, Tyers (2003) developed indices over several decades by counting moose year-round while traveling the YNP road that bisects the NYWR and riding horseback on a network of trails in the southern ABW in the fall.

Moose History in the GYE and Southern ABW

The Shiras moose is found in regions of Alberta, Montana, Idaho, and Colorado. It probably arrived in the GYE in the mid to late 1800's as a pioneer species (Houston 1982; Schullery & Whittlesey 1992; Tyers 2003). Their presence in the southern ABW was first formally reported in the early 1900's by rangers conducting snowshoe patrols (Rush 1942; McDowell & Moy 1942; Stevenson 1920). Montana Biologist Joe Gabb began horseback surveys in the late 1940's in the southern ABW to obtain a more formal moose population assessment at a broader scale (Gaab 1949, 1948). His efforts were also in response to agency concerns over reports of willow degradation from a rapidly expanding moose population (Tyers 2003; Gaab 1949, 1948). These early surveys indicated an expanding moose population in the southern ABW since their arrival in the late 1800's.

When moose arrived on the NYWR and the southern ABW, they encountered an environment in transition due to the effects of European settlement (Ballenberghe & Ballard 1997). Human predation was initially important and then curtailed. Forest succession was altered with attempts to suppress fires. Agency reports suggest that moose had expanded into all suitable habitat in this region by the early to middle of the twentieth century (Tyers 2003). Reports of negative impacts on willows indicated that, at least in some drainages, moose numbers may have stabilized or over-populated the area by the late 1930's. Regulated moose hunting in the southern ABW was introduced in the 1940's to alleviate damage to willow stands in the southern ABW. This may have ended a population eruption triggered by a ban on hunting that dated from the early 1900's and by concerted efforts to eliminate predators from the GYE during the 1910's-1930's (USDA 1936; McDowell & Moy 1942).

Agencies remained concerned about the status of willow in riparian areas in the southern ABW. They speculated that high moose numbers were largely responsible for over-browsing and growth suppression of willow. Montana responded by starting a moose quota hunt in 1945 of 40 permits. By the early 1980's, there were 55 either sex moose hunting permits available (Tyers 2003). However, despite the generous moose hunting quotas, willow in the southern ABW riparian areas was still visibly suppressed in height and over-browsed.

To monitor willow condition trends exclosures were established in Hellroaring, Buffalo Fork, and Slough Creek in the early 1960's. Only the exclosure in Slough Creek has survived. The Slough Creek exclosure demonstrated that willow in the southern ABW was suppressed by herbivory (Erickson 1979; Chadde & Kay 1988; Tyers 2003).

Tyers (2003) assessed historical records of moose observations in the southern ABW through the first half of the 1900's and then implemented a suite of indices to describe the moose population in the same area and the adjacent NYWR from 1985 to 2001. He documented a population crash following the 1988 Yellowstone fires from these indices (Tyers 2003, 2008, 2006). As further evidence of a population decline, hunters were no longer able to fill all available tags in the southern ABW hunting districts. In response, in 1990, Montana issued 42 permits (23 antlered and 19 antlerless). The quota was reduced to 21 (13 antlered and 19 antlerless) in 1991 and to 13 (all antlered) in 1996 (Tyers 2008). The current hunting quota is 2 bulls in the Cooke City unit but none in the units of the southern ABW. The sharp decline in moose numbers was attributed to significant changes in available moose winter habitat (Tyers 2008, 2003, 2006).

Moose are adapted to survive in the harsh conditions of northern latitudes (Telfer & Kelsall 1984). Their large size allows them to reduce predation risk, handle cold weather, and travel long distances in difficult terrain (Telfer & Kelsall 1984). However, to compensate, moose utilize patches of relatively low-quality food that allow for minimal movement and high rates of intake (Saether & Andersen 1990; Regelin et al. 1985; Renecker & Schwartz 1997). In winter, moose use patches of preferred food to minimize travel. Tyers (2003, 2008) documented that moose in the southern ABW balance energetic needs in this harsh winter environment by utilizing patches of willow in riparian meadows and patches of subalpine fir in late successional stage lodgepole pine forests.

Willow forms the most concentrated patches of browse for moose in the southern ABW, but it is mostly browsed in early winter when snow conditions have less impact on moose movements (Tyers 2003). If snow did not restrict moose from willow stands and if twigs were available above the snowpack, it would probably be the primary food item throughout the winter. Tyers (2003) found that moose utilize willow in the ABW for as long as snow conditions allow, then retreat to cover provided by mature double-canopy lodgepole pine forests where the overstory ameliorates snow conditions. Within these forests, they search for areas with patches of small subalpine fir trees (*Abies lasiocarpa*) (<5 meters tall), which are usually found in the greatest density in the oldest lodgepole pine (*Pinus contorta*) forests (Mattson & Despain 1985; McArthur & Pianka 1966; Tyers 2003). Unlike other conifers, subalpine fir is a palatable winter food for moose. It is also a shade tolerant tree that grows in coniferous forests after a canopy of lodgepole pine has formed post-disturbance, which takes several hundred years. It has a unique growth form that produces patches in the understory of the oldest coniferous forests; lower branches root to form an expanding cluster around the parent tree, providing concentrations of browse for moose after they are forced out of willow stands by deep, crusted snow. Loope and Gruell (1973) suggested that with fire suppression in the GYE, moose populations increased as forests aged, and shade-tolerant subalpine fir prospered.

In 1988, the Yellowstone Fires burned much of the old growth forests in the ABW that moose relied on for winter survival. This loss of late successional subalpine fir patches in the mature coniferous forests caused a decline in moose numbers (Tyers 2003; Tyers & Irby 1995). Since willow is only available during the summer and early months of winter, the loss of subalpine fir as winter forage resulted in a population crash. A lack of mature coniferous forests for mid to late winter habitat, coupled with predation from increased grizzly bear and wolf populations, continues to limit the moose population in the southern ABW (Tyers 2006, 2003; Tyers & Irby 1995).

Study Justification

The long-term effects of beaver on willow stand status have not been well documented in the GYE. Scrafford (2018) generalized willow canopy changes since beaver re-establishment in the southern ABW using aerial imagery interpretation for 4 meadows. My study will add 12 years of data and analysis with finer spatial resolution to quantify changes more accurately in willow canopy cover as it relates to beaver re-establishment in 13 meadows. Long-term data such as these are integral in understanding the cause and effect of ecosystem processes in the GYE, uniquely assessing the interactions of 2 obligate species and willow stands. Therefore, this research will fill in gaps in the story of the GYE Yellowstone ecosystem and provide context for the discussion of long-term landscape level changes.

Research on trophic cascades effects and the relationship of herbivory to willow has been a focus across the GYE for decades. However, most studies have been conducted at lower elevations on traditional ungulate winter range, especially the NYWR. Willow response to moose populations in the upper reaches of drainages with severe winter conditions are a significant factor that has not been well documented, except for Tyers (2003). How moose populations interact with willow has not been adequately addressed in the discussion of trophic cascades, despite the ability for moose herbivory to suppress willow growth (Tyers 2003; Chadde & Kay 1988). My research utilizes the findings of Tyers 2003 in the southern ABW and includes 19 additional years, providing a 35-year analysis on the effects of moose populations on willow condition.

Project Origin and Background

The 3818 km^2 ABW was established in 1978 out of National Forest lands in the northern GYE. As required by USFS policy, an initial management plan was prepared in 1982, setting the stage for a more detailed discussion of plan priorities over the next decade (USDA 1987). Research objectives and hypotheses were expected to be identified iteratively as managers had more clarity on questions and opportunities (Tyers 2003).

The purpose of a wilderness management plan is to establish priorities for resource protection, limits to human use, and monitoring programs to track environmental changes. The Wilderness Act encourages the idea that designated areas can serve as laboratories to enhance our understanding of natural processes. The Forest Service was interested in adhering to this concept while managing the ABW. For a variety of reasons, willow stands in the southern ABW were identified as a focus for long-term monitoring. This included the associated riparian areas and beaver and moose, two terrestrial species ecologically linked to this habitat (Dan Tyers personal communication). This is comparable to the focus of research and management occurring across the GYE.

Willow and the riparian systems that support them are considered good indicators of long-term and landscape-level environmental changes in natural settings. Willow can help document trophic cascade effects because they are sensitive to variations in browsing pressure and can reflect changes in ungulate numbers and associated predator populations (Peterson et al. 2020). Therefore, monitoring willow condition involved 13 large riparian meadows in the southern ABW near the YNP boundary, inclusive of Hellroaring, Buffalo Fork, and Slough drainages. Riparian meadows in the Stillwater and Soda Butte drainages adjacent to the ABW were also included.

As the primary herbivores of willow in this high elevation environment, moose and beaver populations were similarly targeted for long-term monitoring. When it was determined that beavers were extirpated, a beaver reintroduction was conducted, and the results were tracked.

As opportunities arose, what began as a monitoring effort intended to track long-term changes in the condition of unique resources in the ABW evolved into more sophisticated studies conducted by the Forest Service from 1985 until 2021 in collaboration with Montana Fish Wildlife and Parks, Yellowstone Park, and Montana State University. These study efforts focused on willow condition, moose ecology and population trends, and the effects of beaver reintroduction on montane riparian areas. Therefore, my objective is to assess the drivers of willow height and canopy cover as it relates to moose and beaver populations and associated impacts on the landscape. To accomplish this, I assessed long-term trends in beaver colony numbers and density. I determined if beaver colony numbers and density have increased or decreased since the last monitoring effort in 2010. I also tested if willow canopy and standing water have increased or decreased since beaver reintroduction. Then I tested whether beaver density and years of activity play a role in willow canopy changes. To address the second part of the main objective, I will assess long-term trends in moose relative abundance to determine if moose abundance has increased or decreased over time. I will also test if moose abundance is related to browsing pressure. Then I will test whether browsing plays a role in influencing willow height in the southern ABW.

CHAPTER TWO

LONG-TERM EFFECTS OF BEAVER REINTRODUCTION ON WILLOW IN THE SOUTHERN ABSAROKA BEARTOOTH WILDERNESS

Introduction

Willow is found in riparian ecosystems throughout the intermountain west. In these environments, willow and beaver typically coexists in a mutualistic relationship. Specifically, it is an example of proximate mutualism where removal of one reduces the performance of the other (Peinetti et al. 2009). Moreover, the decline or absence of either beaver or willow has significant ecological impacts on many other species. Hence, beaver is considered a keystone species and an ecosystem engineer (Naiman et al. 1986, 1988; Jones et al. 1994; Kay 1994; Wright et al. 2002).

The mechanisms that drive the persistence of beaver-willow communities arise from a unique combination of willow life history traits and beaver foraging behavior. Beaver density can be influenced by beaver territorial behavior, willow patch size, and other site conditions. Density can also be influenced by the consistency of forage cover, where patchy distribution of woody vegetation relative to predation risks and distance to water can prevent beaver occupancy (Smith 1997; Peinetti et al. 2009).

The mutualistic relationship between beaver and willow is dynamic. The impacts of beaver presence can have lasting effects on the landscape, even from inconsistent beaver occupation. Some beaver structures, like dams, can affect the landscape long after beaver abandonment depending on how long the dams and ponds last. This can depend on stream gradients, flow rates, and sedimentation. Depending on these site conditions, the physical effects of beaver activity, like dams, can disappear shortly after beaver abandonment or can last for decades (Gurney & Lawton 1996; Peinetti et al. 2009).

Willow is often referred to as a barometer of landscape changes because fluctuations in height and abundance is indicative of ecosystem drivers like herbivory pressure and stream hydrology. Willow presence is determined by available groundwater, so stream incision or a reduced water table may lessen willow abundance. The availability of tall willow suitable for winter food caches is necessary for beaver persistence, especially if other suitable woody vegetation is lacking. However, competition for willow can favor livestock or ungulates over beaver in a heavily browsed environment. In these areas, decades of intense browsing by large herbivores can either eliminate willow or create short, hedged plants unsuitable for beaver use (Baker 2003; Baker et al. 2012).

Beaver and willow likely coexisted in abundance throughout the intermountain west region for thousands of years (Persico & Meyer 2009). However, the ecological balance between beaver and willow maintained in many waterways was disrupted at a landscape scale by fur trapping in the early to mid-1800s, which decimated beaver populations. Since then, beaver-willow communities have been altered progressively by a variety of factors attributed to human intervention (Persico & Meyer 2013; Smith & Tyers 2012, 2008).

For example, this mutualistic balance has been disrupted in some wildland settings because removal of predators by humans allowed for large increases in ungulate numbers resulting in over-browsing of willow and decreases in beaver populations. An iconic example involves the NYWR in Yellowstone Park, where this phenomenon has been studied extensively (Smith & Tyers 2008, 2012; Smith et al. 2020; Persico & Meyer 2013).

The 1,481 km^2 area of lower elevation grasslands and stream corridors on the NYWR attracts wintering ungulates. Two primary factors account for a marked declines in willow stands on this winter range in the 1900's: a combination of intense ungulate herbivory and reduced moisture. With the systematic removal of predators by humans across the broader GYE, high populations of migratory elk resulted in over-browsed willow over several decades, which caused a decline in beaver populations. The lack of beaver dams and impounded water lowered the water table in stream corridors creating stress for riparian plants, including reduced vigor or death for willow stands (Jonas 1955; Wolf et al. 2007; Houston 1982; Engstrom et al. 1991; Peterson et al. 2020).

Consequently, riparian areas on the NYWR and other winter ranges were transformed in the 1900's from a "willow-beaver" state to a persistent alternative condition that Wolf et al. (2007) called an "elk-grassland state". In this condition, individual willow plants are short-statured and die without being replaced by new plants. Therefore, willow stands are limited to small, isolated fragments, and active beaver dams are absent. Because beaver rely on tall, abundant willow stands for dam-building material and winter food caches, intensive elk browsing of willow forced them to abandon small streams on the NYWR. Their absence led to several hydrologic changes, including incised streams, channel widening, and a lowered water table (Warren 1926; Jonas 1955; Wolf et al. 2007; Beschta & Ripple 2018). Willow reproduction rarely occurred in the 1990's due to the combined effects of intensive elk herbivory, beaver dam abandonment, channel incision, and the encroachment of upland plant species (Wolf et al. 2007).

Many efforts have been made to repair degraded beaver-willow communities across the intermountain west (Goldfarb 2018). This includes willow planting, creating replicate beaver dams, beaver reintroductions, and removing livestock access to riparian corridors (Goldfarb 2018). Competition from wild ungulates has been addressed by direct reduction or reintroducing predators, both of which were employed on the NYWR in the 20th century.

The relationship between beaver and willow in wildland settings has especially attracted attention by managers and scientists, prompting various monitoring efforts and studies (Baker et al. 2005; Peinetti et al. 2009; McColley et al. 2011). The circumstances often parallel the example of the NYWR where both predator and ungulate numbers were manipulated, and the status of willow and beaver became a metric of ecosystem health.

In response, I investigated the relationship between beaver populations and willow canopy cover in the southern ABW. In this area, riparian floodplains and willow stands provide a large contribution to biodiversity. Post-glacial lakes that are now meadows with sinuous streams and willow were once occupied by beaver and extensive stands of tall willow until the mid-1900's. As the result of predator control measures, including wolf eradication, a pioneering moose population grew rapidly (Tyers 2003). Quota hunts were used to control the moose population, which ultimately crashed in 1988 following the landscape-level Yellowstone fires. In concert with the heavy browsing impacts on willow, beavers were eradicated by trapping in the middle of the 1900's. By the 1960's, willow was reported to be at "knee-height" and declining markedly (Chadde & Kay 1988; Tyers 2003). In 1978, Tyers documented uniformly repressed willow that was all under 1m tall (Tyers 2020). After several decades of absence, 46 beaver were reintroduced into the Hellroaring, Buffalo, Slough, and Stillwater drainages by the Forest Service and Montana Fish, Wildlife, and Parks starting in 1986.

The results of this reintroduction effort were documented from 1986 to 2021, providing a 35-year perspective on the relationship between beaver and willow in this wildland setting. Monitoring efforts revealed that the beaver population reached carrying capacity in this area by 2000 (Scrafford et al. 2018). Scrafford (2018) concluded that willow canopy cover in 4 large meadows repopulated with beaver increased by 16%. However, no efforts were made to analyze the progression of changes over time, and the analysis of just 4 out of the 13 meadows does not represent the entire area where beaver were reintroduced.

While factors such as reduced herbivory in recent decades have likely supported a recovery of willow height, it is probable that beaver have disproportionately contributed to a resurgence of willow due to their ability to impound water and alter riparian systems. Specifically, I expect that the water impoundment and associated landscape alterations from beaver would be reflected in changes in willow canopy cover. Therefore, our objective is to determine if beaver colony numbers and density have increased or decreased since reintroduction, and if there have been any changes in water and willow canopy cover. Moreover, if there are changes in willow canopy, I want to determine if these changes are correlated with beaver density and the longevity of beaver activity within the vicinity.

Methods

Study Area

The study area includes 4 drainages that flow into YNP and the NYWR, but they are in or near the southern ABW administered by the US Forest Service. These include Hellroaring, Buffalo, Slough, and upper Stillwater drainages. Within these drainages, thirteen riparian meadows were the focus of the study (Table 1, Figure 1). They define all available habitat for beaver in the southern ABW. These meadows were delineated using the boundary or edge of the riparian area, which is generally distinguished by identifying the floodplain and the vegetation transitional zones from grasses and shrubs to coniferous forest.

The average elevation of the meadows in the Hellroaring drainage is 2277m, 2320m in the Buffalo drainage, 2314m in the Slough drainage, and 2583m in the Stillwater drainage. The closest weather station for the study area is in Cooke City, Montana (~2500m, Figure 1). The average annual precipitation is 65.4cm with peak precipitation in May and June. Mean minimum temperature is -15.4 C in January and mean maximum temperature is 23.2 C in July (Western Regional Climate Center 2022).

The study meadows primarily consist of sedges and shrubs such as *Carex spp.* and willow. There were seven primary species of willow present in the study area, including Geyer (*Salix geyeriana*), Booth (*Salix boothii*), Wolf (*Salix wolfii*), Drummond (*Salix drummondiana*), Farr (*Salix farrii*), Eastwood (*Salix eastwoodiae*), and Barclay (*Salix barclayi*). Moose browse willow in these study meadows (Tyers 2003). Higher elevation and deep snow preclude access for other ungulates in the winter. Historically, large moose populations in the early to mid-1900’s have likely contributed to a decline in willow stature and abundance in the southern ABW, but their population crashed after habitat loss caused by the 1988 Yellowstone Fires (Tyers 2003; Tyers & Irby 1995).

Beavers were once abundant in the study area in the early 1900’s but were extirpated through trapping, willow stand degradation, and a potential tularemia outbreak (Smith & Tyers 2012). After several decades of absence, the Gallatin National Forest and Montana Fish, Wildlife, and Parks reintroduced beaver into the study area starting in 1986. From 1986 to 1999, 46 beavers were reintroduced into Christenson’s, Hellroaring, Lake Abundance, and Stillwater Basin meadows. Beaver from these meadows dispersed into the other meadows in the study area.

Table 1: Southern Absaroka-Beartooth Wilderness study area meadow characteristics.

Meadow	Size (Hectares)	Elevation (m)	Drainage
Frenchy’s	337.36	2074	Slough
Stillwater	152.20	2583	Stillwater
Christenson’s	126.39	2339	Buffalo
Holeman’s	89.12	2301	Buffalo
Hellroaring	59.45	2162	Hellroaring
Bull Moose	42.26	2209	Hellroaring
Grizzly	40.46	2379	Hellroaring
Hart’s	18.03	2199	Slough
Upper Lake Creek	11.01	2423	Slough
Elk	8.08	2226	Hellroaring
Lake Abundance	3.73	2560	Slough
Beaver	2.26	2465	Hellroaring
East Fork	1.83	2223	Hellroaring

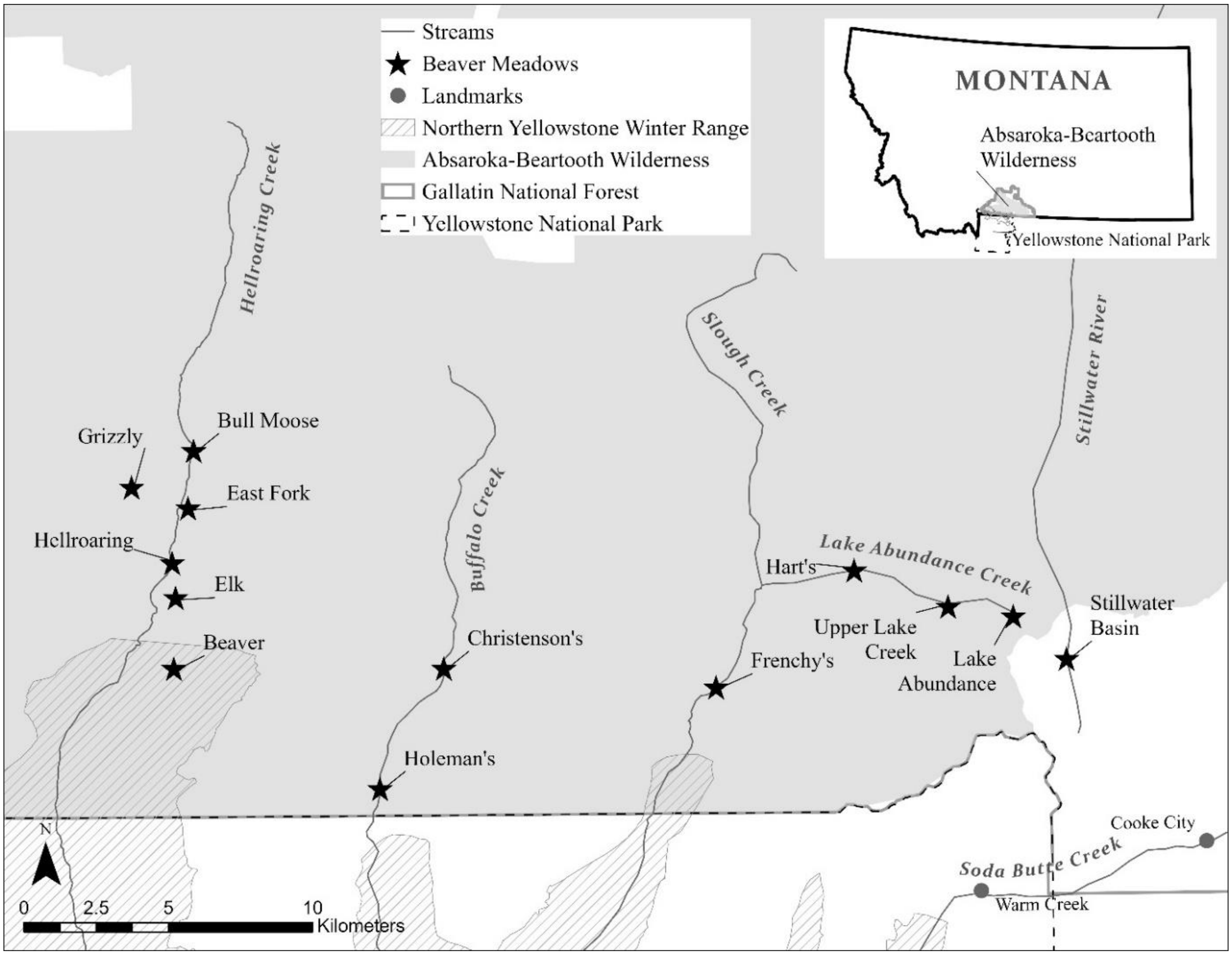

Figure 1: Southern Absaroka-Beartooth Wilderness study area (Montana, USA), including 13 beaver meadows in 4 major drainages in the Southern Absaroka-Beartooth Wilderness.

Beaver Colony Inventories

I used data collected from annual streamside surveys from 1986 through 2010 that recorded the presence and location of all active lodges, dams, and caches along the main channels and all tributaries of the 13 study meadows. I repeated the streamside surveys in 2020 and 2021. Active structures were distinguished by observing freshly cut vegetation, beaver slides, and fresh mud on structures. I mapped active structures using a geographic information system (GIS), and active colonies were determined by identifying clusters of active structures. Clusters of active caches and lodges served as identifiers for estimating the location of an active colony.

GIS-based Vegetative Canopy Assessment

I quantified the progression of changes in willow canopy cover and water surface area in the study area using fine resolution (≤ 1 m) aerial imagery from 1981, 1991, 2005, 2011, and 2019. Imagery from 1981 was used because it provides a reference of the landscape five years before beaver reintroduction. Subsequent aerial imagery was spaced about 10 years apart. Finally, 2019 was used because it was the most recent imagery available. I obtained 1981 imagery from the US Department of Agriculture Farm Service Agency Aerial Photography Field Office and 1991 imagery from the USGS digital orthophoto collection. I acquired images from 2005, 2011, and 2019 from the United States Department of Agriculture (USDA) National Aerial Imagery Program (NAIP). To accurately distinguish vegetation, I used imagery ranging from July to October before snow covered the ground. Some NAIP imagery for a given year did not cover the entire study area because of cloud cover or inclement weather at the time of collection, so I used the previous or next available year’s imagery to complete the dataset.

I delineated polygons of the study meadows using ArcGIS Pro based on visual indicators of obvious visible riparian vegetation cover and estimated floodplain extent. Polygons of delineated riparian meadows often bordered forests and adjacent hillsides, so the polygon boundaries remained the same for all years. I created a systematic grid of points spaced 25m apart on each delineated meadow (n=7,625 GIS points) and each point was then evaluated and classified as willow, water, soil, herbaceous vegetation, conifer, or burned forest. I calculated the percentage of willow cover and standing water for each year by dividing the number of points classified as willow or water, respectively, by the total number of points in the meadow.

Statistical Analysis

Beaver Colony Inventories. I used a one-way analysis of variance (ANOVA) to determine whether beaver colony numbers observed in 2020-2021 have changed since the previous survey effort in 2010. I also used a one-way ANOVA to test whether average colony density in the entire study area has significantly changed since 2010. The latest assessment on beaver colony numbers in 2010, reported by Scrafford (2018), did not include an assessment in the differences in colony trends in all 13 meadows, so I used a linear regression model with an interaction term between meadow and year to test whether the number of active colonies for each meadow increased or decreased from 1986-2020. Initial data exploration revealed a strong curvilinear relationship which was addressed with a second order polynomial transformation to the ‘year’ explanatory variable. The equation for the linear regression model is as follows:

$$\widehat{Colony\,Numbers} = \beta_0 + \beta_1(Year^2) + \beta_2(Meadow) + \beta_3(Year^2 * Meadow) + \varepsilon$$

To determine how beaver colony numbers changed between meadows (1986-2021), I used the R package ‘emmeans’ to evaluate and compare estimated marginal means and trends for each meadow (Lenth 2022). All results were considered significant at a 0.05 α level. The null hypotheses tested were as follows:

H_o: The average number of active colonies in the study area has not changed from 2010 to 2020.

H_o: The average colony density in the study area has not changed from 2010 to 2020.

H_o: Colony numbers have not changed from 1986-2020 in the 13 meadows in the study area.

Canopy Cover Comparison. To determine if the percentage of willow and water canopy cover visible from aerial imagery changed in the study area from 1981 to 2019, I used a multiple linear regression with canopy cover as the response, and year and meadow as explanatory variables for both willow and water cover. I anticipated that water and willow cover change over time would differ for each meadow, so I included an interaction term for the "year" and "meadow" variables for both models. I used an analysis of variance test to determine the significance of including the interaction terms in both models. To determine which meadows experienced significant changes in willow and water canopy cover from 1986 to 2021, I used the R package 'emmeans' to evaluate and compare estimated marginal means and trends for each meadow (Lenth 2022).

The full model for willow canopy change over time is as follows:

$$\widehat{Willow\ Canopy} = \beta_0 + \beta_1(Year) + \beta_2(Meadow) + \beta_3(Year * Meadow) + \varepsilon$$

The full model for water canopy change over time is as follows:

$$\widehat{Water\ Canopy} = \beta_0 + \beta_1(Year) + \beta_2(Meadow) + \beta_3(Year * Meadow) + \varepsilon$$

The null hypotheses tested were as follows:

H_o: The percentage of willow canopy cover in the study area has not changed from 1981 to 2019 in any of the 13 study meadows.

H_o: The percentage of water cover in the study area has not changed from 1981 to 2019 in any of the 13 study meadows.

Drivers of Willow Canopy Changes. I used a binomial regression model to assess the probability of a GIS landcover classification point being classified as willow based on several predictor variables. The response variable is the probability of a GIS landcover point being classified as willow (1) versus being classified as any other landcover category (0). The predictor variables are the number of years a meadow has been occupied by beaver, and beaver colony density. I used beaver colony density instead of beaver colony numbers as a predictor variable because the meadows in this study vary in size, so the number of active colonies is not representative of their potential impacts on the landscape, whereas colony density remains a consistent form of evaluating colony impacts on the landscape even when accounting for meadow sizes. I predicted that the probability of a point transitioning to willow would be positively associated with beaver colony density and the number of years a site has been occupied by beaver.

I created candidate models and used Akaike's information criterion corrected for small sample size (AICc) to assess model support (Anderson & Burnham 2002). The full model includes all predictor variables described above. The formula for the full binomial regression model is as follows:

$$\log(odd\widehat{s\ of}\ willow) = \beta_0 + \beta_1(Beaver\ Colony\ Density) + \beta_2(Years\ Occupied\ by\ Beaver) + \varepsilon$$

All estimates from the binomial regression model were on the log(odds) scale, so to transform to the probability scale, I used the formula: $\frac{\exp(x)}{1+\exp(x)}$, where *x* is the log(odds) estimate.

The null hypothesis tested is as follows:

H_0: The probability of a GIS classified landcover point transitioning to willow is not influenced by beaver colony density or the number of years beaver were active.

Results

Beaver Colony Inventories

I found that beaver colony numbers have not changed significantly from 2010 to 2020 in the study area (p=0.74, Table 2). Similarly, the average beaver colony density has not changed significantly in the same time frame (p=0.67, Table 3).

Table 2: Results of a one-way ANOVA for testing difference in mean colony numbers (n=13) in 2010 and 2020 in the southern Absaroka-Beartooth Wilderness study area.

	df	Sum Sq	Mean Sq	F statistic	p-value
Year	1	0.62	0.615	0.111	0.742
Residuals	24	133.23	5.551		

Table 3: One-way ANOVA for testing difference in mean colony density (n=13) in 2010 and 2020 in the southern Absaroka-Beartooth Wilderness study area.

	df	Sum Sq	Mean Sq	F statistic	p-value
Year	1	0.26	0.259	0.182	0.673
Residuals	24	34.06	1.419		

The total number of active colonies increased since beaver reintroduction starting in 1986 (Scrafford et al. 2018) through the early 2000's and then remained constant through 2020 (Figure 2). However, I found that colony numbers have responded over time differently in each of the 13 study meadows, quantified with a linear regression model with colonies as the response and an interaction between year and meadow explanatory variables (Figure 3). An R^2 value of 0.833 indicates that about 83% of the variation in colony numbers is explained by the model. Furthermore, an analysis of variance test indicates strong support for the inclusion of the polynomial term and interaction terms ($p<0.001$).

Evaluation of estimated marginal means and trends indicates that Christenson's ($p<0.001$), Frenchy's ($p<0.0001$), Grizzly ($p= 0.007$), Hellroaring ($p <0.001$), Holeman's ($p <0.001$), and Stillwater ($p <0.001$) all have significant increases in beaver colony numbers from 1986 to 2020, while the remaining 7 meadows did not.

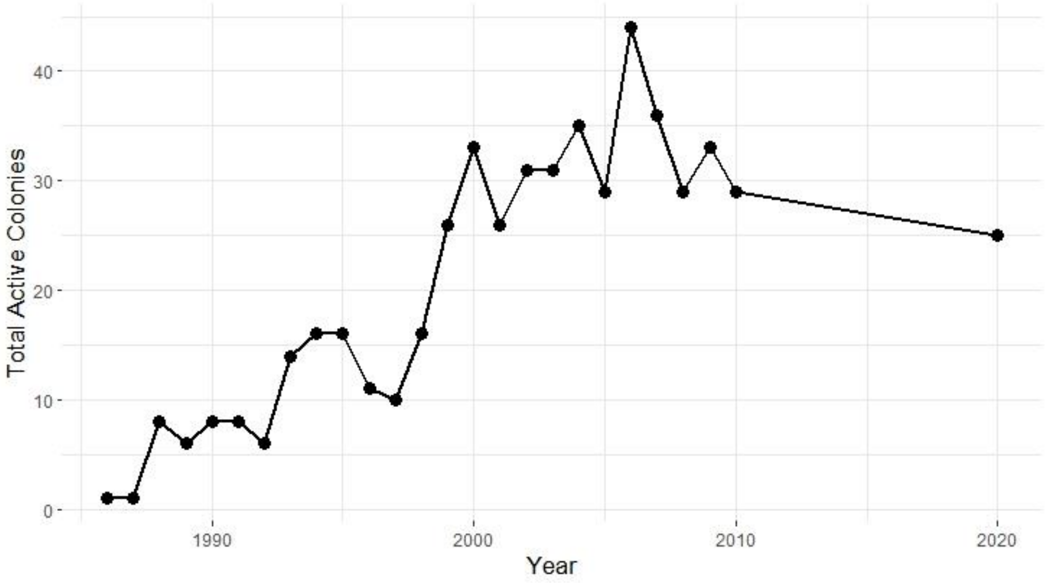

Figure 2: Total number of active beaver colonies from 1986-2020 in the southern Absaroka-Beartooth Wilderness.

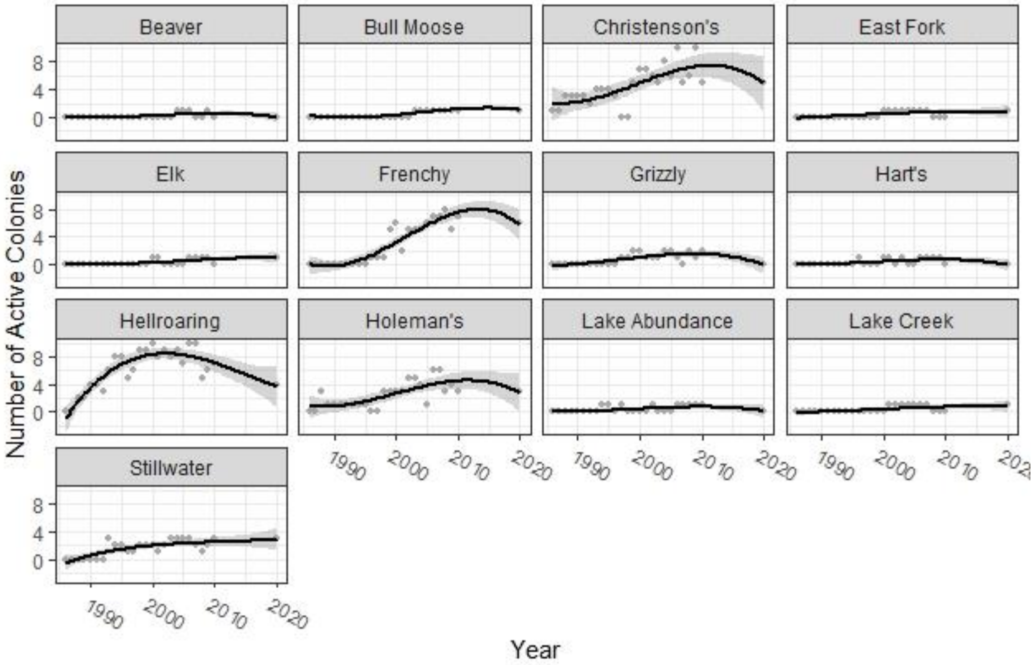

Figure 3: Number of active colonies from 1986 - 2020 for the 13 study meadows in the southern Absaroka-Beartooth Wilderness.

GIS-based Vegetative Canopy Assessment

Average Willow Canopy and Surface Water Trends. I found that the interaction between meadow and year was not significant in explaining variability in water cover (p=0.907), so a simple linear regression model estimating water cover as a function of year was used (Table 4). Surface water changed from an average of 5% in 1981 to an average cover of 8% in 2019, reflected by a statistically significant change in estimated mean water cover over time with the linear model (p=0.015).

Table 4: Results of a linear regression model estimating the average water cover in the study area as a function of year.

Predictors	Estimates	95% Confidence Interval		p-value
		Lower	Upper	
(Intercept)	-144.61	-266.25	-22.96	0.021
Year	0.08	0.01	0.14	0.015
Observations	65			
R^2 / R^2 adjusted	0.090 / 0.075			

I found that the average willow canopy cover for all meadows in the study area significantly increased from 16% in 1981 to 37% 2019 ($p<0.05$). I found that the interaction between year and meadow was significant in explaining the variability in willow cover ($p<0.001$), so the full model was used. An R^2 value of 0.971 indicates that this model explains about 97% of the variation in willow canopy. Willow canopy cover was an average of 16% throughout the 13 study meadows in 1981 and nearly doubled to an average of 37% in 2019. A test of estimated marginal means and slopes indicates that all meadows in the study had significant increases in willow canopy cover from 1981 to 2019 ($p<0.05$). Lake Creek meadow had the highest rate of change from 1981 to 2019, where each year the average percentage of willow canopy cover increased about 1.043%.

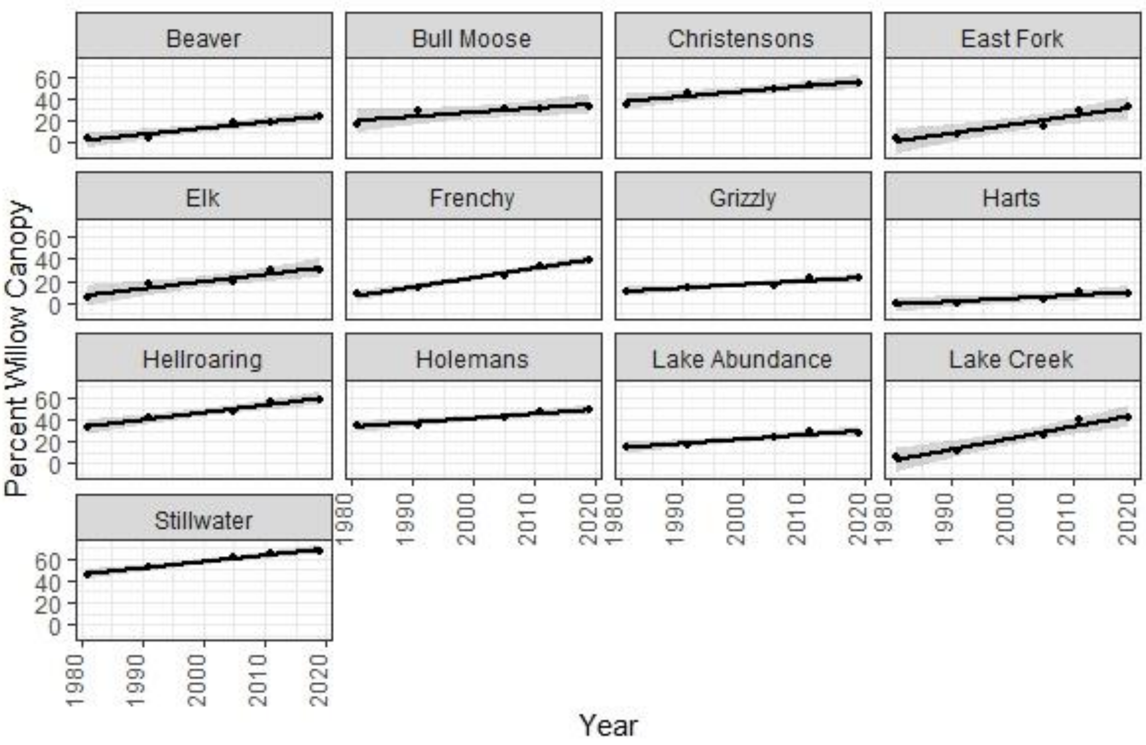

Figure 4: Percent willow canopy cover change over time for the 13 study meadows in the southern Absaroka-Beartooth Wilderness.

Drivers of Willow Canopy Changes. To investigate the drivers behind willow canopy changes, I used a binomial regression model to estimate the probability of a GIS landcover classified point transitioning to willow from one year to the next based on beaver colony density and the number of years beaver had occupied the area. I used a variance inflation factor (VIF) test to check for any multicollinearity between independent variables. A VIF of 1.59 indicated no correlation between the predictor variables. An AICc model selection indicated that the best model included colony density and number of years the area was occupied by beaver (Table 5).

A model weight of 1 for the top model indicated strong support over the other candidate models (Table 5).

I found that the probability of a point transitioning to willow increased by 0.507 for every unit increase in the number of years beaver occupied the area and increased by 0.562 for every unit increase in colony density (colonies/km) ($p<0.001$, Figure 5).

Table 5: AICc model selection for binomial regression model.

Explanatory Variables	K	AICc	ΔAIC_c	weight	Log likelihood
Years Occupied + Colony Density	15	19869.97	0.00	1	-9919.98
Years Occupied	2	39329.81	19459.84	0	-19662.90
Colony Density	2	39844.34	19974.37	0	-19920.17
Null (intercept only)	1	40490.27	20620.30	0	-20244.14

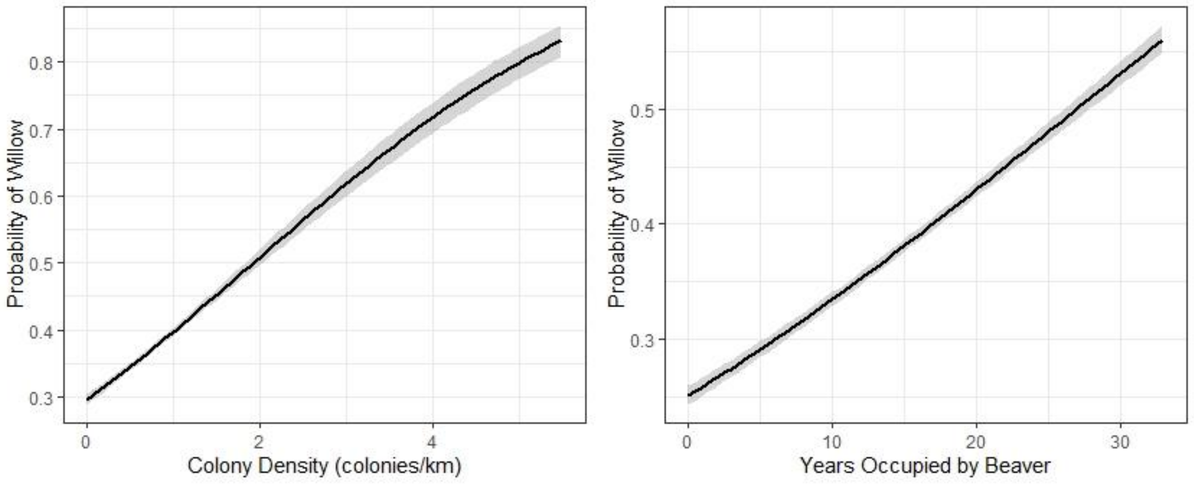

Figure 5: Probability of a GIS point being classified as willow based on beaver colony density and the number of years the site was occupied by beaver. Shaded areas represent a 95% confidence interval.

Discussion

The objective of this study was to determine if beaver had a sustained positive or negative effect on willow canopy cover in the southern ABW. To accomplish this, I repeated streamside surveys for beaver colonies to determine if beaver colony numbers and density had increased or decreased since the last survey effort in 2010 (Scrafford et al. 2018). I then analyzed standing water and willow canopy cover trends from 1981 (five years before beaver reintroduction) to 2019 and explored the relationship between willow canopy changes and beaver colony density and longevity.

Beaver Population in the Southern ABW

Beaver in the southern ABW were extirpated through trapping in the mid 1900's, but their disappearance may also be attributed to a decline in willow condition from over-browsing by moose (Smith & Tyers 2012; Tyers 2003). At the time of beaver reintroduction, there was concern about the likelihood of success of beaver being reintroduced into a heavily browsed landscape. Willow, being the primary food and building source for beaver in the southern ABW, was degraded (Chadde & Kay 1988; Tyers 2003). However, after a moose population decline following 1988 and a subsequent decline in willow browsing (Tyers 2003), Scrafford et al. (2018) determined that willow stands were not degraded enough to prevent a successful reintroduction of beaver.

Scrafford (2018) analyzed beaver colony numbers from 1985 to 2010 and determined that beavers in the southern ABW reached carrying capacity in 2000 and remained at an average of

1.33 colonies per km of stream through 2010. I repeated these colony surveys in 2020 and found no significant change in colony numbers or density.

The widespread persistence of beaver colonies in the southern ABW, despite being reintroduced into an over-browsed environment, may be partially attributed to a source-sink population dynamic. This dynamic is described as having a larger population with quality habitat that enables ancillary habitats, presumably of lower quality, to persist despite stochastic local extinction events (Pulliam 1988; Pulliam et al. 1992; Fryxell 2001). As discussed by Baker (2003), beaver and willow communities may be able to recover in heavily browsed environments if beaver are able to disperse from nearby “source” populations. I found that the 13 study meadows in the southern ABW appeared to reflect such population dynamics.

I found that 6 meadows in the southern ABW study area experienced significant increases in beaver colony numbers since their reintroduction, indicating higher quality habitat. I believe that these meadows act as habitat for source populations in the southern ABW. They include colonies in Christenson’s, Frenchy’s, Hellroaring, Holeman’s, Grizzly, and Stillwater. It is very likely that the size of a meadow plays an important role in whether a meadow can sustain a source population. The larger meadows have more habitat, food, and building materials to sustain more than one active colony. Ancillary meadows that would be considered “sink” populations are Beaver, Bull Moose, East Fork, Elk, Harts, Lake Abundance, and Lake Creek. These sink populations experience stochastic local extinction events with no permanent populations, with the survey efforts finding occasional abandonment by beaver only to return in subsequent years. This supports Baker’s (2003) hypothesis that these source communities are critical for long-term population survival, such as the southern ABW beaver population. It is probable that the source meadows can maintain a large enough meta-population to allow the southern ABW beaver population to persist.

Furthermore, some of the smaller, ancillary meadows had some of the strongest willow recovery. These findings also align with Baker's (2003) assessment of beaver-willow habitat relationships. Baker (2003) offers that beaver can facilitate willow recovery in marginalized areas even if they do not consistently occupy an area. This phenomenon was described as a "positive feedback mechanism", where beaver from source populations periodically occupy marginal habitat and create condition for new establishment and persistence of willow where there was not any before. Therefore, I conclude that once beaver began periodically inhabiting these smaller, marginal habitats in the ABW, willow canopy exhibited a stronger recovery than that of meadows that already had adequate habitat to sustain a long-term population.

In the broader context of source and sink beaver populations, the beaver in the "source" meadows in southern ABW have also likely contributed to the beaver population increase on the NYWR, which is downstream. Commensurate with the decline in elk numbers and an increase in willow, beaver populations have begun to increase on the NYWR (Smith & Tyers 2012). Smith and Tyers (2012) hypothesize that the beaver reintroduction in the southern ABW increased the rate of beaver colonization in YNP.

Beaver and Landcover Changes

Scrafford et al. (2018) surmised that beavers in the southern ABW improved willow communities, as reflected by an increase in willow canopy cover. They found that willow canopy cover increased from 32% in 1981 to 48% in 2011 through a comparison of aerial photos of 4 meadows. In contrast to Scrafford's (2018) approach, I added additional years for aerial photo comparisons and included all 13 study meadows to analyze the changes in willow canopy cover and standing water. I confirmed that willow canopy cover has increased since beaver were reintroduced in the southern ABW in the late 1980's. On average, throughout the entire study area there was nearly a two-fold increase in willow canopy cover ($p<0.05$). Average willow canopy for the southern ABW study meadows increased from 16% in 1981 to 37% in 2019. I surmise that beaver-caused disturbances such as flooding, raised water tables, and redirecting streams facilitated a natural disturbance regime that favors willow growth.

My analysis also showed a change in visible standing water since beaver reintroduction ($p<0.05$). I suggest that beaver have altered the landscape in these meadows to such an extent with dams and canals that a water table increase is intuitive. Average water cover throughout the study area increased from 5% in 1981 to 8% in 2019. The 13 meadows I visited in the 2020 survey effort had extensive marshy areas. These were often covered in vegetation such as sedges (*Carex* spp.) and would not be recognized as water using the simple aerial imagery classification. Therefore, it is very likely that the aerial imagery landcover classifications do not accurately represent the true amount of impounded water in these beaver meadows.

The extent of spatial and temporal data for this project enabled an analysis of the effect of beaver colony density and longevity on willow canopy cover changes. I found that the probability of willow establishment (defined as a GIS point being classified as willow or not) is positively correlated with beaver colony density and the number of years beaver have been present in an area. The disturbances caused by beaver play an important role in willow recovery. It is very likely that beaver activity has facilitated new recruitment of willow plants by promoting asexual reproduction through adventitious roots or buried stems (Johnston et al. 2011; McColley et al. 2011).

The landcover changes over the last 4 decades highlight some important drivers of willow recruitment in a wildland setting. As beaver alter the landscape, we see significant changes in willow and water cover in all study meadows. This phenomenon is supported by the concept of a "shifting habitat mosaic", wherein ecosystems like floodplains and riparian areas experience frequent disturbances that cause constant changes in successional states as the landscape is altered by external factors (Mouw et al. 2012; Wimberly 2006). In this case, beaver activity facilitates a disturbance regime through redirecting streams, impounding water, trapping sediments, and revegetating parts of the floodplain.

Implications

The NYWR in YNP has garnered the most attention in the debate over causes of willow decline (Peterson et al. 2020; Smith & Tyers 2012). It is a good natural laboratory to address variation in willow response spatially and temporally given the size of this winter range, unique assemblage of ungulates and carnivores, and the long-term monitoring that has occurred (Houston 1982; Despain et al. 1987; Singer et al. 1998; Yellowstone National Park 1997; Wagner 2006; Wolf et al. 2007; Peterson et al. 2020). Because it is juxtaposed to my study area, conditions on the NYWR offer comparisons on the role of beaver and willow in the ecology of the wildland riparian system in the southern ABW; acknowledging the differences that the ABW is at higher elevation and moose are the primary wintering ungulate utilizing willow. The ecology of the southern ABW is simpler than on the ungulate wintering areas in Rocky Mountain and Yellowstone National Parks (Peterson et al. 2020; Tyers 2003). Still, some comparison is valid. Specifically, why has willow recovered in the southern ABW but not to the same extent on the NYWR?

The effects of climate warming and disrupted fire cycles were factors affecting both of these areas, as was a significant decline in willow distribution, abundance, and condition from ungulate herbivory (Tyers 2003, 2020; Peterson et al. 2020). Bilyeu et. al. (2008) addressed the loss of beavers in YNP, which they believed was responsible for stream incision resulting in the inability of willow to fully recover to normal height. They added that very heavy elk browsing suppressed willow while reducing browsing promoted willow recovery (Bilyeu et al. 2008; Smith & Tyers 2012; Smith et al. 2020). They were unsure if the changes that have occurred on the NYWR in the last 100 years can allow for a conversion of the current "elk-grassland" state back to a "beaver-willow" state. Peterson et al. (2020) conjectured that, "if beavers do not reestablish a much greater presence across the northern range landscape, it is possible that the elk-grassland state that persisted for much of the twentieth century will prevail as a stable state in many areas." They added that an increase in beaver colonies across the NYWR, "will need to continue if woody plant communities are to recover to their fullest extent."

Stream incision from erosion, exacerbated by a loss of beaver and willow, is consistently documented on the NYWR (Wolf et al. 2007; Kay 1990; Smith et al. 2020) but not in the southern ABW (Peterson et al. 2020; Kay 1990; Wolf et al. 2007; Tyers 2003). Therefore, I conclude that the southern ABW streams and willow communities were not degraded enough to prevent the recovery of a beaver-willow community as described by Peterson et al. (2020). The reduction in moose browsing and reintroduction of beaver enhanced the riparian areas in the southern ABW and increased willow canopy cover.

Another important difference between the southern ABW and the NYWR is the topography. The southern ABW beaver-willow riparian areas occur in post-glacial lakes with gentle topography and wide valleys, whereas areas on the NYWR such as Blacktail Creek with extensive channel erosion have steeper slopes with narrow stream corridors (Johnston et al. 2014). Therefore, steeper topography may contribute to riparian areas being more vulnerable to erosion and stream incision when exposed to over-browsing. These characteristics may also make the sites on the NYWR more vulnerable to hydrologically disconnecting to the floodplain, whereas the flat wetland meadows in the southern ABW are more likely to retain a high water table during times of over-browsing or disturbance.

The differences in willow recovery in the southern ABW versus the adjacent NYWR may also be attributable to varying degrees of ungulate utilization. The southern ABW has experienced a decline in moose browsing which has remained low since the population crash after 1988 (see chapter 3). However, Painter et al. (2020) describes that although elk browsing has decreased, willow has not recovered uniformly because of an increase in bison numbers on the NYWR.

Furthermore, Baker (2003) describes that an important factor in the recovery of beaver-willow communities in marginalized areas is having a “source” population that facilitates periodic beaver activity in places that are degraded. These “source” populations then create a positive feedback mechanism by periodically inhabiting marginal habitat and facilitating new willow growth. My findings show evidence of this phenomenon in the ABW, but the NYWR beaver population does not have a well-documented, resilient source population that has the capacity to facilitate new beaver-willow communities in marginalized habitat (Smith & Tyers 2012. This may explain why beaver-willow communities were not able to re-establish more uniformly on the NYWR.

Considering these contrasts and similarities between the NYWR and the southern ABW, I found that the beaver population in the southern ABW has remained at carrying capacity for 20 years, and willow canopy cover has continued to increase since the last analysis in 2011 by Scrafford et al. (2018), changing from 35.5% canopy cover in 2011 to 37.1% in 2019. This confirms the hypothesis that beavers are beneficial to willow communities such as those in the southern ABW, but also suggests that the longevity of beaver presence benefits willow dominated wetlands. The duration of this study has shown that if beavers are allowed to persist in a wildland setting with willow-dominated plant communities, their presence has the potential to enhance and restore riparian systems. Managers should consider this when exploring options of reducing negative effects of over-browsing or restoring wetlands and riparian systems.

CHAPTER THREE

WILLOW RESPONSE TO CHANGING MOOSE RELATIVE ABUNDANCE AND HERBIVORY IN THE SOUTHERN ABSAROKA BEARTOOTH WILDERNESS

Introduction

Willow stands occupy a small percentage (<5%) of the American west, including the GYE (Naiman et al. 1993). Although this vegetation occupies a very limited portion of the landscape, they are a ecologically valuable part of riparian areas because they support diverse aquatic and terrestrial flora and fauna (Naiman et al. 1993; Smith et al. 2020; Skagen et al. 1998). Willows also have deep roots that stabilize stream banks and reduce erosion (Naiman et al. 1993; Polvi et al. 2014). Willows often reproduce asexually through disturbances, like flooding events or when beaver harvest stems, which facilitates willow stand expansion (McColley et al. 2011; McColley 2007; Kay & Chadde 1992; Johnston et al. 2011; Marshall et al. 2014; Baker et al. 2005). This resiliency and quick recovery from disturbances makes willow a critical component of complex riparian systems.

However, because of its growth form, association with riparian habitats, and high food value, willow may be substantially altered by fire, flooding, sediment movement, drought, and browsing (Marshall et al. 2014; Brookshire et al. 2002; Cooper et al. 2006). Research has shown that willow is generally tolerant of browsing and may increase production at moderate levels of browsing, while heavy and repeated utilization may suppress growth (Wolff 1978; Tyers 2003; Bilyeu 2006).

Consequently, changes in willow height have been used to describe the effects of elk populations and associated browsing in many areas, including the NYWR (Johnston et al. 2007; Painter & Tercek 2020). Moreover, among other trees and shrubs like aspen (*Populus tremuloides*) and cottonwood (*Populus* spp.), willow (*Salix* spp.) is often the dominant overstory vegetation in riparian systems in the GYE. Therefore, willow abundance and stature are also used as a metric of riparian status and overall ecosystem health.

Willow establishment appears to have undergone a dramatic decline after the 1930's in a variety of wildland settings, including the GYE, resulting in changes in distribution and vigor. This has been extensively documented on the NYWR in the GYE (Peterson et al. 2020). For willow on the NYWR, this has been attributed to the combined effects of elk herbivory, beaver dam abandonment, channel incision, and replacement by upland plant species (Peterson et al. 2020).

Peterson et al. (2020) chronicled this phenomenon on the NYWR by describing changes through the twentieth century, centered on fluctuations in willow populations in relation to elk and beaver numbers. They describe a transition from a "beaver-willow state", where riparian zones were once dominated by tall willow stands maintained by beaver along small streams and in larger meadows. Photo comparisons show a decline in the stature and abundance of willows during this period (Kay 1990). They also noted that willow establishment appears to have decreased dramatically after the 1930's resulting in dead and suppressed willow that were replaced by grasses and herbaceous plants in many areas. These transformed riparian areas took on the persistent alternative condition Wolf et. al. (2007) called the "elk-grassland state". In this status, individual willow plants are short in stature and die without being replaced by new plants. Willow stands are ultimately limited to small, scattered fragments; and active beaver dams are absent.

By contrast, researchers have described a recent increase in willow height on the NYWR as an indicator of top-down trophic cascade, where reduced elk numbers after predator recovery released willow from browsing pressure following decades of over-browsing (Singer et al. 1998; Chadde & Kay 1991; Belile 2016; Beschta et al. 2020; Peterson et al. 2020). Frequent correlations have been made between willow height recovery and elk population trends, suggesting that reduced elk browsing is the primary driver behind NYWR willow recovery (Baker et al. 2005; Ripple & Beschta 2006; Beyer et al. 2007). However, willow utilization on the NYWR is not restricted to elk. Elk, mule deer, moose, and increasing bison numbers have resulted in continued suppression of willow growth in some areas, making it difficult to completely ascribe changes in elk populations to willow recovery.

Documenting the changes in vegetation after the extirpation and then restoration of large carnivores (wolves, grizzly bears, and mountain lions) on the NYWR has greatly increased our understanding of the cascading effects that can reverberate through ecosystems. Moreover, the NYWR example in Yellowstone is not unique. A similar cycle has been demonstrated in other ecoregions and various National parks of western North America, including Olympic, Rocky Mountain, Wind Cave, Yosemite, and Zion in the United States and Banff, Jasper, Kootennay and YoHo in Canada (Peterson et al. 2020).

I investigated evidence of a comparable ungulate boom and bust cycle in the southern ABW, which was also marked by a decline and apparent recovery of willow (Tyers 2003). Previously robust willow stands were dramatically suppressed during the period when moose numbers were increasing and have rebounded in recent decades following a moose population crash after the landscape-level Yellowstone fires (Tyers 2003; Tyers & Irby 1995).

The southern ABW has glaciated topography with extensive post-glacial lake beds that are now willow-dominated wetlands. At these higher elevation sites, snow accumulation usually precludes access for elk, bison, and mule deer. Therefore, winter browsing effects can be ascribed to moose (Tyers 2003; Chadde & Kay 1988). Consequently, the association between browsing measurements and the moose population can be used to assess the effects of local moose numbers on willow status (Tyers 2003).

Moose Population and Willow Stand Monitoring

Moose population monitoring requires an understanding of their habitat requirements and adaptations for survival in northern latitude winter environments. Moose are uniquely adapted to harsh winter conditions. This includes a larger body size to reduce the risk of predation and deal with cold weather, and they are also able to travel long distances quickly in difficult terrain. (Telfer & Kelsall 1984). However, to compensate, moose need to find digestible food in patches that enable high rates of intake (Saether & Andersen 1990). Moose must optimize food consumption in areas with limited food availability, which often means finding an adequate supply of low-quality woody twigs to meet nutritional requirements throughout the winter (Peek et al. 1992; Peterson 1955; Renecker & Schwartz 1997; Tyers 2003; Telfer & Kelsall 1984).

Moose distribution and home range depends on available forage, especially in winter when large quantities of nutritious and digestible food are rare. As browsers, moose feed primarily on woody vegetation during the winter when more digestible food is less available (Geist 1971; Peek et al. 1992; Tyers 2003). Among the many tree and shrub species moose utilize, willow is significant. In some areas, it is the primary determinant of moose habitat relationships because it can provide large amounts of critical forage in concentrated patches (Peterson 1955; Wolff 1978; Coady 1982; Renecker & Schwartz 1997; Tyers 2003). Coady (1982) summarized North American moose ecology from Wyoming to Alaska and concluded that shrub communities, particularly riparian willow stands, are the most critical winter habitat.

Available biomass determines the ability of moose to meet energy needs utilizing willow. The best foraging opportunities are where willow height can extend above the snow and where willow canopy cover is greatest (Geist 1971; Eastman & Ritcey 1987; Joyal 1987; Thompson & Euler 1987; Oldemeyer & Regelin 1987; Kelsall & Telfer 1974; Tyers 2003). The survival chances of individual moose and the fate of a moose population can be determined by the availability of large patches of browse during winter, especially willow stands.

Therefore, to assess moose habitat use and track annual variation and trends, especially long-term impacts on primary foods such as willow, monitoring moose abundance is necessary (Tyers 2003). However, population analysis is difficult for moose because they are usually solitary and occupy habitats with poor observability (Tyers 2003; Gasaway et al. 1986; Ballenberghe & Peek 1971; Crête 1989; Burkholder et al. 2017; Nadeau et al. 2017). Timmerman and Buss (1997) recommended developing indices of moose populations involving consistent, long-term repetitive sampling in moose habitat that is accessible to observers (Tyers 2003; Timmerman & Buss 1997). For example, Tyers (2003) developed indices over several decades by counting moose year-round while traveling the YNP road that bisects the NYWR and riding horseback on a network of trails in the southern ABW in the fall.

There have also been other approaches to moose population monitoring that include monitoring browse utilization of plant communities (Crête 1989; Keigley and Fager 2006; Seaton et al. 2011). Keigley and Fager (2006) reported that a reduced moose population was reflected in increased willow growth, thus suggesting that land managers could use willow status as a metric moose abundance to make informed decisions on hunting quotas. Furthermore, Crête (1989) found a significant positive linear relationship between moose density and deciduous browse removal in Quebec, Canada.

Moose Population History in the Southern ABW

Tyers (2003) reported on moose population status and winter habitat condition in the southern ABW in 2003. This was previously poorly documented. His findings have corollaries with what Smith et al. (2020) describe for the relationship between elk and willow on the NYWR. Likely, moose arrived and spread across the GYE in the late 1800's. Observations in the early 1900's indicate that the moose population in the southern ABW area was small, with few reported sightings (McDowell & Moy 1942). During this time, willow was reportedly tall and robust (McDowell & Moy 1942; Chadde & Kay 1988). In 1921, the U.S Forest Service began more extensive patrols (non-systematic snowshoe surveys conducted from December to April) to discourage poaching and monitor wildlife near YNPs northern boundary. A small but growing moose population was observed. In the 1930’s, the population was reported to be expanding and concern for the condition of willow stands was documented in agency reports. Over-winter utilization of willow by moose was estimated at 90% and about three quarters of the willows in moose winter range were reported to be dead (Tyers 2003). Periodic horseback surveys were conducted through the 1940’s with reports of an increasing moose population and severely over-browsed willow stands. In response, Montana authorized a moose hunt with 40 permits in 1945. Agency reports in the 1960’s indicated declining moose numbers and deteriorating willow stands (Kehrberg 1964; Tyers 2003). In 1985, when population monitoring for this project began, the hunting quota for moose was 55 with no restriction on age or sex. Willow was reduced to scattered patches and uniformly shorter than the average snowpack. Tall willows were no longer a component of winter moose range (Tyers 2003).

In 1985, a group of State and Federal agencies started a long-term study to assess the population status and winter ecology of the Shiras moose in the southern ABW and NYWR. Tyers (2003) reported the findings from 1985 to 2001 and continued population and habitat monitoring on an annual basis. He reported a marked decline in the population following the landscape level Yellowstone fires in 1988 because most forested hillsides adjacent to willow stands burned.

Moose in the southern ABW rely on woody vegetation during winter months when other digestible food is unavailable. To optimize time spent foraging, moose find patches of forage. Though limited in area and distribution, willow stands form the most concentrated patches of browse on the landscape (Tyers 2003). Willow is browsed mostly in early winter when snow conditions have less impact on moose movements. Tyers (2003) found that moose utilize willow stands if snow conditions allow, then retreat to cover provided by mature double canopy forests where the overstory ameliorates snow conditions and moose can feed on dense patches of subalpine fir (*Abies lasiocarpa*) < 5m tall in the understory. Subalpine fir is a shade-tolerant conifer species that grows in late-successional stage lodgepole pine forests.

The long-term implications of moose population trends and willow status in the ABW have yet to be determined. Therefore, my objective was to determine if moose abundance and associated browsing influence willow height in the ABW. I accomplished this using long-term data collection on moose relative abundance, browsing rates, and willow condition in the southern ABW.

I first tested whether moose relative abundance increased or decreased from 1986 to 2021 using a suite of indices that were started in 1986 by Tyers (2003). I then tested whether changes in moose relative abundance in the southern ABW are correlated with browsing and willow height. Finally, I tested the relationship between browsing and willow height throughout the study area to determine if willow height fluctuates in response to browsing.

I hypothesized that moose relative abundance has declined throughout the past 36 years, and that this decline is reflected in moose browsing rates on willow. Furthermore, I expected that lower moose abundance has resulted in a release of browsing pressure and contributed to a recovery of willow height in the study area. This has implications for interpreting the trophic cascade effect and status of ecological process in a wildland setting and will provide a means for managers to monitor moose relative abundance through willow stand monitoring.

Methods

Study Area

The study area is in the northern region of the GYE, specifically in the southern ABW and associated areas (Figure 6). There are 4 primary drainages that comprise this study area: Hellroaring Creek, Slough Creek, Buffalo Creek, and Stillwater Creek. Much of the study area is north of the YNP boundary, but parts of the NYWR are included in the data collection.

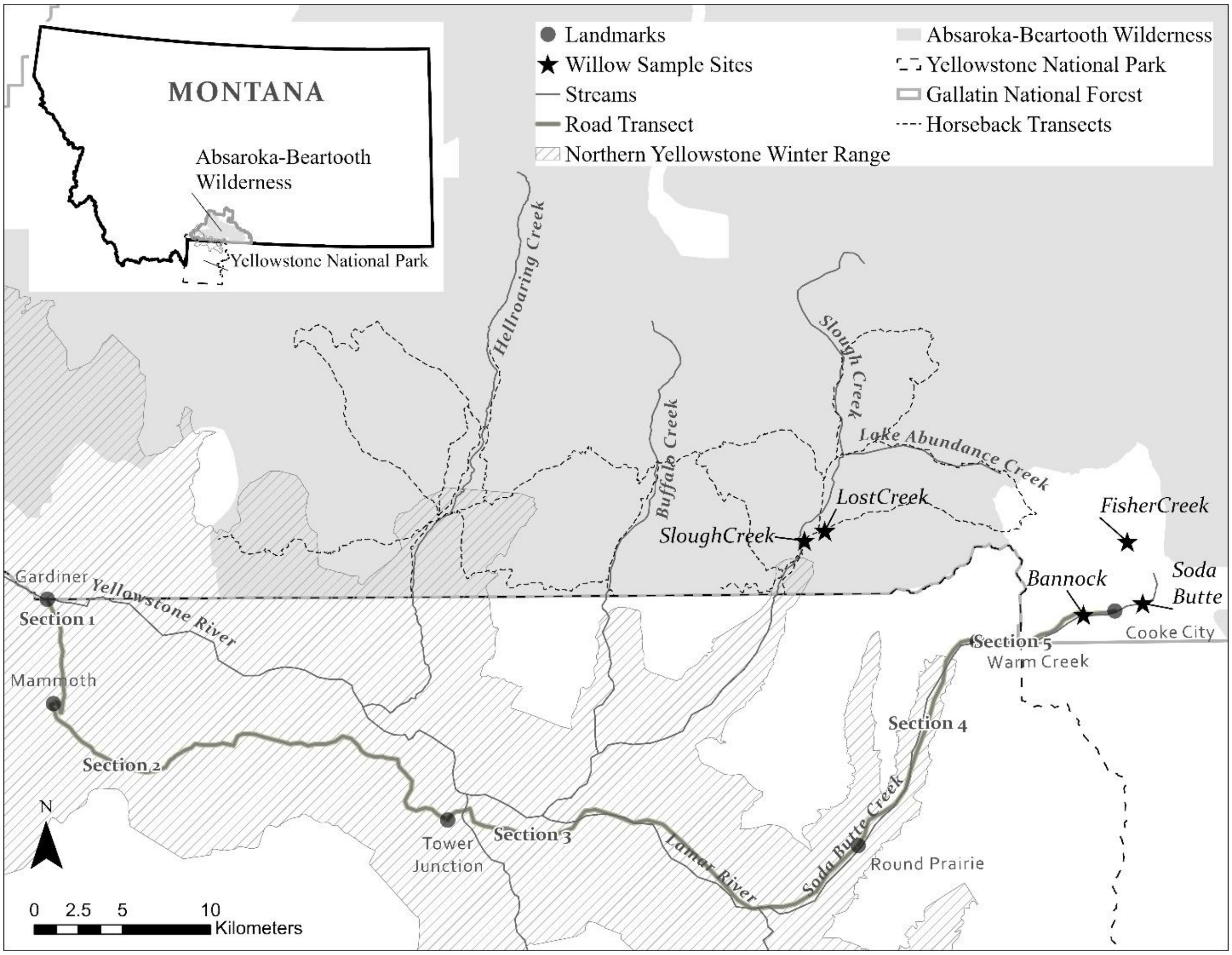

Figure 6: Southern Absaroka-Beartooth Wilderness study area (Montana, USA), including willow sample sites and moose relative abundance transects.

The closest weather station for the Southern ABW study area is in Cooke City, Montana (~2500m, Figure 6). The average annual precipitation is 65.4cm with peak precipitation in May and June. Mean minimum temperature is -15.4 C in January and mean maximum temperature is 23.2 C in July (Western Regional Climate Center 2022). Vegetation in the study area has changed over time after a stochastic fire event in 1988, with much of the old growth coniferous forests burning and transitioning to a new successional stage of young lodgepole pine (Tyers 2003). Vegetation in the study area varies depending on the elevation. Sage steppe is typically found at lower elevations (2,000m), then transitions to coniferous forests at higher elevations (3,000m). Forest types are primarily comprised of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), and whitebark pine (*Pinus albicaulis*). Willow is the most prominent woody riparian vegetation that occurs along streams and wetlands.

The NYWR is defined by the wintering limitations of elk, with elk and bison being the primary ungulates utilizing this range for winter habitat (Singer et al. 1994; Tyers 1981; Yellowstone National Park 1997). Moose winter here too but are scattered in areas of suitable habitat that are at higher elevations than elk and bison (Tyers 2006). The partitioning of ungulates in the study area is determined primarily by access to forage and by snow in the winter. Therefore, elk and bison are mostly restricted to lower elevations, while moose, adapted to harsh winter conditions, are found at higher elevations. The study plots and areas north of the YNP boundary are all above 2000 m, which contributes to deeper snow that precludes winter access for elk and bison, resulting in moose as the primary wintering ungulates in the southern ABW study area (Tyers 2003). The average elevation for the southern ABW study sites is 2250

m. In contrast, the average elevation of the elk winter range is about 1900 m (Yellowstone National Park 1997).

Moose Relative Abundance

Horseback Transects. Moose relative abundance over time was assessed through a series of count transects along the southern ABW trail system. These transects include 177 km of trail through the ABW, inclusive of all the drainages in the study area (Figure 6). Data collection on moose distribution and abundance via horseback transects was first conducted in 1947, 1948, and 1949 by Joe Gabb (Montana Fish and Game) who searched for moose every fall for these three years. This route was repeated annually from 1985 to 2021 between July and late October, with sampling concentrated in September.

These transects span 4 drainages and cover difficult terrain, so transects take multiple days and trips to complete. Several efforts, such as those done by Joe Gabb in the 1940's, was primarily to look for moose, but most transects were done by Forest Service crews that conducted other tasks along the way, including trail maintenance and outfitter camp inspections. In recent years, we also enlisted the help of area outfitters. My efforts in 2019, 2020, and 2021 included riding the trails solely to look for moose and to document beaver colony locations. Party size throughout the study duration ranged from 1 to 6. The days spent covering the transect each fall ranged from 5 to 66, which in some years included multiple repetitions. Moose sightings were recorded as the number of moose seen per day of searching, with information on the sex and approximate age of each moose observed.

The logistic limitations associated with this index meant several sections of the transect were duplicated during surveying efforts while others were not, and we were unable to account for variations in habitat quality, moose observability, and distance from transect throughout the entire trail system. Therefore, I used the measure of moose observed per survey day to accommodate the variations in survey efforts. From 1942 to 2021, the total number of days spent searching was 1,363.

Road Transects. I also assessed moose relative abundance over time using transects along the 89 km stretch of paved road from Gardiner to Cooke City, the only road in YNP open year-round. Each trip from one end of the road to the other is considered one transect, regardless of the direction of travel. At least 4 transects were completed each month from 1987-2021 (n=2,947 transects). Each transect records the number of moose seen, sex, approximate age, cover type, and location along road transect. Transects were completed with a party size that ranged from 1-5. The time it took for each transect ranged from 2 to 3 hours. Several transects were completed with the sole purpose of searching for moose. Most of the time, the road was driven for other reasons, but crews were instructed to search for and record moose sightings. Sampling occurred between January 1987 and December 2021. The transect was divided into 5 sections to accommodate varying habitat characteristics (Figure 6). To assess moose relative abundance trends in varying habitat types with varying degrees of changes after the 1988 Yellowstone fires, I analyzed moose sighting trends within each section in addition to the overall transect.

- Section 1 is defined as the section covering the Gardner River canyon and includes broken topography with arid grasslands and sagebrush. This section was not burned by the 1988 Yellowstone Fires.

- Section 2 includes the section of road from Mammoth to Tower Junction and includes diverse vegetation such as open grasslands, Douglas fir, mature spruce-fir, and some patches of willow and aspen. This section was heavily burned by the 1988 Yellowstone Fires.

- Section 3 includes the road section from Tower Junction to Round Prairie following the Lamar River and includes an open valley with grasslands and sagebrush. This area was not burned by the 1988 Yellowstone Fires.

- Section 4 includes the road section from Round Prairie to Warm Creek and includes mature lodgepole pine forests. Despite being heavily forested, this area was not burned by the 1988 Yellowstone fires.

- Section 5 includes the road section from Warm Creek to Cooke City and includes large willow stands and old growth spruce fir forest. The area north of this road section burned in the 1988 Yellowstone Fires.

Willow Permanent Plots

To determine if willow height and browsing pressure has changed over time and if moose browsing pressure is correlated with willow height trends, I analyzed permanent willow plots that were created in 1988 and monitored every spring through 2021, excluding 1993, 1994, 1998, 1999, 2000, 2001, 2018, and 2019. 179 plots were established in 5 locations that were known to be available to wintering moose: Fisher Creek, Soda Butte Creek, Bannock Creek, Lost Creek, and Slough Creek (Figure 6). Each location contains an average of 10 plots for each species present in that willow community (Table 6). Species include one birch and seven willow species: Bog Birch, Booth, Drummond, Farr, Wolf, Barclay, Eastwood, and Geyer (Table 7). Plots were established along linear transects, with each plot tagged to allow for repeated sampling across years. Measurements for each plot included the height of the tallest live leader, the total number of new twigs, and the number of new twigs browsed within a 0.5-meter circular radius (Table 8). Browsing pressure was recorded as the number of twigs browsed divided by the total number of twigs.

Table 6: Southern Absaroka-Beartooth Wilderness study area sampling locations and descriptions, including number of sample plots, elevation, and species present.

Location	# Plots	Elevation	Species Present
Bannock Creek	57	2286 m	Bog Birch, Booth, Drummond, Farr, Wolf
Soda Butte Creek	36	2365 m	Barclay, Booth, Drummond’s, Farr
Slough Creek	41	2070 m	Booth, Drummond, Geyer, Wolf
Lost Creek	15	2073 m	Booth, Drummond, Wolf
Fisher Creek	30	2682 m	Eastwood

Table 7: Description of one birch and 7 willow species in the southern Absaroka-Beartooth Wilderness study area (adapted from Heinze 1992).

Species	Stature and Height	Ecological Zone(s)
Bog Birch / Dwarf Birch (BEGL) (*Betula glandulosa*)	Low to medium shrub: ~2m	Subalpine, Montane
Barclay Willow (SABA) (*Salix barclayi*)	Medium shrub: ~4 m	Subalpine
Booth Willow (SABO) (*Salix boothii*)	Medium to large shrub: ~1-4m	Subalpine
Drummond Willow (SADR) (*Salix drummondiana*)	Low to medium shrub: ~1-4 m	Montane, Subalpine
Eastwood Willow (SAEA) (*Salix eastwoodiae*)	Low to medium shrub: ~1-2 m	Subalpine
Farr Willow (SAFA) (*Salix farriae*)	Low shrub: ~0.2-0.5 m	Subalpine, Montane
Geyer Willow (SAGE) (*Salix geyeriana*)	Medium to large shrub: ~1.4-7 m	Montane
Wolf Willow (SAWO) (*Salix wolfii*)	Low to medium shrub: ~0.2-2 m	Subalpine, Montane

Table 8: Willow permanent plot measurements. Includes height (cm), total number of new twigs, new twigs browsed, and browsing pressure.

Variable	Method
Height (cm)	Measures height of the tallest live leader within 0.5m radius
# Twigs	Measures the total number of new twigs
# Browsed	Measures the total number of new twigs browsed
Browsing Pressure	Measures the percentage of twigs browsed (Number of twigs browsed ÷ number of new twigs)

Exclosure

To test the response of willow from a complete release of browsing for 60 years, I analyzed willow height and canopy changes in and out of an 18x18 meter exclosure within the Slough Creek study area. The area inside the exclosure was 325 m^2, surrounded by fence about 3m tall. In 1961, 2 linear transects were established inside the exclosure stretching from one corner to the other (25 m and 26 m long), and 2 more transects were placed outside the exclosure at each of the eastern corners of the exclosure boundary to measure willow canopy and height when removed from browsing and exposed to browsing (21.6 m and 27,6 m long). Data were not recovered for 1961 or 1962, but records were found for 1963, 1964, 1965, and partial records for 1979 (Chadde & Kay 1988). In 1986, 6 new transects were established outside of the exclosure (30.5 m long) and were sampled in addition to the original 4 that were established in 1961 (Tyers, 2003). Species presence, average willow height, and percent of willow canopy intersecting the transect were recorded along each of the linear transects (Chadde & Kay 1988; Tyers 2003). These transects were read approximately every 10 years through 2021.

Camera points were established in 1962 to provide a visual reference for the response of willow from a complete release of browsing. Three camera points were established, but camera point 2 was destroyed after being washed out by Slough Creek. Camera points 1 and 3 remained permanently marked with metal stakes throughout the study duration and were revisited in 1962, 1986, 2009, and 2020.

Statistical Analysis

Horseback Transects. I used a linear regression model to assess the relationship between year and the average number of moose seen per day of searching on the horseback transects (n=1,291 days of searching) from 1985 to 2021. I did not include the transects from 1947-1949 in the linear regression model because I could not justify extrapolating moose abundance trends across the 36-year gap from 1949 to 1985. Initial data exploration revealed violations of normality evident in a heavily left skewed data distribution. This was corrected by applying a logarithmic transformation to model an exponential decay curve. The formula for the model is as follows:

$$\log(\widehat{Moose\ Per}\ Day) = \beta_0 + \beta_1(Year) + \varepsilon$$

The null hypothesis tested was:

H_o: The average number of moose observations per day of searching did not change throughout the study duration (1986 – 2021).

Road Transects. To determine the relationship between year and the average number of moose observed per transect per year (n=1,291), I used a linear regression model. A second order polynomial transformation to the explanatory variable "year" was used to help correct violations of the normality assumption. The model equation is as follows:

$$Average\ \widehat{Moose}/Transect = \beta_0 + \beta_1(Year^2) + \varepsilon$$

The complete road transect included five segments that differed in suitable moose habitat. To determine the combined effects of year and road transect on moose observations, I created a linear model that considered the interaction between year (polynomial-transformed) and road segment. The full model is as follows:

$$\begin{aligned} &Average\ \widehat{Moose}\ /\ Transect \\ &\quad = \beta_0 + \beta_1(Year^2) + \beta_2(Road\ Section) + \beta_3(Year^2 * Road\ Section) + \varepsilon \end{aligned}$$

To determine how the effect of year on moose observations changed between road segments, I used the R package ‘emmeans’ to evaluate and compare estimated marginal means for each road segment.

The null hypotheses tested were:

H_o: The average number of moose observed per transect did not change throughout the duration of the study (1987 – 2021).

H_o: The average number of moose observed per transect throughout the study duration (1987 – 2021) were the same for all road sections.

Willow Permanent Plots. To determine if willow height changed significantly in the study area from 1987 to 2021, I used a multiple linear regression to model willow height as a function of year. I anticipated that willow height would vary between species and location, so I included interaction terms between species and year, and location and year in our proposed full model. The equation for the full multiple linear regression model to estimate how willow height has changed over time is as follows:

$$\widehat{Height} = \beta_0 + \beta_1(Year) + \beta_2(Species) + \beta_3(Location) + \beta_4(Year * Species) + \beta_5\,(Year * Location) + \varepsilon$$

I created a set of 9 candidate models and used Akaike’s information criterion corrected for small sample size (AICc) to assess model support for willow height in response to year, species, and location (Anderson & Burnham 2002). I evaluated interaction terms using the ‘emmeans’ package in R to test differences in estimated marginal means and trends. All results were considered significant at a 0.05 α level.

The null hypothesis tested is as follows:

H_o: Willow height among species at all sampling locations did not change throughout the duration of the study (1987 – 2021).

I also tested the average browsing pressure (% twigs browsed) as a function of year to determine if moose browsing had significantly changed from 1987 to 2021. I anticipated that accessibility to browse varied for each location, and browse palatability varies for each species, so I included an interaction between year and species, and year and location in our proposed full model. The equation for the full multiple linear regression model to estimate how moose browsing has changed over time is as follows:

$$\widehat{Browsing} = \beta_0 + \beta_1(Year) + \beta_2(Species) + \beta_3(Location) + \beta_4(Year * Species) + \beta_5\,(Year * Location) + \varepsilon$$

I created a set of 9 candidate models and used AICc to assess model support for browsing in response to year, location, and species. I evaluated interaction terms using the ‘emmeans’ package in R to test differences in estimated marginal means and trends. All results were considered significant at a 0.05 α level.

The null hypothesis tested is as follows:

H_o: Willow browsing among species at all sampling locations did not change throughout the duration of the study (1987 – 2021).

To determine if browsing had a significant effect on willow height, I modeled willow height as a function of explanatory variables using a multiple linear regression (n=4,735 willow plot assessments). The response variable was willow height (cm), and I considered combinations of three explanatory variables: sampling location, species, and browsing pressure (Table 8). I created a set of 9 candidate models and used Akaike's information criterion corrected for small sample size (AICc) to assess model support (Anderson & Burnham 2002). The full model included an interaction effect between browsing and willow species, as well as an interaction between browsing and sampling location.

I predicted that willow height would be negatively associated with browsing pressure because high levels of browsing can suppress willow growth. I also predicted that the rate of height recovery and browsing rates will differ for each willow species and sampling location under the premise that location can influence winter accessibility to willow, and the different willow species have different maximum heights and palatability.

An interaction between willow species and moose browsing is justified by the range of palatability of various species to moose and the height variability of different species that influences access to browse in the winter (Tyers 2003). An interaction between moose browsing and location was also suggested because of the variation in available browse species and the variation in elevation which could influence snow depth and accessibility for moose in the winter. The equation for the full multiple linear regression model to estimate the effects of browsing on willow height is as follows:

$$\widehat{Height} = \beta_0 + \beta_1(Browsing) + \beta_2(Species) + \beta_3(Location) + \beta_4(Browsing * Species) + \beta_5\,(Browsing * Location) + \varepsilon$$

I evaluated interaction terms using the ‘emmeans’ package in R to test differences in estimated marginal means and trends. All results were considered significant at a 0.05 α level. The null hypothesis tested was as follows:

H_o: Moose utilization (browsing) has no relationship to willow height at all sampling locations throughout the duration of the study (1987 – 2021).

Fisher creek willow stand was anomalous because it is the only site with one willow species and is also the only location to have Eastwood willow. When Fisher Creek data was included in the models that contained both species and location explanatory variables, a highly inflated VIF indicated extreme multicollinearity between species and location (VIF > 6). Once Fisher Creek was removed, the models had small VIF values for species and location parameters (≤ 2.09), indicating no issues with multicollinearity. Therefore, I analyzed Fisher Creek separately using a linear regression model to test if willow height and browsing changed significantly over time, and if browsing had a significant effect on willow height at this location throughout the study.

Exclosure. I used a two-way ANOVA to test for significant differences between average height and canopy cover in and out of the exclosure among and between sampling years. I used a Tukey’s honest significant difference post-hoc test to evaluate differences between inside and outside the exclosure among and between years. All results were considered significant at a 0.05 α level. The null hypothesis tested were as follows:

H_o: Average willow height inside the exclosure was not statistically different from outside the exclosure among years (1962-2020).

H_o: Average willow canopy inside the exclosure was not statistically different from outside the exclosure among years (1962-2020).

Moose Abundance, Browsing, and Willow Height. To address whether moose abundance influences browsing and willow height in the southern ABW, I used a linear regression model to estimate the response of average browsing pressure (% twigs browsed) and average willow height (cm) to relative moose abundance. I used average values of browsing pressure and height for all transects for each year to represent the average for the entire study area. For the explanatory variable (moose relative abundance), I used yearly averages of the number of moose observed per day of searching on the horseback transect. I used this index as opposed for the road transect for this model because it is the most representative of the trends of moose abundance for the southern ABW because the trails cover the entire study area.

To test for any multicollinearity between independent variables, I used a variance inflation factor (VIF). I tested the VIF of a model with both moose relative abundance and average browsing as predictors of willow height but observed an inflated VIF of 3.7, which indicates browsing and moose abundance are reasonably correlated. Therefore, I elected to run two separate models: one estimating average willow height as a function of moose abundance, and one estimating average browsing pressure as a function of moose abundance. Exploratory analysis indicated no significant violations of assumptions using the linear model approach for both models. The equations for the two linear models are as follows:

$$\widehat{Height} = \beta_0 + \beta_1(Moose\ Abundance) + \varepsilon$$

$$\widehat{Browsing} = \beta_0 + \beta_1(Moose\ Abundance) + \varepsilon$$

The null hypotheses tested were as follows:

H_o: Moose relative abundance had no effect on average willow height in the southern ABW.

H_o: Moose relative abundance had no effect on average browsing pressure in the southern ABW.

Results

Moose Relative Abundance Indices

Horseback Transects. In the 1940’s, the number of moose observed during fall monitoring efforts ranged from 30 to 106 moose. The average number of moose seen per day during this period ranged from 1.58 to 3.79 moose per day of searching. From 1985 through 1992, the number of moose observed ranged from 12 to 49 and the number of moose seen per day of searching ranged from 1.33 to 3.06 during this sampling period. The total number of moose observed, and the average moose seen per day remained comparatively low from 1995 through 2021, with the number of moose observed ranging from 0 to 22, and the average number of moose per day ranging from 0 to 0.43 (Figure 7). A linear regression with an exponential decay transformation indicates that from 1984-2021, the average number of moose observed per day of searching declined about 18% every year ($R^2 = 0.338$, Figure 8).

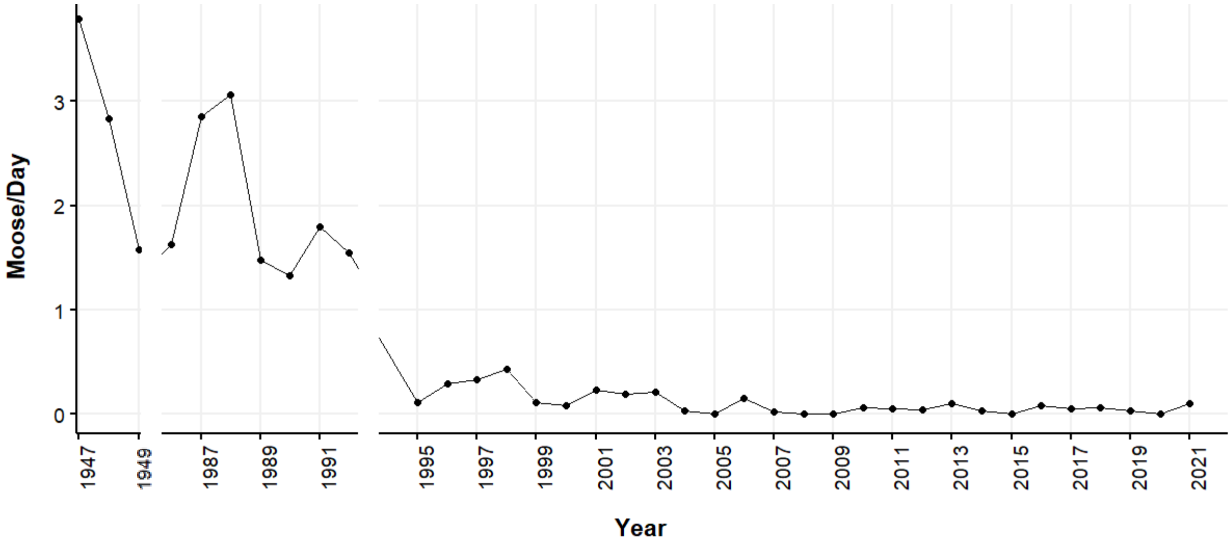

Figure 7: Number of moose observed per day of searching on horseback transects from 1947-1949; 1985-1992; and 1995-2021 along the 177km of trails in the southern Absaroka-Beartooth Wilderness.

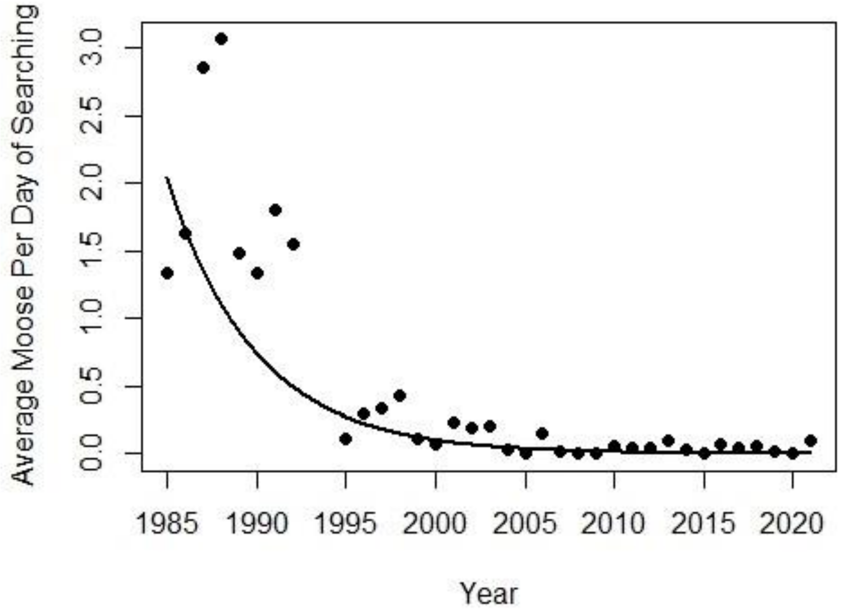

Figure 8: Fitted linear regression model with an exponential decay transformation that models the average number of moose observed per day of searching the 177 km of trails on the horseback transects from 1984-2021 in the southern Absaroka-Beartooth Wilderness.

Road Transect. The average number of moose observed while driving the road from Gardiner to Cooke City declined from 1987 through 2021 ($n=2,947$). The highest number of moose observed per transect was in 1988, with an average of 1.6 moose observed per transect during this year. The lowest number of moose observed per transect was in 1995, with an average of 0.024 moose observed per transect. Results of a linear regression model considering year with a polynomial transformation ($R^2=0.609$) suggests that the average number of moose observed per transect declined from 1987 through about 2010, then increased slightly from about 2010 to 2021 (Figure 9).

I found that road sections 4 and 5 had the highest number of moose observed per transect, with an average of 0.13 and 0.21 average moose per transect throughout the study duration, respectively (Figure 10). Section 1 had no observations throughout the study (Figure 10). A linear model considering the interaction of year (with a polynomial transformation) and road section found both year and road segment were important in explaining average moose observations ($p<0.05$). Using estimated marginal means, I determined that the effect of year on moose observations differed across the road segments (Figure 11). Sections 1 ($p=1.00$) and 3 ($p=0.95$) experienced no significant change in the average number of moose observed per transect over time. Trends in these sections overlapped with those in section 2, where the average moose observations declined slightly from 1987-2021, but the slope was only marginally significant ($p=0.053$). The change over time in section 2 was also similar to that observed in section 5, where moose observations decreased ($p<0.001$) across the study period. Notably, average moose observations per year increased for section 4 ($p<0.001$).

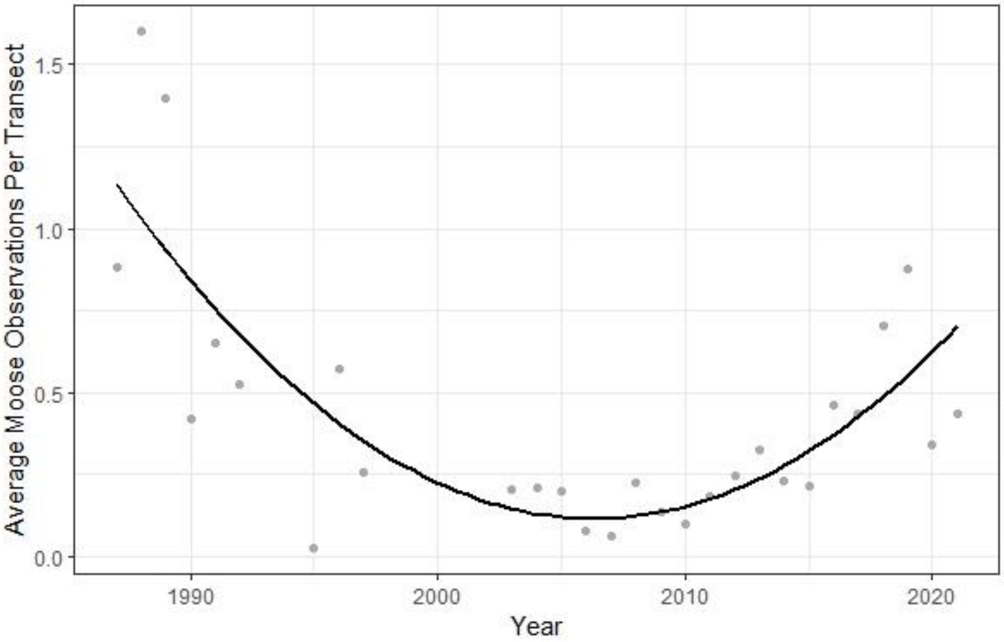

Figure 9: Estimated number of moose observed per 89 km road transect from Gardiner to Cooke City, MT (including all sections) as a function of year (polynomial transformed); 1987-2021.

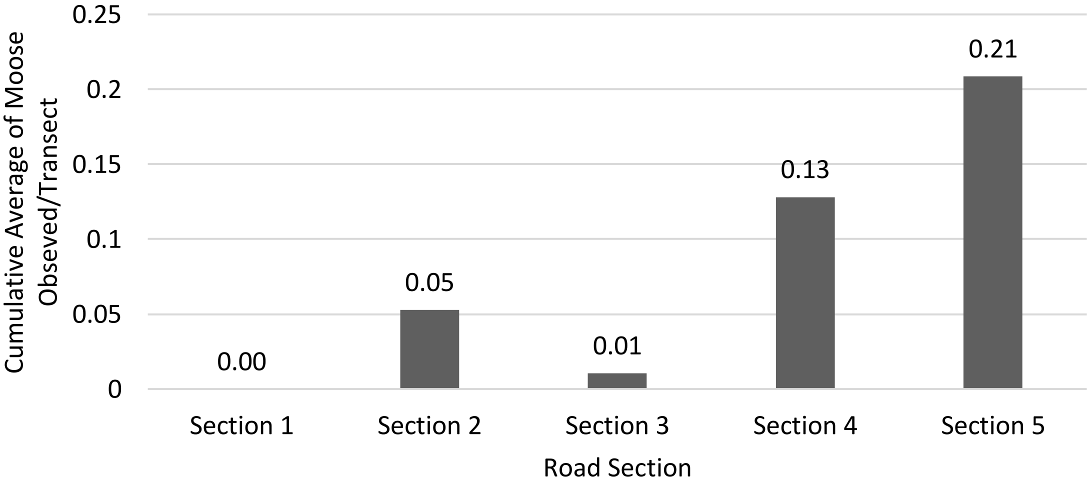

Figure 10: Average moose observed per 89 km road transect section throughout the study duration (1987-2021).

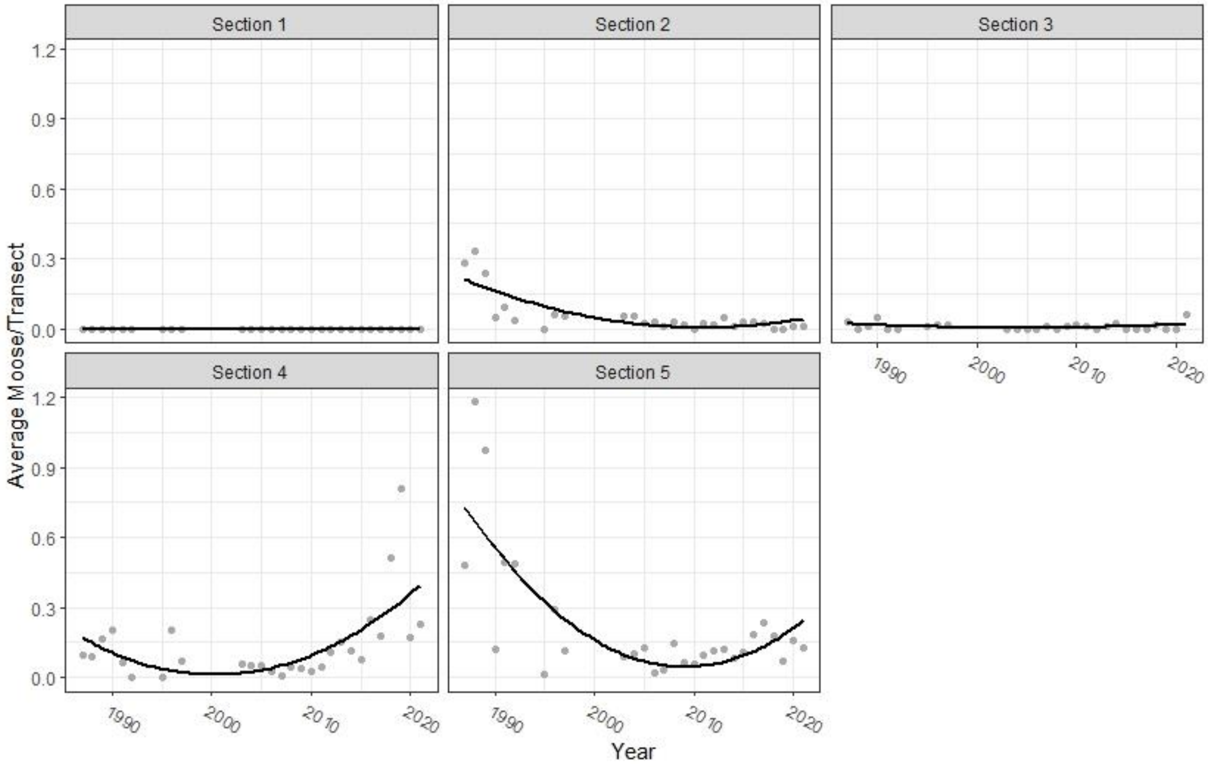

Figure 11: Estimated change in the average number of moose observed per road transect section throughout the study period, 1987-2021.

Willow Permanent Plots

Willow Height Over Time. Average willow height for all species increased from an average of 113cm in 1988 throughout the study area to an average of 190cm in 2021. I found strong support for the full multiple linear regression model that estimates willow height as a function of year, location, and species, with an interaction term between year and species, and year and location. A model weight of 1 indicates strong support for this full model over the other candidate models (Table 9).

Table 9: AICc comparison of candidate models of willow height as a function of explanatory variables (year, species, and location), including interaction terms between year and species, and year and location.

Explanatory variables	K	AIC_c	ΔAIC_c	AIC_c weight	Log likelihood
Year*Species+Year*Location	21	42225.38	0.00	1	-21091.57
Year * Species	15	43386.51	1161.13	0	-21678.19
Year * Location	9	43778.56	1553.18	0	-21880.26
Year + Species	9	43801.99	1576.61	0	-21891.97
Year + Location	6	44377.59	2152.21	0	-22182.79
Species	8	44715.71	2490.33	0	-22349.83
location	5	45200.10	2974.72	0	-22595.04
Year	3	45626.61	3401.23	0	-22810.30
Intercept Only	2	46267.40	4042.02	0	-23131.70

I found that the willow height increased significantly from 1987 to 2021 for Slough Creek Cabin, Bannock, Lost Creek, and Soda Butte willow sites ($p<0.001$, Figure 12). Slough Creek Cabin willow site had the largest rate of change, with an estimated average increase of 6.49 cm in willow height every year. Bannock had the lowest rate of change, with an estimated average increase of 1.65 cm in willow height every year.

I also found that willow height increased significantly from 1987 to 2021 for Bog Birch, Geyer willow, Barclay willow, Booth willow, Drummond willow, Farr willow, and Wolf willow ($p<0.001$, Figure 13). Geyer willow had the largest rate of change over time, with an estimated average increase of 6.70 cm in height per year. All other species increased at an estimated rate ranging between 2.40 cm per year and 3.32 cm per year. When analyzing Fisher Creek separately, I found that willow height significantly increased from 1987 to 2021, but only by about an estimated 0.16% per year ($p=0.043$).

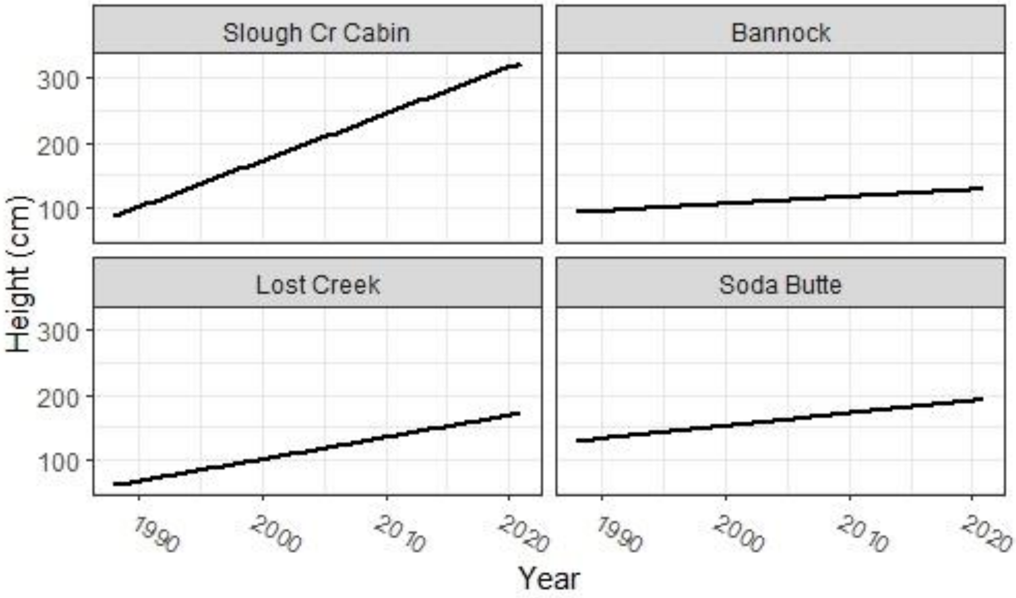

Figure 12: Estimated willow height (cm) in response to year (1987) for Slough Creek Cabin, Bannock, Lost Creek, and Soda Butte sampling locations.

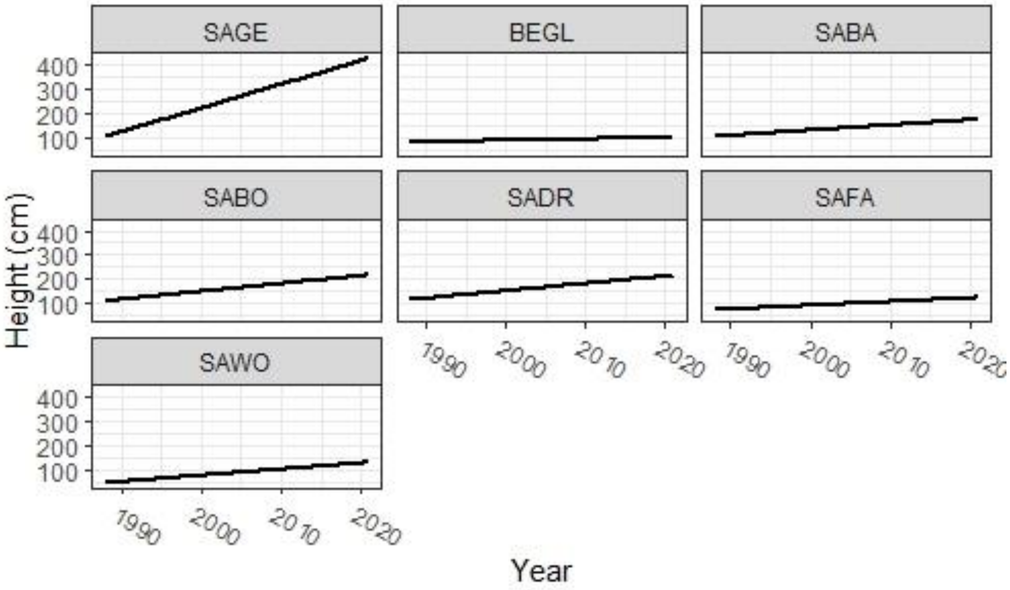

Figure 13: Estimated willow height (cm) in response to year (1987-2021) for 6 willow species and 1 birch (Geyer, Barclay, Booth, Drummond, Farr, Wolf, and Bog Birch).

Moose Browsing Over Time. I found strong support for the full model that estimates moose browsing (% of twigs browsed) as a function of year, location, and species, with an interaction term between year and location, and year and species (AICc weight =1, Table 10).

Table 10: AICc comparison of candidate models of browsing (%twigs browsed) as a function of explanatory variables (year, species, and location), including interaction terms between year and species, and year and location.

Explanatory Variables	k	AICc	ΔAICc	AICc weight	Log Likelihood
Year*Species + Year*Location	21	31811.54	0.00	1	-15884.65
Year*Location	9	31930.62	119.07	0	-15956.29
Year + Location	6	31956.71	145.17	0	-15972.35
Year*Species	15	32215.46	403.92	0	-16092.67
Year + Species	9	32239.05	427.51	0	-16110.50
Year	3	32283.92	472.38	0	-16138.96
Location	5	33905.20	2093.66	0	-16947.59
Species	8	34050.95	2239.40	0	-17017.45
Intercept Only	2	34079.08	2267.53	0	-17037.54

I found that browsing significantly decreased at Bannock, Lost Creek, Slough Creek Cabin, and Soda Butte willow sites ($p<0.001$, Figure 15). Bannock and Soda Butte sites had the most significant decline in moose browsing from 1987 to 2021, with an estimated decline of 1.29% in Bannock and 1.11% decline in Soda Butte every year. I also found that browsing pressure declined for all species ($p<0.001$, Figure 16). The rate of decline for moose browsing ranged from 0.621% per year (Farr willow) to 1.186% per year (Barclay willow). When analyzing Fisher Creek (and associated Eastwood willow) separately, I found no significant change in moose browsing from 1987 to 2021 ($p=0.731$).

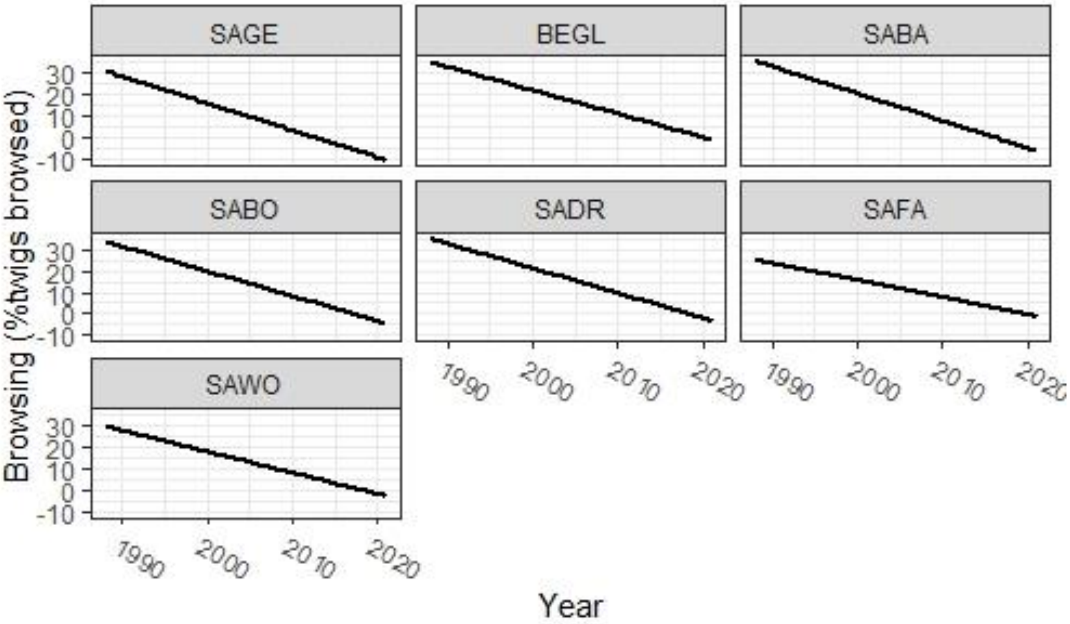

Figure 14: Moose browsing (%twigs browsed) over time (1987-2021) for 6 willow and 1 birch species.

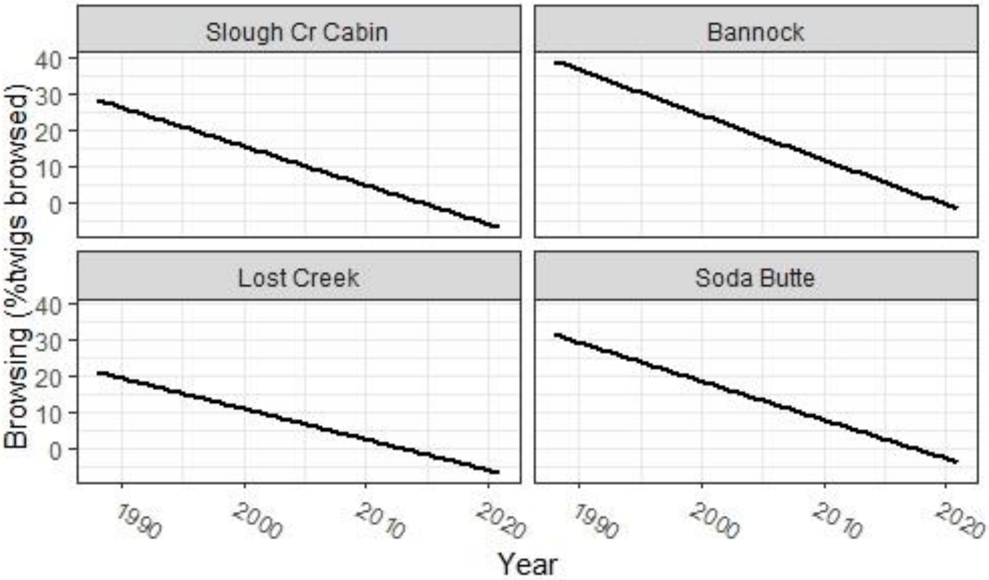

Figure 15: Moose browsing (%twigs browsed) over time (1987-2021) for each study location in the southern Absaroka-Beartooth Wilderness.

Willow Height in Response to Browsing. I found that there is a correlation between willow height and moose browsing pressure. The AICc model selection for the response of willow height as a function of browsing, location, and species indicated that the best supported model of willow height was the most complex model, considering all individual parameters and interactions between browsing and willow species, and browsing and location (Table 11). This model had a model weight of 1, indicating strong support over the other candidate models (Table 11).

Table 11: AICc comparison of candidate models of willow height as a function of explanatory variables (browsing, species, and location), including interaction terms between browsing and species, and browsing and location.

Explanatory variables	K	AIC_c	ΔAIC_c	AIC_c weight	Log likelihood
Browsing*Species + Browsing*Location	21	43430.51	0.00	1	-21694.14
Browsing*Species	15	44144.87	714.36	0	-22057.38
Browsing + Species	9	44355.78	925.27	0	-22168.87
Browsing*Location	9	44666.26	1235.75	0	-22324.11
Species	8	44715.71	1285.19	0	-22349.83
Browsing + Location	6	44989.18	1558.67	0	-22488.58
Location	5	45200.10	1769.59	0	-22595.04
Browsing	3	45989.71	2559.20	0	-22991.85
Intercept only	2	46267.40	2836.89	0	-23131.70

The effects of browsing on willow height was significant for Slough Creek Cabin, Lost Creek, Bannock, and Soda Butte, with the strongest relationship at Slough Creek Cabin sampling location ($p<0.001$). For these locations, a negative slope indicates that higher browsing pressure was correlated with lower willow height (Figure 17). The effect of browsing on willow height was statistically different between all locations ($p<0.05$) except for Lost Creek and Soda Butte ($p=0.1552$).

The effects of browsing on willow height was significant for Geyer ($p<0.001$), Bog Birch ($p<0.001$), Booth ($p<0.001$), Drummond ($p<0.001$), Farr ($p<0.001$), Barclay ($p=0.002$), and Wolf willow ($p<0.001$) (Figure 16). The strongest correlation between height and browsing was on Geyer's willow, with about an estimated 3.063cm decline in willow height for each percentage increase in moose browsing. A post-hoc test conducting pairwise comparisons of estimated marginal means of willow height as a function of browsing for each species also indicates that the effects of browsing on willow height varies between willow species (Figure 16). Specifically, the effect of browsing on height of Geyer willow is statistically significant from all other species ($p<0.001$). When analyzing Fisher Creek (containing only Eastwood willow) separately, I found that moose browsing appeared to have no significant effect on willow height ($p=0.283$, Table 12).

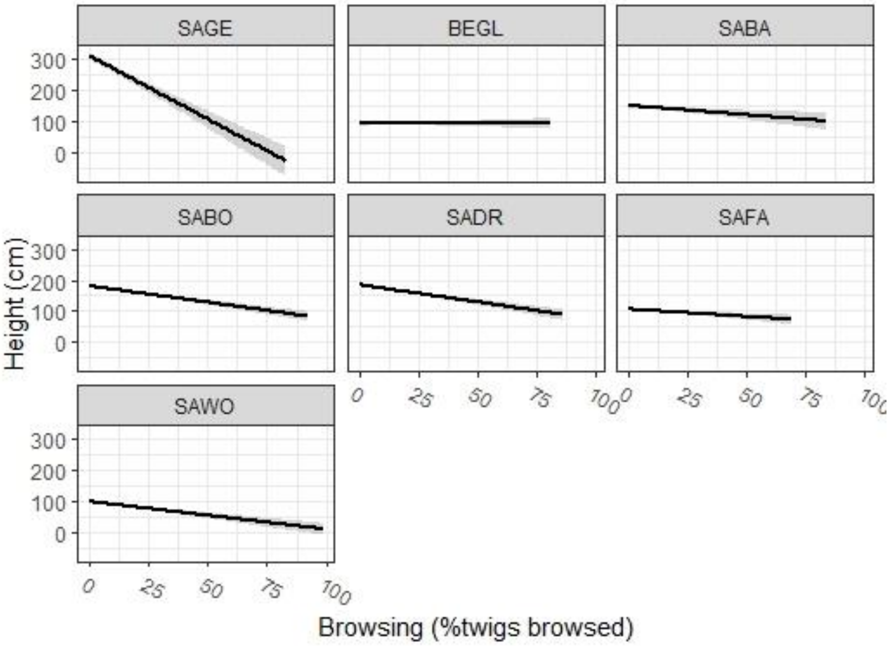

Figure 16: Average willow height (cm) as a function of browsing (%twigs browsed) for 6 willow species and 1 birch in the southern Absaroka-Beartooth Wilderness study area.

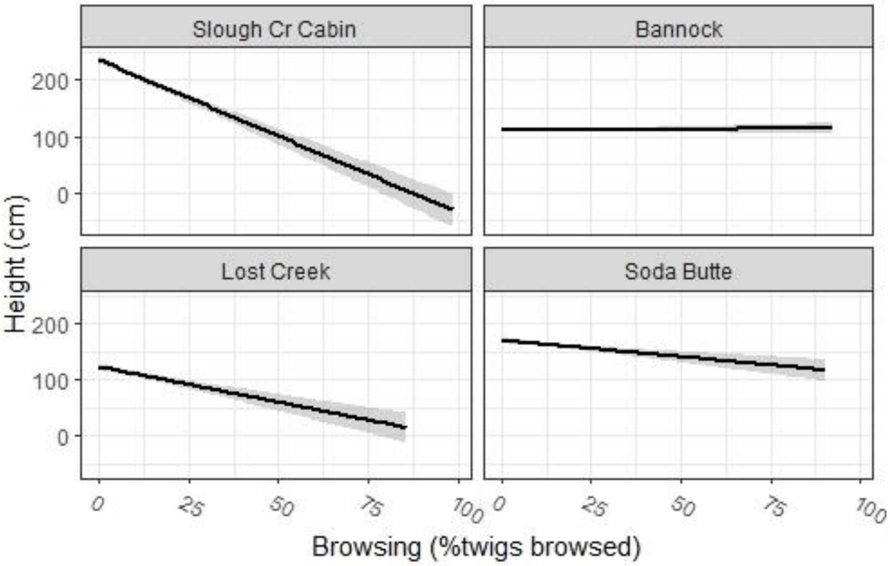

Figure 17: Average willow height (cm) as a function of browsing (%twigs browsed) for Slough Creek Cabin, Bannock, Lost Creek, and Soda Butte study locations in the southern Absaroka-Beartooth Wilderness.

Exclosure

I found that willow height inside the Slough Creek exclosure increased in height sooner than willow outside (Figure 18). The average height inside the exclosure remained at 120cm inside the exclosure from 1963 to 1965 before increasing to 300cm in 1986. From 1986 to 2020 willow height inside the exclosure fluctuated until it reached an average of 345cm in 2020 (Table 12). The average height outside of the exclosure remained below 100cm from 1963 through 1979. Then it increased to an average height of 263 cm in 2007. Willow outside the exclosure then increased to 312 cm in 2020.

Table 12: Average willow height (cm) and percent canopy cover in and out of the Slough Creek exclosure; 1963-2020.

Year	Height Inside (cm)	Height Outside (cm)	% Canopy Inside	% Canopy Outside
1963	120	80	46	32
1964	120	75	55	34
1965	115	80	47	30
1979	no records	190	no records	36
1986	300	89	100	37
1995	205	120	100	61
1997	252	163	99	84
2007	294	259	100	95
2009	317	287	100	96
2020	345	312	100	99

A two-way ANOVA indicated that average willow height (cm) was not significantly different inside and outside of the exclosure from 1963 through 1965 ($p>0.05$, Figure 18). In 1986, average willow height inside the exclosure increased significantly while willow outside of the exclosure did not ($p<0.001$). Willow height inside the exclosure remained significantly taller inside than outside the exclosure from 1986 through 2007 ($p<0.001$). Average willow height outside the exclosure did not experience significant increases until 1997 (Figure 18). Average willow height outside the exclosure then began to increase until it caught up with the average height inside (Figure 18).

Average willow canopy in and out of the exclosure was not significantly different from 1963 to 1965 ($p>0.05$). In 1986, willow height inside the exclosure increased to 100% canopy cover, while willow canopy outside had no significant change (Figure 19). Average willow canopy inside the exclosure remained at about 100% from 1986 to 2020. Willow canopy outside the exclosure began to gradually increase after 1995 but remained significantly less than inside the exclosure until it reached 84% canopy cover in 1997 ($p<0.05$, Figure 19). From there, willow canopy cover inside and outside the exclosure were not statistically different through 2020, with average willow canopy reaching 99% outside the exclosure in 2020.

The camera points visited in 1963, 1981, 2009, and 2020 provide visual references that corroborate these findings, demonstrating differences in willow height inside and outside the exclosure among and between years (Appendix E). Photos from 1963 indicate willow stature is short both inside and outside the exclosure, then 18 years later in 1986 willow height inside the exclosure noticeably increased while willow height outside remained short. Then in 2009 the photos indicate a recovery of willow height outside the exclosure until willow height appears very similar inside and outside in the 2020 photograph (Appendix E).

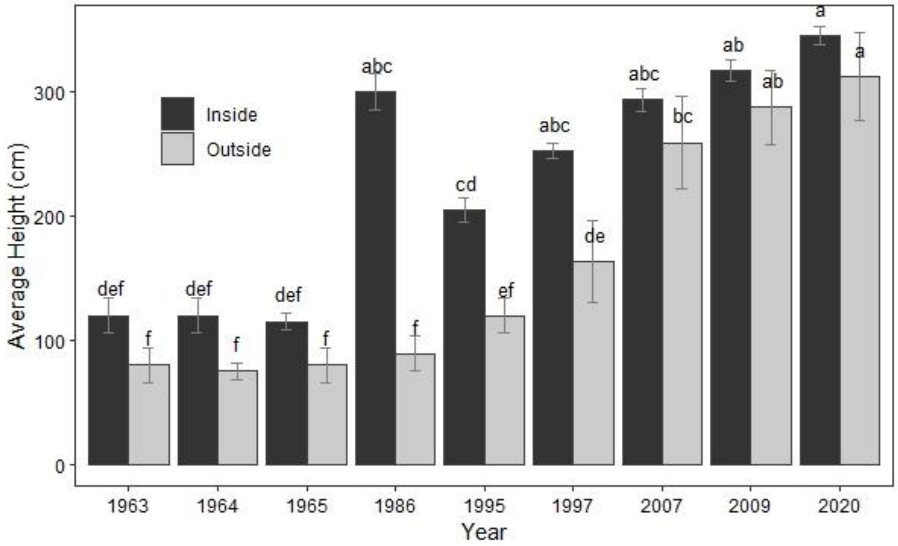

Figure 18: Average willow height (cm) comparisons in and out of the Slough Creek exclosure among and between years. Matching letters indicate no statistically significant difference and different letters indicate significance using a 2-way ANOVA within and between years ($p < 0.05$). Error bars indicate ± 1 standard deviation.

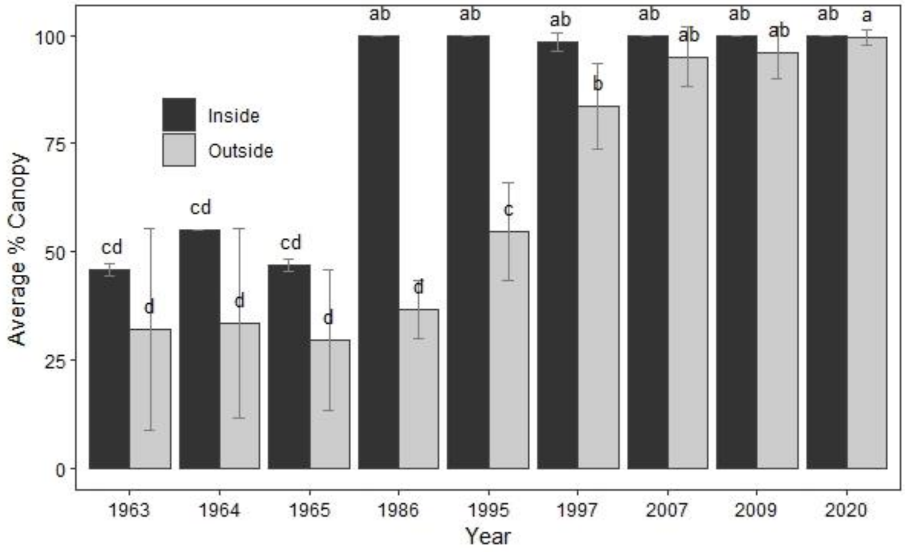

Figure 19: Average percent willow canopy cover comparisons in and out of the slough creek exclosure among and between years. Matching letters indicate no statistically significant difference and different letters indicate significance using a 2-way ANOVA within and between years ($p < 0.05$). Error bars indicate ± 1 standard deviation.

Moose Abundance, Browsing, and Willow Height

I found a positive linear relationship between moose relative abundance and average browsing pressure ($p<0.001$). For each unit increase in relative abundance (average moose observed per day), average browsing pressure (% twigs browsed) increased by 20% (Figure 20). I also found a negative linear relationship between average willow height (cm) and relative moose abundance ($p<0.001$). For each unit increase in moose relative abundance, average willow height declined by 40 cm (Figure 20).

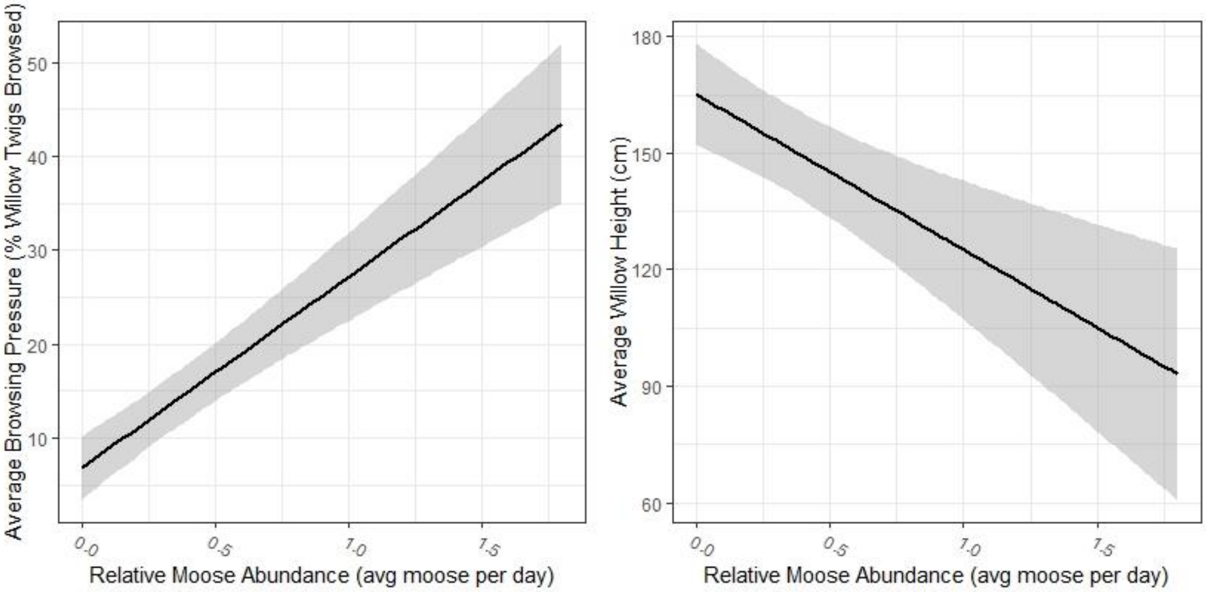

Figure 20: (left) average willow browsing pressure (% willow twigs browsed) as a function of moose relative abundance (average moose observed per day) in the southern Absaroka-Beartooth Wilderness ($R^2=0.72$); and (right) average willow height (cm) as a function of moose relative abundance (average moose observed per day) in the southern Absaroka-Beartooth Wilderness ($R^2=0.39$). Shaded areas represent 95% confidence intervals.

Discussion

The objective of this study was to determine if moose populations influence the condition of willow in the southern ABW. To accomplish this, I analyzed moose abundance indices and permanent willow plots established by Tyers (2003) in 1986 and explored the relationship between moose abundance, browsing, and willow height. I found that moose abundance and associated browsing is a defining factor of willow height in the southern ABW.

Moose Relative Abundance

Tyers (2003, 2006) hypothesized that moose numbers in the southern ABW declined after winter range habitat loss caused by the 1988 Yellowstone Fires. The continuation of horseback transects through 2021 corroborated Tyers' (2003) findings, but also indicated that the moose population in the southern ABW still has not fully recovered to pre-fire levels. The horseback transects from 1947 through 2021 indicated an exponential decline in moose relative abundance, where moose sightings generally declined from 1947 through 1995, then remained consistently low from 1995 through 2021. The index of moose observed along the road from Gardiner to Cooke City also indicated a decline in moose numbers after 1988.

The limitations of monitoring a population with such low abundance over a large area commonly result in relatively weak statistics and small datasets (Nadeau et al. 2017). Therefore, long-term studies, like this one, with consistent and repetitive methods for monitoring moose are valuable. Although long-term monitoring associated with this project in the southern ABW is not robust enough to provide estimates of the entire moose population, the longevity and consistency associated with the indices of moose abundance appear to successfully reflect trends in moose relative abundance.

Willow Height and Browsing

Commensurate with the decline in moose relative abundance, I found that browsing rates on willow in the study area declined from 1985 to 2021. I also found that willow height has increased during this time. My analysis revealed a very strong correlation between willow height and browsing, indicating strong evidence to support the hypothesis that browsing was an important limiting factor of willow height. This supports the findings of similar studies on the NYWR, where willow height increased with decreased browsing (Painter & Tercek 2020; Beschta et al. 2020). However, willow height on the NYWR did not increase uniformly. Painter (2020) found that although willow height appeared to increase in response to reduced elk browsing along streams, willows in meadows appeared to remain suppressed because of increasing bison numbers. Other researchers such as Cooper & Hobbs (2013) argue that this is because parts of the NYWR riparain areas are hydrologically disconnected from the floodplain, and that both access to groundwater and herbivory are important drivers of willow recovery.

The results from the Slough Creek exclosure offer insights into this discussion. The willow inside and outside the exclosure had the same access to groundwater and same site conditions, other than a removal from browsing inside the exclosure. Even though the willow inside had the same access to groundwater as the willow outside, it became significantly taller than the willow outside the exclosure which was exposed to browsing. This provides further evidence to support the hypothesis that, in the southern ABW, browsing is a very important driver of willow height.

An important comparison between the studies on the NYWR, such as Painter et al. (2020), and my study area in the southern ABW is the difference in topography and floodplain characteristics. The NYWR consists of relatively high gradient streams and small meadows that are degraded to such an extent that willow in meadows likely have reduced access to groundwater (Peterson et al. 2020; Painter et al. 2015; Ripple & Beschta 2006). These areas are frequently described as being heavily incised with dry adjacent meadows. In contrast, the major stream corridors in the southern ABW have extensive willow stands on what were formerly post-glacial lake beds (Peterson et al. 2020; Tyers 2003; Smith & Tyers 2012, 2008). These areas did not have the same level of stream incision and hydrological disconnect from the floodplain (Smith & Tyers 2008, 2012; Tyers 2003). Therefore, I conclude that, because access to groundwater was probably not a problem for willow in the southern ABW, especially after beaver reintroduction (see chapter 2), willow height was able to respond to a release of browsing pressure.

Furthermore, the methodology of my study differs from other studies, such as Painter (2020), because rather than focusing on tall willow species' height in response to browsing, I observed height and browsing trends for all deciduous browse species present in a willow community. This includes short statured willow, tall willow, and one birch species. I found that the influence of browsing on willow height in my study area differed among the species and location of willow communities.

While Painter (2020) found that willow recovery was different for willow along streams than in meadows, in the southern ABW I found that willow height increased everywhere except for the highest elevation sampling location (Fisher Creek) that had short statured willow. Fisher Creek differs from the other sampling locations in the southern ABW because of its species composition, elevation, and winter accessibility. This location contains entirely Eastwood willow, meaning that the height of this willow stand does not exceed 2 meters. This sample site is also at the highest elevation and receives snow sooner than the other locations. Despite the adaptations moose must have to navigate snowy environments, their movements and access to food are determined by snow depth and hardness (Peek 1971; Tyers 2003; Telfer & Kelsall 1984; Peek 1997). The short stature of Eastwood willow, combined with deep snow at this high elevation site, means that moose likely have limited access to this willow stand throughout the winter. Tyers' (2003) research on snow conditions in moose winter range observed snow conditions in the same transect locations. Tyers found that from 1987 to 1991, Fisher Creek willow was consistently buried and inaccessible to moose between January and April (Tyers 2003).

I also found that the extent to which moose browsing impacts willow height also varies among browse species. Except for Eastwood willow (associated with Fisher Creek), I found that a reduction in browsing pressure had a significant impact on willow height for all species in the study area. The most noticeable relationship between height and browsing was in Geyer and Booth willow. These are also the tallest species of willow sampled in this study. Therefore, I infer that Geyer and Booth were most accessible to moose in the winter and also more vulnerable to over-browsing when moose densities were higher and had a more distinct and noticeable recovery in height when released from browsing.

Several studies also suggest that the nutritional quality of different species of willow play an important role in browse selection of willows. Different willow species potentially have different nutritional content and secondary compounds that may contribute to heterogenous browsing patterns (Risenhoover 1989; Stolter et al. 2005; Burkholder et al. 2017). In addition to accessibility above the snow, secondary compounds may also be a motivator for moose utilization of specific willow species present in the study area.

This study revealed several apparent preferences for browse species within willow communities based on the average browsing pressure throughout the study duration. The most heavily browsed species, on average, was Bog Birch. Through all years of data collection Bog Birch appeared to be selectively targeted by moose, which is not only reflected in the data but was also included in notes from crews collecting data. Although it is not in the *Salix* genus, it appears to be highly palatable to moose in the southern ABW. Apparent browse preference based on average browsing pressure is followed, in order, by Drummond, Eastwood, Booth, Barclay, Farr, Geyer, then Wolf. It is important to note that the species with higher browsing rates, except for Bog Birch, are all tall species of willow that have higher phenotypic expressions of height (Heinze 1992).

It may be likely that the nutritional value of some willow species drives heterogenous browsing rates. However, given that the moose population declined because of burned habitat and the loss of sub-alpine fir (Tyers 2003) and the uniform decline in browsing in all willow species in the study area from 1988 to 2021, it may be possible that snow depth is more important for predicting moose browse preference than species palatability. That is, the moose that remain may not be as selective because there are limited browse resources available to them throughout the winter. Burkholder et al. (2017) conducted a study on moose browsing heterogeneity in the Mount Hagin Wildlife Management area and found that one of the most palatable species for moose in southern Montana included Wolf willow. In the southern ABW, however, Wolf willow was one of least browsed species, probably because of its short stature and the fact that it is buried under the snow throughout much of the winter. This confirms the findings from Tyers (2003), who found that moose preference for winter browse species in the southern ABW is predominantly driven by snow, not palatability.

Slough Creek Exclosure

Analysis of the Slough Creek exclosure corroborates the hypothesis that browsing is a primary determinant of willow height in the southern ABW by providing a comparison of long-term willow response to a complete release of browsing. Willow height and canopy cover increased at a much faster rate inside the exclosure than outside. From 1963 to 1986, willow height inside the exclosure nearly doubled when removed from browsing. By 1986, willow inside was more than double the height outside ($p<0.05$), and the willow outside the exclosure had not changed ($p>0.05$). After the 1988 fires and the subsequent moose population decline, willow canopy increased outside the exclosure began a more noticeable increase, indicating a release from browsing pressure. Previous studies on the Slough Creek exclosure also indicated a shift in species composition for willow inside the exclosure that was completely protected from browsing (Chadde & Kay 1988; Tyers 2003). Specifically, taller willow like Geyer appeared to become dominant, while short willow like Wolf was outcompeted by 1997 (Tyers 2003).

It is possible that elk were able to access the area around the exclosure in early winters and years with mild snow conditions when elk could expand to periphery habitat. However, Tyers (2003), through analysis of track intercept transects documented almost exclusive use by moose in the meadows near the Slough Creek exclosure. Furthermore, the correlation between the moose population crash and the subsequent increase in willow height outside the exclosure provides further evidence to support the conclusion that moose were the primary wintering ungulate utilizing willow near the exclosure. Elk were observed in this portion of the study area on rare occasions, usually associated with mild winter conditions and shallow snow (Dan Tyers & Doug Smith personal communication).

Moose Abundance and Willow Height

Many studies have found a connection between browsing and willow height (Ripple & Beschta 2006; Wagner 2006; Yellowstone National Park 1997; Smith & Tyers 2012). On the NYWR, researchers have hypothesized that elk populations are responsible for changes in willow height, but also acknowledge that increasing bison numbers limit the potential of recovery in all areas (Painter & Tercek 2020; Beschta et al. 2020; Ripple et al. 2010). My study area offers a circumstance where moose are the dominant wintering ungulate utilizing willow (Tyers 2003), thus allowing a direct comparison between ungulate numbers and willow height. I found a positive linear relationship between moose relative abundance in the southern ABW and willow browse rates. I also found a negative linear relationship between moose relative abundance and willow height. This provides further support for the hypothesis that moose populations are an important driver of willow height in the southern ABW.

Management Implications

Many studies connect ungulate population trends to foraging effects on habitat, including changes in browsing impacts on deciduous vegetation. Changes in annual browse utilization rates or long-term patterns in plant status are often linked to animal population trends, especially on winter range. It is not a surrogate for population surveys, but these monitoring efforts are used to interpret population trends regarding ecological balance. That is, connecting ungulate population size to browsing impacts helps describe habitat relationships (Burkholder et al. 2017; Burkholder 2012; Seaton et al. 2011; Crête 1989). This is especially true for deciduous browse species and is central to literature addressing habitat condition of the NYWR (Ripple & Beschta 2006; Wagner 2006; Yellowstone National Park 1997; Smith & Tyers 2012).

The connection between moose and willow across most moose winter ranges means that willow condition is often used as a barometer of moose population fluctuations. This metric has proved useful in tracking moose population cycles of eruption, crash, and stabilization (Ballenberghe & Ballard 1997; Peek 1997; Renecker & Schwartz 1997). The findings from this study support other research that uses browsing rates as measurement tools for moose population monitoring (Burkholder et al. 2017; Seaton et al. 2011; Crête 1989). These studies found that moose browsing was correlated with population trends, suggesting that monitoring browsing is an important component of moose research. The association between moose and willow is a pattern seen across the intermountain west, including the southern ABW (Peek 1974; Pyke et al.

1977; Ballenberghe & Ballard 1997; Tyers 2003). Moose populations can be very difficult to survey, but this connection plays a role in population monitoring and the development of indices. I demonstrated that willow status can be used as indicator of local moose population trends in the southern ABW.

Furthermore, willow condition in response to moose abundance reflects on the ecological status of riparian areas. Willow provides food and habitat for a variety of aquatic and terrestrial species, including songbirds and insects (Baril 2009; Ripple & Beschta 2012). Willow stand degradation from over-browsing may have negative implications for riparian biodiversity. On the NYWR, a decline in willow has been cited to have implications for hydrologically disconnected floodplains and a subsequent loss of willow dominated plant communities (Wolf et al. 2007; Beschta & Ripple 2010; Peterson et al. 2020). Wolf et al. 2007 refers to this phenomenon as a transition from a “beaver-willow” state to an “elk-grassland” state, where the loss of willow, beaver, and other riparian species contribute to accelerated erosion, widened streams, lower water table, and more exposed sand and gravel.

The longevity and consistency of data collection for this project sets it apart from other research on ungulate populations and the associated effects of browsing on willow. These findings suggest that a reduction in moose browsing has played an important role in the recovery of willow across this landscape. This has implications for interpreting the status of ungulate population on other winter ranges, especially the NYWR, and for evaluating the ecological condition for riparian areas and associated habitat. I confirmed a decline in moose numbers in the southern ABW is associated with an improvement in willow condition within their range.

Therefore, the ecological story of willow and moose in the southern ABW has similarities to the trophic cascade phenomenon on the NYWR in YNP (Smith et al. 2020; Ripple et al. 2013). There, reduced elk numbers have been cited as the cause for an increase in willow height (Painter & Tercek 2020). My study provides a direct comparison for trophic cascades reflected in willow. I conclude that a trophic cascade is occurring in the southern ABW, where reduced moose numbers have caused a recovery in willow height.

CHAPTER FOUR

SUMMARY AND IMPLICATIONS

The objective of this study was to examine willow condition in response to changes in beaver and moose populations in the southern ABW. I analyzed 37 years of willow condition and beaver and moose population trends to determine how beaver activity and moose populations effect willows in the southern ABW. My analysis revealed that beaver populations, after gradually increasing since their reintroduction in 1986, have remained at carrying capacity over the last 20 years and have contributed to an increase in willow canopy cover across the southern ABW. Since their reintroduction, willow canopy cover has increased from 16% in 1981 (five years before reintroduction) to 37% in 2019 across 13 study meadows. I also found that moose numbers declined and have remained low since their population crash after the 1988 Yellowstone fires (Tyers 2003). This population decline, reflected in moose relative abundance indices, has increased willow height and had a positive linear relationship to browsing pressure. Analysis of 58 years of data from a browsing exclosure corroborates the hypothesis that a decline in moose numbers has caused a resurgence in willow height, and browsing is a limiting factor for willow height in the southern ABW.

The status of willow has been a topic of discussion for several decades throughout the intermountain west. The potential causes of willow decline and recovery has historically been debated because of its contribution to biodiversity and potential for reflecting changes in the environment (Tyers 1981; Painter & Tercek 2020; Beschta & Ripple 2018; Ripple et al. 2013). Olympic, Rocky Mountain, Wind Cave, and Zion National Parks have been the focus of these assessments, although there are many less celebrated locations where willow declines have also occurred (Beschta & Ripple 2009).

Addressing the condition of willow in wildland settings provides opportunities to observe how ecological processes affect willow status (Zeigenfuss et al. 2002; Baker et al. 2005; Wolf et al. 2007; Bilyeu 2006; Bilyeu et al. 2008; Beschta & Ripple 2009; Smith & Tyers 2012; Peterson et al. 2020). In Rocky Mountain National Park, Baker et al. (2005) investigated the effects of beaver and elk herbivory on willow. They concluded that beaver cutting along with intense elk browsing suppressed willow. However, they also described a system with low ungulate densities where beaver and willow benefited from a mutualistic relationship.

Beaver-Willow Communities in Heavily Browsed Environments

Extensive literature surrounding the topic of willow response to beaver and ungulate populations supports the observation that willow can be suppressed from over-browsing and beaver can promote recovery of degraded environments (Peterson et al. 2020; Beschta & Ripple 2016; Smith & Tyers 2012). However, some literature also suggests that if a system is degraded to a point where successional vegetation changes occur, beaver cannot establish or persist and favorably change the environment. Wolf et al. (2007) and Peterson et al. (2020) describe this scenario as a transition to an alternative stable state, where the species composition shifts from a “beaver-willow” community to an “elk-grassland” community with a lowered water table and fewer riparian species. It is argued that when an environment is disrupted enough to change species composition for a prolonged period, it is likely irreversible (Peterson et al. 2020). This raises an important question: when is a riparian system altered to such an extent that a transition to an alternative stable state occurs?

In YNP's NYWR, several publications offer descriptions of the landscape transitioning to new states of species composition after disturbances from elk over-browsing and the disappearance of beaver (Wolf et al. 2007; Kay 1990; Smith et al. 2020). Bilyeu et al. (2008), for example, describes the loss of beavers in YNP and how beaver decline in combination with intense elk herbivory facilitated loss of willow and caused stream incision. Important comparisons can be made with my study area in the southern ABW, where willow was historically over-browsed by moose, but stream incision was not documented (Smith & Tyers 2008, 2012; Tyers 2003). Therefore, I conclude that stream incision is an important indicator for a "tipping point" of a degraded system being beyond recovery.

Another important difference between the southern ABW and the NYWR is the topography. The southern ABW beaver-willow riparian areas occur in post-glacial lakes with gentle topography and wide valleys. This topography may contribute to more resilient riparian areas, making them less likely to experience stream incision during times of over-browsing and high seasonal water flow (Smith & Tyers 2008, 2012; Tyers 2003). Many of the study areas cited on the NYWR do not have the same topography. Areas such as Blacktail Creek (Marshall et al. 2014, 2013) and Crystal Creek that have extensive channel erosion have steeper slopes with narrow stream corridors that may be more vulnerable to erosion and stream incision when exposed to over-browsing.

Furthermore, in degraded systems with historical over-browsing, beaver may not be able to establish or persist in new areas if they do not have a stable population elsewhere to sustain beaver activity in degraded systems. Baker (2003) describes that a “source-sink” beaver population dynamic is an important factor in the recovery of beaver-willow communities in marginalized areas, where a location with sufficient food and building material supports a stable “source” population that is capable of producing offspring that can disperse to less viable “sink” habitat in marginalized areas. This population dynamic can facilitate a positive feedback in marginalized habitat, where even periodic beaver activity can promote water impoundment and new willow growth. My findings show evidence of this phenomenon in the southern ABW, but the NYWR beaver population does not have a well-documented, resilient source population that has the capacity to facilitate restoration of beaver-willow communities in marginalized habitat (Smith & Tyers 2008, 2012). This may explain why beaver-willow communities have not been able to re-establish more uniformly across the NYWR in recent years. Smith and Tyers (2012) surmised that the recent increase in beaver on the NYWR may be in part because of beaver migrating from the “source” population in the southern ABW. The extent of environmental degradation on the NYWR may mean that some of the NYWR beaver populations might continue to rely on the “source” populations in the southern ABW in addition to other areas with likely source populations, such as the Yellowstone River.

I conclude that the streams and willow communities in the southern ABW were not degraded enough to prevent the recovery of a beaver-willow community as described by Peterson et al. (2020). Reduced moose browsing and beaver reintroduction enhanced the riparian areas and increased willow canopy cover. Managers should consider this distinction when contemplating restoration of riparian areas in an over-browsed environment, especially when considering beaver reintroduction to facilitate riparian recovery.

Monitoring Moose

Moose can be difficult to count (Tyers 2003; Timmerman & Buss 1997; Gasaway et al. 1986; Hinton et al. 2022). Traditional survey efforts using aircraft on grid patterns have been useful (Gasaway et al. 1986). However, this seems to only be successful in areas with open canopies, such as expansive taiga or near-arctic shrub fields. My study shows a relationship between browsing and moose relative abundance, indicating that browsing measurements may be an important tool for monitoring trends in local moose populations, especially in combination with several indices of relative abundance.

Implications for these findings may include offering insights to land managers who may use willow stature as an indication of ungulate numbers. In the southern ABW, willow height appears to directly reflect local moose abundance. This confirms other studies that have promoted willow monitoring as an important component of moose population research, where changes in willow condition and browse rates are offered to be a useful and important component of moose population monitoring on a local scale (Burkholder et al. 2017; Seaton et al. 2011; Crete 1989).

Trophic Cascade in the Southern ABW

Researchers in YNP have documented an increase in willow height, especially on the NYWR, which some attributed to a reduction in elk numbers following wolf reintroduction in 1995-96 (Beschta & Ripple 2010; Ripple & Beschta 2006, 2003; White et al. 2013). These researchers introduced the concept of a top-down trophic cascade effect. This theory hypothesizes that the reintroduction of wolves in YNP, combined with an increase in other predators like cougars and grizzly bears, caused elk numbers to decline, resulting in reduced browsing and an increase in willow height. Changes in willow height in relation to elk numbers are cited as evidence to support the presence of a top-down trophic cascade effect on the NYWR (Smith et al. 2020; Ripple & Beschta 2012).

The ecology of the NYWR is similar to my study area in the southern ABW, where willow stands have historically been over-browsed but have also experienced a recovery in height. An important distinction, however, is that willow herbivory in the southern ABW is primarily limited to moose because of the higher elevation and winter conditions (Tyers 2003). Furthermore, willow on the NYWR is cited to have increased, but not uniformly (Painter & Tercek 2020). This is likely due to a loss of beaver habitat and increasing bison numbers that suppress willow growth potential through trampling and herbivory even though elk numbers have decreased (Beschta et al. 2020; Painter & Tercek 2020).

The longevity of the research on moose abundance, browsing, and willow height in the southern ABW sets it apart from other studies analyzing the effects of ungulate numbers on willow. These data include 37 years of willow measurements and span periods of moose population increase, the 1988 crash, and stabilization at lower density. My findings provide evidence to support the hypothesis that a moose population crash caused a decline in willow browsing, which in turn allowed willow to increase in height. Therefore, I conclude that the ecology of the southern ABW provides evidence of a similar trophic cascade as described by researchers on the NYWR (Peterson et al. 2020), reflected in reduced moose numbers and a recovery in willow height.

Ungulate browsing on willow communities has the potential to drastically alter ecosystems, such as what occurred in parts of YNP's NYWR and other famous ecological research areas like Rocky Mountain National Park (Peterson et al. 2020; Baker et al. 2005). In these circumstances, willow browsing from ungulates were enough to alter vegetative communities resulting in a transition to an alternative stable state. This phenomenon is described by Wolf et al. (2007) in parts of the NYWR where "beaver-willow" communities transitioned to "elk-grassland" communities. In some cases, these changes may not recover for long periods, or may never return to their previous state. Intense elk browsing, in addition to areas where beavers are unable to re-establish, have led researchers in YNP to question whether the previous beaver-willow communities will ever revert to their original states or if this will occur only in favorable locations.

The southern ABW, juxtaposed to YNP's NYWR, was able to recover from historic over-browsing and beaver extirpation. My findings show that a reduction in moose numbers and associated browsing, commensurate with a reintroduction of beaver, enhanced the willow communities in these riparian meadows. These findings suggest that under the right circumstances, willow communities have the potential to recover from a previously degraded state.

REFERENCES CITED

Anderson DR, Burnham KP (2002) Avoiding Pitfalls When Using Information-Theoretic Methods. The Journal of Wildlife Management 66:912–918

Baker B, Ducharme H, Mitchell DCS, Stanley TR, Peinetti HR (2005) Interaction of Beaver and Elk Herbivory Reduces Standing Crop of Willow 15:110-118

Baker B, Peinetti HR, Coughenour MB, Johnson TL (2012) Competition favors elk over beaver in a riparian willow ecosystem. Ecosphere 3:1–15

Baker B, Peinetti R, Coughenour M (2005) Resilience of Willow Stems After Release From Intense Elk Browsing. Rangeland Ecology & Management 58:575–581

Baker BW (2003) Beaver (Castor canadensis) in heavily browsed environments. Lutra 46:173–181

Baker BW, Hill EP (2003) Beaver (Castor canadensis). In: Wild mammals of North America: biology, management, and conservation. Feldhamer, GA, Thompson, BC, & Chapman, JA, editors. Johns Hopkins University Press, Baltimore, Maryland, USA pp. 288–310.

Ballenberghe V van, Ballard WB (1997) Ecology and Management of the North American moose. Smithsonian Institution Press, Washington and London, USA

Ballenberghe V van, Peek J (1971) Radiotelemetry Studies of Moose in Northeastern Minnesota. The Journal of Wildlife Management 35:63–71

Baril LM (2009) Change in Deciduous Woody Vegetation, Implications of Increased Willow (Salix spp.) Growth for Bird Species Diversity, and Willow Species Composition in and Around Yellowstone National Park’s Northern Range. M.S. Thesis, Montana State University, Bozeman, MT, USA

Barmore W (1980) Population characteristics, distribution, and habitat relationships of six ungulate species in Yellowstone National Park. Final Report. Mammoth, Wyoming, USA

Belile DL (2016) Spatio-temporal analysis of ungulate browsing on willow (Salix spp.) communities within the Northern Range of Yellowstone. M.S. Thesis, Oglala Lakota College, Missoula, MT, USA

Beschta RL, Ripple WJ (2018) Can large carnivores change streams via a trophic cascade? Ecohydrology 12:1–13

Beschta RL, Ripple WJ (2009) Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401–2414

Beschta RL, Ripple WJ (2010) Recovering Riparian Plant Communities With Wolves in Northern Yellowstone, U.S.A. Restoration Ecology 18:380–389

Beschta RL, Ripple WJ (2016) Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction. Biological Conservation 198:93–103

Beschta RL, Ripple WJ, Kauffman JB, Painter LE (2020) Bison limit ecosystem recovery in northern Yellowstone. Food Webs 23:1–12

Beyer H, Merrill E, Varley N, Boyce M (2007) Willow On Yellowstone's Northern Range: Evidence for a Trophic Cascade? Ecological Applications 17:1563–1571

Bilyeu D (2006) Effects of elk browsing and water table on willow growth and physiology: implications for willow restoration in Yellowstone National Park. Ph.D. Dissertation, Colorado State University, Fort Collins, CO, USA

Bilyeu DM, Cooper DJ, Thompson Hobbs N (2008) Water Tables Constrain Height Recovery of Willow on Yellowstone's Northern Range. Ecological Applications 18:80–92

Bowyer T, Ballenberghe V van, Kie J (1997) The Role of Moose in Landscape Processes: Effects of Biogeography, Population Dynamics, and Predation. In: Wildlife and Landscape Ecology. Springer New York pp. 265–287

Brookshire J, Kauffman B, Lytjen D, Otting N (2002) Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia 132:559–566

Burkholder BO (2012) Seasonal distribution, winter habitat selection and willow utilization patterns of the Shiras moose on the Mount Haggin Wildlife Management Area. M.S. Thesis, Montana State University, Bozeman, MT, USA

Burkholder BO, DeCesare NJ, Garrott RA, Boccadori SJ (2017) Heterogeneity and power to detect trends in moose browse utilization of willow communities. Alces 53:23–39

Cederlund G, Okarma H (1988) Home range and habitat use of adult female moose. Journal of Wildlife Management 52:336–343

Chadde S, Kay C (1988) Willows and Moose: a Study of Grazing Pressure, Slough Creek Exclosure, Montana, 1961-1986. Research Note 24. Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana. Missoula, Montana, USA

Chadde SW, Kay CE (1991) Tall-willow Communities on Yellowstone’s Northern Range: A Test of the ‘Natural-Regulation’ Paradigm. In: The Greater Yellowstone Ecosystem: Redefining America’s Wilderness Heritage. Keiter, RR & Boyce, MS, editors. Yale University Press, New Haven, CT pp. 231–262

Coady J (1982) Moose. In: Wild Mammals of North America. Chapman, J & Feldhammer, G, editors. The John Hopkins University Press, Baltimore, Maryland pp. 902–922.

Cooper DJ, Dickens J, Hobbs NT, Christensen L, Landrum L (2006) Hydrologic, geomorphic and climatic processes controlling willow establishment in a montane ecosystem. Hydrological Processes 20:1845–1864

Coughenour MB, Singer FJ (1996) Elk Population Processes in Yellowstone National Park Under the Policy of Natural Regulation. Ecological Applications 6:573–593

Crète M (1989) Approximation of K carrying capacity for moose in eastern Quebec. Canadian Journal of Zoology 67:373–380

DeCesare NJ, Newby JR, Boccadori VJ, Chilton-Radandt T, Thier T, Waltee D, Podruzny K, Gude JA (2016) Calibrating minimum counts and catch-per-unit-effort as indices of moose population trend. Wildlife Society Bulletin 40:537–547

Despain D, Houstan D, Meagher M, Schullery P (1987) Wildlife in Transition: Man and Nature on Yellowstone’s Northern Range. Roberts Rinehart Publishers, Boulder, Colorado, USA

Eastman D, Ritcey R (1987) Moose habitat relationships and management in British Columbia. Sweedish Wildlife Research (Supplement) 1:101–118

Engstrom DR, Whitlock C, Fritz SC, Wright HE (1991) Recent environmental changes inferred from the sediments of small lakes in Yellowstone’s northern range. Journal of Paleolimnology 1991 5:2 5:139–174

Erickson G (1979) Slough Creek big game exclosure: A reevaluation after 20 years. Unpublished Report.

Fryxell JM (2001) Habitat suitability and source–sink dynamics of beavers. Journal of Animal Ecology 70:310–316

Gaab JE (1948) Absaroka Unit moose survey – 1947. Unpublished report pp 1-16

Gaab JE (1949) Absaroka Unit Moose Survey - 1948. Unpublished report on file at Montana Department of Fish, Wildlife, and Parks pp. 1–9

Gasaway W, DuBois S, Reed D, Harbo S (1986) Estimating moose population parameters from aerial surveys. Biological Papers of the University of Alaska 22:1–99

Geist V (1971) The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the old world deer and the genus Bison. Quaternary Research 1:285–315

Goldfarb B (2018) Eager: The Surprising, Secret Life of Beavers and Why They Matter. Chelsea Green Publishing, White River Junction, Vermont, USA

Gurney WSC, Lawton JH (1996) The Population Dynamics of Ecosystem Engineers. Oikos 76:273

Haines A (1955) Journal of a Trapper. Oregon Historical Society, New York, USA

Heinze DH (1992) Willows of Montana. Billings, Montana, USA

Hinton JW, Wheat RE, Schuette P, Hurst JE, Kramer DW, Stickles JH, Frair JL (2022) Challenges and opportunities for estimating abundance of a low-density moose population. The Journal of Wildlife Management 86:1–18

Houston DG (1982) The northern Yellowstone elk: ecology and management. Macmillan Publishing Co. , New York, USA

Johnston DB, Cooper DJ, Hobbs NT (2011) Relationships between groundwater use, water table, and recovery of willow on Yellowstone’s northern range. Ecosphere 2:1–20

Johnston DB, Cooper DJ, Hobbs TN (2007) Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture. Ecologia 154:467–478

Jonas RJ (1955) A population and ecological study of the beaver (Castor canadensis) of Yellowstone National Park. M.S. Thesis, University of Idaho, Moscow

Jones CG, Lawton JH, Shachak M (1994) Organisms as Ecosystem Engineers. Ecosystem Management 69:373–386

Joyal R (1987) Moose habitat investigations in Quebec and management implications. Sweedish Wildlife Research (Supplement) 1:139–152

Kay C (1990) Yellowstone’s Northern Elk Herd: Critical Evaluation of the ‘Natural Regulation’ Paradigm. Ph.D. Dissertation, Utah State University, Logan, UT, USA

Kay CE (1994) Impact of native ungulates and beaver on riparian communities in the intermountain west. Natural Resources and Environmental Issues 1:23–44

Kay CE, Chadde S (1992) Reduction of Willow Seed Production by Ungulate Browsing in Yellowstone National Park. In: Symposium on Ecology and Management of Riparian Shrub Communities. Ogden, Utah pp. 92–99

Kehrberg E v. (1964) Wildlife management plan, Gardiner Ranger District.

Kelsall J, Telfer E (1974) Biogeography of moose with particular reference to western Canada. Canadian Naturalist 101:117–130

Lenth R (2022) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.4-1. https://CRAN.R-project.org/package=emmeans

Leopold A, Cain SA, Cottam CM, Gabrielson IN, Kimball TL (1963) Wildlife Management in the National Parks. National Park Service, USA

Levine R, Meyer GA (2019) Beaver-generated disturbance extends beyond active dam sites to enhance stream morphodynamics and riparian plant recruitment. Scientific Reports 9:1–12

Marshall KN, Cooper DJ, Thompson Hobbs N (2014) Interactions among herbivory, climate, topography and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. Journal of Ecology 102:667–677

Marshall KN, Thompson Hobbs N, Cooper DJ (2013) Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proc R Soc Lond B Biol Sci 280

Mattson DJ, Despain DG (1985) Grizzly bear habitat component mapping handbook for the Yellowstone Ecosystem. National Park Service, and U.S. Forest Service

McArthur PH, Pianka ER (1966) An optimal use of a patchy environment. American Naturalist 100:603–609

McColley SD (2007) Restoring Aspen Riparian Stands with Beaver on the Northern Yellowstone Winter Range. M.S. Thesis. Montana State University, MT, USA

McColley SD, Tyers DB, Sowell BF (2011) Aspen and Willow Restoration Using Beaver on the Northern Yellowstone Winter Range. Restoration Ecology 20:450–455

McDowell LE, Moy M (1942) Montana moose survey, Hellroaring-Buffalo Fork-Slough Creek unit.

Meiman PJ, Thorne MS, Skinner QD, Smith MA, Dodd JL (2009) Wild Ungulate Herbivory of Willow on Two National Forest Allotments in Wyoming. Rangeland Ecology & Management 62:460–469

Mouw JEB, Chaffin JL, Whited DC, Hauer FR, Matson PL, Stanford JA (2012) Recruitment and Successional Dynamics Diversify the Shifting Habitat Mosaic of an Alaskan Floodplain. River Research and Applications 29:671–685

Müller-Schwarze D (2011) The Beaver: Its Life and Impact, Second Edition. Cornell University Press, USA

Nadeau MS, DeCesare NJ, Brimeyer DG, Bergman EJ, Harris RB, Hersey KR, Huebner KK, Matthews PE, Thomas TP (2017) Status and trends of moose populations and hunting opportunity in the western United States. Alces 53:99–112

Naiman RJ, Decamps H (1997) The Ecology of Interfaces: Riparian Zones. Annual Review of Ecology and Systematics 28:621–658

Naiman RJ, Decamps H, Pollock M (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. Ecological Applications 3:209–212

Naiman RJ, Johnston CA, Kelley JC (1988) Alteration of North American Streams by Beaver. BioScience 38:753–762

Naiman RJ, Melillo JM, Hobbie JE (1986) Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor Canadensis). Ecology 67:1254–1269

National Research Council (2002) Ecological Dynamics on YNP's Northern Range. National Academies Press, Washington, D.C., USA

Nordengren C, Hofgaard A, Ball JP (2003) Availability and quality of herbivore winter browse in relation to tree height and snow depth. Annales Zoologici Fennici 40:305–314

NRC (2002) Ecological Dynamics on Yellowstone's Northern Range. Committee on Ungulate Management in Yellowstone National Park, Division of Earth and Life Sciences, National Research Council, USA

Oldemeyer J, Regelin W (1987) Forest succession, habitat management, and moose on the Kenai National Wildlife Refuge. Swedish Wildlife Research (Supplement) 1:163–179

Painter LE, Beschta RL, Larsen EJ, Ripple WJ (2015) Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? Ecology 96:252–263

Painter LE, Tercek MT (2020) Tall willow thickets return to northern Yellowstone. Ecosphere 11(5)

Peek J (1997) Habitat relationships. In: Ecology and Management of the North American Moose. Franzmann, A & Schwartz, C, editors. Smithsonian Institution Press, Washington and London pp. 351–376.

Peek J, Mackie R, Dusek G (1992) Overwinter survival strategies of North American Cervidae. Alces (supplement) 1:156–161

Peek JM (1971) Moose-snow relationships in Northeastern Minnesota. In: Symposium on Snow and Ice in Relation to Wildlife and Recreation. Iowa State University, Ames p. 280.

Peinetti H, Baker BW, Coughenour MB (2009) Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. Ecological Modelling 220:998–1012

Peinetti H Raul, Baker BW, Coughenour MB (2009) Simulation modeling to understand how selective foraging by beaver can drive the structure and function of a willow community. Ecological Modelling 220:998–1012

Persico L, Meyer G (2013) Natural and historical variability in fluvial processes, beaver activity, and climate in the Greater Yellowstone Ecosystem. Earth Surface Processes and Landforms 38:728–750

Peterson R (1955) North American Moose. University of Toronto, Toronto, Ontario

Peterson R, Beschta R, Cooper D, Hobbs T, Johnston D, Larsen E, Marshall K, Painter L, Ripple W, Rose J, Smith D, Wolf E (2020) Indirect Effects of Carnivore Restoration on Vegetation. In: Yellowstone Wolves. Smith, D, Stahler, D, & MacNulty, D, editors. The University of Chicago Press, Chicago and London.

Polvi LE, Wohl E, Merritt DM (2014) Modeling the functional influence of vegetation type on streambank cohesion. Earth Surface Processes and Landforms 39:1245–1258

Pulliam HR (1988) Sources, Sinks, and Population Regulation. The American Naturalist 132:652–661

Pulliam HR, Dunning JB, Jianguo Liu (1992) Population dynamics in complex landscapes: a case study. Ecological Applications 2:165–177

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: A selective review of theory and test. Quarterly Review Biology 52:137–154

Regelin W, Schwartz C, Franzmann A (1985) Seasonal energy metabolism of adult moose. Alces 22:83–90

Renecker L, Schwartz C (1997) Food habits and feeding behavior. In: Ecology and Management of the North American Moose. Franzmann, A & Schwartz, C, editors. Smithsonian Institution Press, Washington and London pp. 403–440.

Renecker LA, Hudson RJ (1992) Thermoregulatory and behavioral responsees of moose. Is large body size an adaptation or constraint? Alces (supplement) 1

Ripple WJ, Beschta RL (2006) Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96–106

Ripple WJ, Beschta RL (2012) Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation 145:205–213

Ripple WJ, Beschta RL (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299–313

Ripple WJ, Beschta RL, Fortin JK, Robbins CT (2013) Trophic Cascades From Wolves to Grizzly Bears in Yellowstone. Journal of Animal Ecology 83:223–2

Ripple WJ, Painter LE, Beschta RL, Cormack GC (2010) Wolves, Elk, Bison, and Secondary Trophic Cascades in Yellowstone National Park 3(1)

Risenhoover KL (1989) Composition and quality of moose winter diets in interior Alaska. Journal of Wildlife Management. 53: 586-577

Ritter TD (2018) Ecosystem Pioneers: Beaver Dispersal and Settlement Site Selection in the Context of Habitat Restoration. Montana State University

Ritter TD, Gower CN, Mcnew LB (2019) Habitat conditions at beaver settlement sites: implications for beaver restoration projects. Restoration Ecology 28:196–205

RStudio Team (2022) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/

Rush W (1942) Untitled agency correspondence - W. M. Rush to L. McDowell and M. Moy, USDA Forest Service. 1–3

Saether B, Andersen R (1990) Resource limitation in a generalist herbivore, the moose Alces alces: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68:993–999

Schladweiler P, Stevens DR (1973) Reproduction of Shiras Moose in Montana. The Journal of Wildlife Management 37:535–544

Schullery P, Whittlesey L (1992) The documentary record of wolves and related wildlife species in the Yellowstone National Park area prior to 1882. 4th ed. National Park Service, Yellowstone National Park, Wyoming, USA

Scrafford MA, Tyers DB, Patten DT, Sowell BF (2018) Beaver Habitat Selection for 24 Yr Since Reintroduction North of Yellowstone National Park. Rangeland Ecology & Management 72:266-273

Seaton CT, Paragi TF, Boertje RD, Kielland K, Dubois S, Fleener CL (2011) Browse biomass removal and nutritional condition of moose Alces alces. Wildlife Biology 17:55–66

Singer FJ, Mark LC, Cates RC (1994) Ungulate Herbivory of Willows on Yellowstone's Northern Winter Range. Source: Journal of Range Management 47:435–443

Singer FJ, Zeigenfuss LC, Cates RG, Barnett DT (1998) Elk, Multiple Factors, and Persistence of Willows in National Parks. The Wildlife Society Bulletin 26:419–428

Skagen SK, Melcher CP, Howe WH, Knopf FL (1998) Comparative Use of Riparian Corridors and Oases by Migrating Birds in Southeast Arizona. Conservation Biology 12(4):896-909

Smith DW (1997) Dispersal Strategies and Cooperative Breeding in Beavers. Ph.D. Dissertation, University of Nevada, Reno, USA

Smith DW, Stahler DR, MacNulty DR (2020) Yellowstone Wolves: Science and Discovery in the World's First National Park. University of Chicago Press, USA

Smith DW, Tyers DB (2008) The Beavers of Yellowstone. Yellowstone Science 16:4–15

Smith DW, Tyers DB (2012) The History and Current Status and Distribution of Beavers in Yellowstone National Park. Northwest Science 86:276

Soulé ME, Estes JA, Berger J, Martinez C, Rio D (2003) Ecological Effectiveness: Conservation Goals for Interactive Species. Conservation Biology 17(5):1238-1250

Stephenson T, Ballenberghe V van, Peek J, MacCracken J (2006) Spatio-Temporal Constraints on Moose Habitat and Carrying Capacity in Coastal Alaska: Vegetation Succession and Climate. Rangeland Ecology and Management 59:359–372

Stevenson (1920) Hellroaring - Slough Creek game patrols, 1919-20. Unpublished report on file at Gardiner Ranger District 1–5

Stolter C, Ball JP, Julkenunen-tiitto R, Lieberei R, Ganzhorn JU (2005) Winter browsing of moose on two different willow species: food selection in relation to plant chemistry and plant response. Canadian Journal of Zoology 83:807-819

Telfer ES, Kelsall JP (1984) Adaptations of some large North American mammals for survival in snow. Ecology 65:1828–1834

Thompson I, Euler D (1987) Moose habitat in Ontario: A decade of change in perception. Sweedish Wildlife Research (Supplement) 1:181–193

Timmerman H, Buss M (1997) Population and harvest management. In: Ecology and Management of the North American Moose. Franzmann, A & Schwartz, C, editors. Smithsonian Institution Press, Washington, D.C., USA

Tyers D (2020) Long-Term Trends in Beaver, Moose, and Willow Status in the Southern Portion of the Absaroka-Beartooth Wilderness. In: Yellowstone Wolves. Smith, D, Stahler, D, & MacNulty, D, editors. University of Chicago Press, Chicago and London pp. 211–213.

Tyers D (2008) Moose Population History on the Northern Yellowstone Winter Range. Yellowstone Science 16:3–11

Tyers D (1981) The Condition of the Northern Winter Range in Yellowstone National Park - a Discussion of the Controversy. M.S. Thesis, Montana State University, Bozeman, USA

Tyers D, Irby L (1995) Shiras Moose Winter Habitat Use in the Upper Yellowstone River Valley Prior to and After the 1988 Fires. Alces 31:35–43

Tyers DB (2006) Moose population history on the Northern Yellowstone Winter Range. Alces 42:133–149

Tyers DB (2003) Winter ecology of moose on the Northern Yellowstone Winter Range. Ph.D. Dissertation, Montana State University, Montana, USA

USDA (1936) Absaroka winter game studies 1935-1936. Unpublished report on file at Livingston Ranger District 1–111

USDA (1987) Gallatin National Forest, forest plan. USDA Forest Service

Visscher DR, Merrill EH, Fortin D, Frair JL (2006) Estimating woody browse availability for ungulates at increasing snow depths. Forest Ecology and Management 222:348–354

Wagner FH (2006) Yellowstone’s Destabilized Ecosystem: Elk Effects, science, and Policy Conflict. Oxford University Press, Oxford, New York, USA

Warren ER (1926) A Study of the Beaver in the Yancey Region of Yellowstone National Park. Roosevelt Wild Life Forest Experiment Station, USA

Western Regional Climate Center (2022) Cooke City, MT climate summary.

White PJ, Garrott RA, Plumb GE (2013) Predation: wolf restoration and the transition of Yellowstone elk. In: Yellowstone’s wildlife in transition. Harvard University Press, Cambridge, Massachusetts, USA pp. 69–93.

Wimberly MC (2006) Species Dynamics in Disturbed Landscapes: When does a Shifting Habitat Mosaic Enhance Connectivity? Landscape Ecology 21:35–46

Wolf EC, Cooper DJ, Hobbs NT (2007) Hydrologic Regime And Herbivory Stabilize an Alternative State in Yellowstone National Park. Ecological Applications 17:1572–1587

Wolff JO (1978) Burning and Browsing Effects on Willow Growth in Interior Alaska. The Journal of Wildlife Management 42:135–140

Wright JP, Jones CG, Flecker AS (2002) An Ecosystem Engineer, the Beaver, Increases Species Richness at the Landscape Scale. Oecologia 132:96–101

Yellowstone National Park (1997) Yellowstone’s Northern Range: Complexity and Change in a Wildland Ecosystem. Yellowstone National Park, National Park Service, Mammoth Hot Springs, Wyo., USA

Zeigenfuss LC, Singer FJ, Williams SA, Johnson TL (2002) Influences of Herbivory and Water on Willow in Elk Winter Range. The Journal of Wildlife Management 66:788–795

APPENDICES

APPENDIX A

BEAVER COLONY NUMBERS IN 13 STUDY MEADOWS FROM 1986-2020

Table A1: Beaver colony numbers from 1987-2020 in the southern Absaroka-Beartooth Wilderness study area. Gray sections represent areas where beavers were not yet present.

Year	Frenchy	Christenson	Holeman	Hellroaring	Bull Moose	East Fork	Grizzly	Elk	Beaver	Hart's	Upper Lake Creek	Lake Abundance	Stillwater	Total
1986		1												**1**
1987		1												**1**
1988		3	3	2										**8**
1989		3	1	2										**6**
1990		3	1	4										**8**
1991		3	1	4										**8**
1992		2	1	3										**6**
1993		4	1	6									3	**14**
1994		4	1	8								1	2	**16**
1995		4	1	8								1	2	**16**
1996	1	3	0	5						1		0	1	**11**
1997	1	0	0	6			1			0		1	1	**10**
1998	1	0	3	9			1			0		0	2	**16**
1999	5	5	3	9			2			0		0	2	**26**
2000	6	7	3	10		1	2	1		1		0	2	**33**
2001	2	7	3	8		1	1	1		1	1	0	1	**26**
2002	5	6	5	9		1	1	0		0	1	1	2	**31**
2003	5	5	5	8	1	1	1	0		1	1	0	3	**31**
2004	5	8	4	9	1	1	2	0	1	0	1	0	3	**35**
2005	6	6	1	7	1	1	2	0	1	0	1	0	3	**29**
2006	7	10	6	10	1	1	1	1	1	1	1	1	3	**44**
2007	7	5	6	10	1	1	0	1	0	1	1	1	2	**36**
2008	8	6	3	5	1	0	2	1	0	1	0	1	1	**29**
2009	5	10	4	6	1	0	1	1	1	1	0	1	2	**33**
2010	7	5	3	7	1	0	2	0	0	0	0	1	3	**29**
2020	6	5	3	4	1	1	0	1	0	0	1	0	3	**25**

APPENDIX B

AVERAGE WILLOW HEIGHT AND BROWSING RATES FOR ALL SPECIES AND SAMPLING LOCATIONS (1988-2021)

Table B1: Average height (cm) of 7 willow and 1 birch species for each sampling location in the southern Absaroka-Beartooth Wilderness (1988-2021).

Year	*Bannock*	*Fisher Creek*	*Lost Creek*	*Slough Cr Cabin*	*Soda Butte*
1988	119.35	108.97	74.30	93.93	162.17
1989	115.08	112.43	64.00	94.67	169.28
1990	115.32	125.13	51.18	86.98	154.50
1991	108.45	116.77	60.14	95.98	152.69
1992	91.12	118.47	58.40	92.95	149.64
1995	93.00	87.97	84.83	127.60	136.11
1996	87.83	91.40	87.50	129.95	127.17
1997	85.38	85.10	96.13	148.90	120.11
2002	91.97	98.97	114.38	188.88	123.94
2003	92.21	88.87	118.38	186.36	131.31
2004	94.27	88.14	114.99	205.80	132.74
2005	98.17	96.44	111.67	205.09	139.51
2006	100.09	93.14	128.13	229.95	135.33
2007	102.36	92.13	135.82	233.87	139.07
2008	109.81	101.73	137.73	250.83	146.19
2009	114.35	100.10	141.50	258.44	155.86
2010	116.98	101.00	145.86	272.49	169.22
2011	111.75	95.87	149.36	280.29	168.17
2012	119.11	103.20	146.14	287.54	175.72
2013	126.16	106.60	149.64	288.73	185.44
2014	122.40	110.37	148.86	291.32	199.14
2015	123.09	113.20	149.14	291.80	204.50
2016	129.56	116.30	151.00	295.37	211.25
2017	135.37	113.97	153.71	296.88	200.31
2020	144.68	118.70	153.47	263.15	212.61
2021	152.32	122.97	152.40	238.90	210.78

Table B2: Average height (cm) for 7 willow and 1 birch species in the southern Absaroka-Beartooth Wilderness study plots (1988-2021).

Year	*Bog Birch*	*Barclay*	*Booth*	*Drummond*	*Eastwood*	*Farr*	*Geyer*	*Wolf*
1988	86.40	135.00	132.38	140.03	108.97	97.25	125.27	64.48
1989	83.20	135.17	130.22	145.47	112.43	95.85	125.64	60.83
1990	100.10	123.00	119.83	133.68	125.13	96.90	101.64	57.13
1991	90.80	121.33	124.88	128.42	116.77	94.25	115.64	55.70
1992	84.10	120.00	113.95	126.10	118.47	85.40	109.82	45.96
1995	82.50	119.50	128.17	132.37	87.97	77.45	162.27	51.67
1996	80.30	113.50	126.10	127.23	91.40	71.20	160.91	51.05
1997	83.50	104.00	126.70	129.90	85.10	74.10	196.82	50.70
2002	91.00	121.33	147.33	131.77	98.97	78.45	253.27	69.85
2003	89.88	119.83	147.70	137.87	88.87	79.20	256.91	69.65
2004	91.25	116.00	151.48	143.44	88.14	82.35	265.54	82.11
2005	95.60	115.03	156.28	150.18	96.44	84.23	262.19	75.71
2006	88.01	124.03	161.70	156.46	93.14	89.28	302.09	90.09
2007	83.26	124.57	170.14	162.92	92.13	85.31	298.11	91.81
2008	95.65	131.83	177.68	176.43	101.73	95.47	308.09	98.61
2009	93.63	137.33	187.18	181.97	100.10	100.20	318.91	103.72
2010	95.38	158.83	194.31	193.77	101.00	100.55	343.09	109.61
2011	86.38	150.33	194.82	191.50	95.87	101.75	355.91	111.33
2012	94.75	161.83	196.73	200.07	103.20	112.75	375.00	112.17
2013	87.38	173.50	204.62	210.67	106.60	116.10	374.55	113.56
2014	92.88	177.00	203.44	210.17	110.37	125.95	393.00	112.94
2015	83.88	162.50	209.22	209.30	113.20	126.50	402.36	113.44
2016	101.25	181.50	209.42	216.13	116.30	132.85	408.64	120.06
2017	97.88	171.83	210.00	216.67	113.97	132.95	408.45	124.17
2020	112.13	208.33	209.96	205.87	118.70	134.80	346.82	133.33
2021	135.13	184.17	200.23	208.67	122.97	145.05	315.91	128.67

Table B3: Average percentage of twigs browsed (% twigs browsed out of all twigs) of 7 willow and 1 birch species for each sampling location in the southern Absaroka-Beartooth Wilderness study area (1988-2021).

Year	*Bannock*	*Fisher Creek*	*Lost Creek*	*Slough Cr Cabin*	*Soda Butte*
1988	22.83	0.04	6.20	14.97	18.19
1989	49.01	0.92	41.06	67.88	50.61
1990	45.29	0.39	18.90	18.59	43.57
1991	36.91	0.13	24.09	28.74	22.83
1992	48.45	0.00	26.55	25.44	27.17
1995	31.21	0.52	23.29	14.62	19.41
1996	30.16	2.25	10.17	10.60	25.08
1997	20.85	0.24	9.81	10.06	28.60
2002	15.74	1.97	7.46	12.94	4.36
2003	24.80	1.93	4.18	19.70	22.30
2004	16.05	1.25	3.09	22.01	9.46
2005	14.06	0.02	0.45	7.62	7.25
2006	7.89	0.02	0.39	4.14	3.08
2007	13.49	0.03	0.18	0.34	7.42
2008	12.34	0.67	0.06	0.18	2.21
2009	1.46	0.00	0.00	0.00	1.26
2010	18.66	0.00	0.00	0.00	12.04
2011	6.04	0.00	0.00	0.03	5.76
2012	9.15	0.00	0.00	0.07	4.50
2013	7.38	0.01	0.00	0.09	1.28
2014	1.76	0.00	0.00	0.23	2.68
2015	5.67	1.81	0.00	4.33	4.57
2016	8.70	1.51	0.00	1.48	9.51
2017	7.29	1.60	0.00	0.72	3.67
2020	6.39	0.00	0.00	0.10	3.70
2021	5.59	0.00	0.11	0.00	3.21

Table B4: Average percentage of twigs browsed (% twigs browsed out of all twigs) for 7 willow and 1 birch species in the southern Absaroka-Beartooth Wilderness study area (1988-2021).

Year	*Bog Birch*	*Barclay*	*Booth*	*Drummond*	*Eastwood*	*Farr*	*Geyer*	*Wolf*
1988	26.66	27.84	15.32	20.30	0.04	16.43	24.53	9.04
1989	37.59	51.25	60.87	58.20	0.92	36.13	64.95	44.96
1990	27.15	49.81	36.21	36.48	0.39	32.38	33.96	27.49
1991	34.23	37.62	28.24	28.57	0.13	19.05	36.30	38.13
1992	35.63	32.21	37.73	35.87	0.00	24.24	35.06	34.78
1995	34.64	17.53	19.65	30.01	0.52	18.18	10.76	30.05
1996	29.60	23.58	20.85	22.03	2.25	20.19	6.52	26.54
1997	18.10	24.73	20.47	23.52	0.24	20.28	1.24	11.96
2002	18.93	6.60	13.93	10.93	1.97	6.32	8.50	9.98
2003	26.60	19.70	20.29	27.01	1.93	16.50	8.74	20.55
2004	20.09	9.26	16.13	17.28	1.25	9.19	13.16	13.21
2005	20.77	5.98	10.92	10.49	0.02	5.50	1.14	7.42
2006	9.28	2.77	5.28	5.89	0.02	2.73	0.16	6.48
2007	19.08	4.37	6.29	8.30	0.03	10.32	0.00	3.66
2008	7.18	4.34	5.73	5.69	0.67	5.53	0.00	5.90
2009	0.20	1.88	0.45	1.10	0.00	1.22	0.00	1.84
2010	19.72	7.09	8.91	9.73	0.00	15.22	0.00	11.65
2011	3.99	4.72	4.78	4.78	0.00	4.32	0.00	0.00
2012	6.56	3.42	2.69	6.90	0.00	5.51	0.00	8.24
2013	8.23	0.62	2.50	4.08	0.01	3.93	0.00	3.48
2014	1.88	1.23	1.60	1.45	0.00	1.74	0.00	0.98
2015	5.23	6.91	4.78	4.20	1.81	3.72	0.79	6.09
2016	7.75	6.60	5.94	6.98	1.51	9.73	0.13	3.64
2017	5.51	5.26	3.51	4.23	1.60	5.67	0.17	3.66
2020	0.78	5.21	3.01	6.48	0.00	2.51	0.00	2.82
2021	1.14	3.07	2.37	6.28	0.00	2.74	0.00	1.82

APPENDIX C

MODEL SUMMARIES AND RESULTS

Table C1: Results of multiple linear regression model estimating beaver colony numbers as a function of year (polynomial transformed) and meadow.

Predictors	Estimates	95% Confidence Interval		p-value
		Lower	Upper	
(Intercept)	0.15	-0.22	0.53	0.424
Year [1st degree]	2.46	-4.5	9.41	0.488
Year [2nd degree]	-1.28	-8.23	5.68	0.718
Meadow [Bull Moose]	0.19	-0.34	0.73	0.48
Meadow [Christenson's]	4.31	3.77	4.84	<0.001
Meadow [East Fork]	0.19	-0.34	0.73	0.48
Meadow [Elk]	0.12	-0.42	0.65	0.671
Meadow [Frenchy]	2.81	2.27	3.34	<0.001
Meadow [Grizzly]	0.58	0.04	1.11	0.035
Meadow [Hart's]	0.15	-0.38	0.69	0.572
Meadow [Hellroaring]	5.96	5.43	6.5	<0.001
Meadow [Holeman's]	2.23	1.7	2.77	<0.001
Meadow [Lake Abundance]	0.19	-0.34	0.73	0.48
Meadow [Lake Creek]	0.15	-0.38	0.69	0.572
Meadow [Stillwater]	1.42	0.89	1.96	<0.001
Year [1st degree] * Bull Moose	4.61	-5.22	14.45	0.356
Year [2nd degree] * Bull Moose	1.78	-8.05	11.61	0.722
Year [1st degree] * Christenson's	27.99	18.16	37.83	<0.001
Year [2nd degree] * Christenson's	-11.03	-20.86	-1.19	0.028
Year [1st degree] * East Fork	2.55	-7.28	12.39	0.61
Year [2nd degree] * East Fork	0.01	-9.83	9.84	0.999
Year [1st degree] * Elk	2.61	-7.22	12.45	0.601
Year [2nd degree] * Elk	1.92	-7.91	11.75	0.701
Year [1st degree] * Frenchy	44.04	34.21	53.87	<0.001
Year [2nd degree] * Frenchy	-7.3	-17.13	2.54	0.145
Year [1st degree] * Grizzly	5.26	-4.57	15.09	0.293
Year [2nd degree] * Grizzly	-5.96	-15.79	3.87	0.234
Year [1st degree] * Hart's	0.91	-8.92	10.74	0.855
Year [2nd degree] * Hart's	-1.6	-11.43	8.23	0.749
Year [1st degree] * Hellroaring	26.5	16.67	36.34	<0.001
Year [2nd degree] * Hellroaring	-37.24	-47.07	-27.41	<0.001
Year [1st degree] * Holeman's	18.79	8.95	28.62	<0.001
Year [2nd degree] * Holeman's	-6.9	-16.73	2.93	0.168
Year [1st degree] * Lake Abundance	0.84	-8.99	10.67	0.867
Year [2nd degree] * Lake Abundance	-0.93	-10.77	8.90	0.852
Year [1st degree] * Lake Creek	2.46	-7.38	12.29	0.623
Year [2nd degree] * Lake Creek	0.6	-9.24	10.43	0.905
Year [1st degree] * Stillwater	13.02	3.18	22.85	0.01
Year [2nd degree] * Stillwater	-4.21	-14.04	5.63	0.401
Observations	338			
R2 / R2 adjusted	0.852 / 0.833			

Table C2: Results of a multiple linear regression model estimating willow canopy as a function of year and meadow, with an interaction term between year and meadow.

Predictors	Estimates	95% Confidence Interval		p-value
		Lower	Upper	
(Intercept)	-1108.9	-1501.08	-716.72	<0.001
Year	0.56	0.36	0.76	<0.001
Meadow [Bull Moose]	373.73	-180.9	928.36	0.181
Meadow [Christenson’s]	236.44	-318.19	791.06	0.394
Meadow [East Fork]	-460.03	-1014.65	94.6	0.101
Meadow [Elk]	-177.32	-731.95	377.31	0.522
Meadow [Frenchy]	-592.62	-1147.24	-37.99	0.037
Meadow [Grizzly]	494.94	-59.68	1049.57	0.079
Meadow [Harts]	549.51	-5.11	1104.14	0.052
Meadow [Hellroaring]	-188.38	-743.01	366.24	0.496
Meadow [Holeman’s]	364.95	-189.68	919.58	0.191
Meadow [Lake Abundance]	348.01	-206.62	902.64	0.212
Meadow [Lake Creek]	-953.06	-1507.69	-398.44	0.001
Meadow [Stillwater]	4.59	-550.03	559.22	0.987
Year * Meadow [Bull Moose]	-0.18	-0.46	0.1	0.197
Year * Meadow [Christenson's]	-0.1	-0.38	0.18	0.463
Year * Meadow [East Fork]	0.23	-0.05	0.51	0.099
Year * Meadow [Elk]	0.09	-0.19	0.37	0.506
Year * Meadow [Frenchy]	0.3	0.02	0.58	0.034
Year * Meadow [Grizzly]	-0.25	-0.52	0.03	0.081
Year * Meadow [Harts]	-0.28	-0.56	0	0.048
Year * Meadow [Hellroaring]	0.11	-0.17	0.39	0.422
Year * Meadow [Holeman’s]	-0.17	-0.45	0.11	0.227
Year * Meadow [Lake Abundance]	-0.17	-0.45	0.11	0.224
Year * Meadow [Lake Creek]	0.48	0.2	0.76	0.001
Year * Meadow [Stillwater]	0.02	-0.26	0.3	0.886
Observations	65			
R2 / R2 adjusted	0.982 / 0.971			

Table C3: Estimated probability of a GIS landcover point being classified as willow (1) vs another landcover category (0), considering the number of years a meadow was occupied by beaver, and the average colony density.

		95% Confidence Interval		
Predictors	Probability	Lower	Upper	p-value
(Intercept)	0.230	0.223	0.239	<0.001
Colony Density	0.562	0.552	0.572	<0.001
Years Occupied	0.507	0.507	0.510	<0.001
Observations	30500			

Table C4: Results of a linear regression model with an exponential decay transformation that estimates the average number of moose observed per day of searching along horseback transects from 1984-2021.

		95% Confidence Interval		
Predictors	Estimates	Lower	Upper	p-value
(Intercept)	403.01	201.75	604.28	<0.001
Year	-0.2	-0.3	-0.1	<0.001
Observations	35			
R2 / R2 adjusted	0.338 / 0.318			

Table C5: Results of a linear regression model estimating the average moose observed per road transect as a function of year (polynomial transformed).

		95% Confidence Interval		
Predictors	Estimates	Lower	Upper	p-value
(Intercept)	0.43	0.34	0.52	<0.001
Year [1st degree]	-0.81	-1.3	-0.32	0.002
Year [2nd degree]	1.35	0.86	1.85	<0.001
Observations	28			
R2 / R2 adjusted	0.638 / 0.609			

Table C6: Results of a multiple regression model estimating the average moose observed per road transect as a function of year and road section, with an interaction between year and road section.

		95% Confidence Interval		
Predictors	Estimates	Lower	Upper	p-value
(Intercept)	0	-0.04	0.04	1.000
Year [1st degree]	0	-0.46	0.46	1.000
Year [2nd degree]	0	-0.46	0.46	1.000
Section [Section 2]	0.06	0	0.11	0.046
Section [Section 3]	0.01	-0.04	0.07	0.713
Section [Section 4]	0.14	0.08	0.19	<0.001
Section [Section 5]	0.22	0.17	0.28	<0.001
Year [1st degree] * Section [2]	-0.66	-1.31	-0.01	0.048
Year [2nd degree] * Section [2]	0.41	-0.25	1.06	0.220
Year [1st degree] * Section [3]	-0.01	-0.66	0.64	0.976
Year [2nd degree] * Section [3]	0.07	-0.59	0.72	0.842
Year [1st degree] * Section [4]	0.77	0.11	1.42	0.022
Year [2nd degree] * Section [4]	1	0.35	1.65	0.003
Year [1st degree] * Section [5]	-1.91	-2.57	-1.26	<0.001
Year [2nd degree] * Section [5]	1.56	0.9	2.21	<0.001
Observations	140			
R2 / R2 adjusted	0.661 / 0.623			

Table C7: Results of the multiple linear regression model that estimates willow height as a function of year for each sampling location and willow species. "Geyer" is the indicator variable for the species*year interaction terms, and "Slough Creek Cabin" is the indicator variable for the location*year interaction terms.

			95% Confidence Interval		
Predictors	Estimates	SE	Lower	Upper	P-value
(Intercept)	-19274.9	604.24	-20459.56	-18090.24	<0.001
Year	9.75	0.3	9.16	10.34	<0.001
Species [BEGL]	8514.07	1015.99	6522.15	10505.99	<0.001
Species [SABA]	6665.36	1155.04	4400.83	8929.88	<0.001
Species [SABO]	6896.23	731.12	5462.82	8329.63	<0.001
Species [SADR]	7463.33	764.32	5964.83	8961.82	<0.001
Species [SAFA]	7202.55	877.28	5482.59	8922.52	<0.001
Species [SAWO]	8284.01	809.94	6696.07	9871.94	<0.001
Location [Bannock]	9663.56	471.74	8738.68	10588.44	<0.001
Location [Lost Creek]	6182.84	601.93	5002.73	7362.96	<0.001
Location [Soda Butte]	8454.16	547.38	7380.98	9527.35	<0.001
Year * Species [BEGL]	-4.31	0.51	-5.3	-3.31	<0.001
Year * Species [SABA]	-3.38	0.58	-4.51	-2.25	<0.001
Year * Species [SABO]	-3.48	0.36	-4.19	-2.76	<0.001
Year * Species [SADR]	-3.76	0.38	-4.51	-3.01	<0.001
Year * Species [SAFA]	-3.66	0.44	-4.52	-2.8	<0.001
Year * Species [SAWO]	-4.2	0.4	-4.99	-3.41	<0.001
Year * Location [Bannock]	-4.85	0.24	-5.31	-4.39	<0.001
Year * Location [Lost Creek]	-3.12	0.3	-3.71	-2.53	<0.001
Year * Location [Soda Butte]	-4.22	0.27	-4.76	-3.69	<0.001
Observations	3955				
R2 / R2 adjusted	0.644 / 0.642				

Table C8: Results of a linear regression model estimating Fisher Creek willow height (cm) over time (1987-2021).

		95% Confidence Interval		
Predictors	Estimates	Lower	Upper	p-value
(Intercept)	-217.77	-529.35	93.81	0.17
Year	0.16	0.01	0.32	0.043
Observations	780			

Table C9: Results of a multiple linear regression model that estimates moose browsing (%twigs browsed) as a function of year for each location and willow species. "Geyer" is the indicator variable for the species*year interaction terms, and "Slough Creek Cabin" is the indicator variable for the location*year interaction terms.

			95% Confidence Interval		
Predictors	Estimates	SE	Lower	Upper	p-value
(Intercept)	2518.75	161.97	2201.19	2836.31	<0.001
Year	-1.25	0.08	-1.41	-1.09	<0.001
Species [BEGL]	-1051.24	272.35	-1585.19	-517.28	<0.001
Species [SABA]	-321.93	309.62	-928.96	285.1	0.299
Species [SABO]	-433.59	195.98	-817.83	-49.35	0.027
Species [SADR]	-519.66	204.88	-921.35	-117.97	0.011
Species [SAFA]	-1460.64	235.16	-1921.7	-999.59	<0.001
Species [SAWO]	-639.45	217.11	-1065.11	-213.78	0.003
Location [Bannock]	731.85	126.46	483.92	979.77	<0.001
Location [Lost Creek]	-304.38	161.35	-620.73	11.96	0.059
Location [Soda Butte]	346.87	146.73	59.19	634.55	0.018
Year * Species [BEGL]	0.52	0.14	0.26	0.79	<0.001
Year * Species [SABA]	0.16	0.15	-0.14	0.46	0.298
Year * Species [SABO]	0.22	0.1	0.03	0.41	0.027
Year * Species [SADR]	0.26	0.1	0.06	0.46	0.011
Year * Species [SAFA]	0.73	0.12	0.5	0.96	<0.001
Year * Species [SAWO]	0.32	0.11	0.11	0.53	0.003
Year * Location [Bannock]	-0.36	0.06	-0.48	-0.24	<0.001
Year * Location [Lost Creek]	0.15	0.08	-0.01	0.31	0.062
Year * Location [Soda Butte]	-0.17	0.07	-0.31	-0.03	0.02
Observations	3955				
R2 / R2 adjusted	0.442 / 0.439				

Table C10: Results of a linear regression that estimates moose browsing (%twigs browsed) for Fisher Creek over time (1987-2021).

		95% Confidence Interval		
Predictors	Estimates	Lower	Upper	p-value
(Intercept)	5.41	-22.09	32.91	0.7
Year	0	-0.02	0.01	0.731
Observations	780			

Table C11: Results of a multiple linear regression model that estimates willow height (cm) as a function of moose browsing (%twigs browsed), willow species, and sampling location, and interactions between browsing and species, and browsing and location. The indicator variable for willow species is "Geyer", and the indicator variable for location is "Slough Creek Cabin".

Predictors	Estimates	95% CI Lower	Upper	p-value
(Intercept)	311.27	303.58	318.97	<0.001
Browsing	-4.09	-4.47	-3.7	<0.001
Species BEGL	-145.71	-160.39	-131.02	<0.001
Species SABA	-139.73	-155.83	-123.63	<0.001
Species SABO	-88.05	-97.51	-78.6	<0.001
Species SADR	-98.19	-108.23	-88.15	<0.001
Species SAFA	-158.35	-170.35	-146.35	<0.001
Species SAWO	-159.98	-170.82	-149.14	<0.001
Location Bannock	-73.7	-80.47	-66.93	<0.001
Location Lost Creek	-80.62	-88.66	-72.58	<0.001
Location Soda Butte	-21.24	-28.88	-13.59	<0.001
PctBrowsed * BEGL	2.22	1.58	2.85	<0.001
PctBrowsed * SABA	2.14	1.38	2.89	<0.001
PctBrowsed * SABO	1.91	1.44	2.38	<0.001
PctBrowsed * SADR	2.11	1.63	2.58	<0.001
PctBrowsed * SAFA	2.04	1.42	2.66	<0.001
PctBrowsed * SAWO	1.96	1.44	2.47	<0.001
PctBrowsed * Bannock	1.89	1.6	2.18	<0.001
PctBrowsed * Lost Creek	0.86	0.42	1.3	<0.001
PctBrowsed * Soda Butte	1.36	0.99	1.72	<0.001
Observations	3955			
R2 / R2 adjusted	0.517 / 0.514			

Table C12: Results of a linear regression model estimating willow height (cm) as a function of moose browsing (%twigs browsed) at Fisher Creek.

Predictors	Estimates	95% Confidence Interval Lower	Upper	p
(Intercept)	104.41	102.8	106.01	<0.001
PctBrowsed	-0.44	-1.24	0.36	0.283
Observations	780			

Table C13: Results of a two-way ANOVA comparing average willow height in and out of the Slough Creek exclosure among and between years.

Parameter	df	Sum sq	Mean sq	F value	p-value
In/Out	1	20296	20296	29.783	1.24e-06
Year	8	527712	65964	96.797	< 2e-16
In/Out:Year	8	42162	5270	7.734	7.58e-07

Table C14: Results of a two-way ANOVA comparing average willow canopy cover in and out of the Slough Creek exclosure among and between years.

Parameter	df	Sum sq	Mean sq	F value	p-value
In/Out	1	1248	1248	18.299	7.76e-05
Year	8	41815	5227	76.667	< 2e-16
In/Out:Year	8	5059	632	9.276	6.18e-08

Table C15: Results of a linear regression model estimating average browsing pressure (% twigs browsed) as a function of moose relative abundance (average moose observed per day) in the southern Absaroka-Beartooth Wilderness.

			95% Confidence Interval		
Predictors	Estimates	std. Error	Lower	Upper	p
(Intercept)	6.82	1.64	3.43	10.21	<0.001
Moose/Day	20.35	2.59	14.98	25.71	<0.001
Observations	25				
R2 / R2 adjusted	0.728 / 0.716				

Table C16: Results of a linear regression model estimating average willow height (cm) as a function of moose relative abundance (average number of moose observed per day) in the Southern Absaroka-Beartooth Wilderness.

			95% Confidence Interval		
Predictors	Estimates	std. Error	Lower	Upper	p
(Intercept)	165.05	6.26	152.11	177.99	<0.001
Moose/Day	-39.95	9.91	-60.45	-19.46	0.001
Observations	25				
R2 / R2 adjusted	0.414 / 0.389				

APPENDIX D

POST-HOC TESTS

Table D1: Estimated marginal mean slopes of beaver colony numbers from 1986-2020 in the 13 southern Absaroka-Beartooth Wilderness study area.

Meadow	Year trend	SE	df	p-value
Beaver	0.0190	0.0246	299	0.4396
Bull Moose	0.0456	0.0246	299	0.0651
Christenson’s	0.2283	0.0246	299	<.0001
East Fork	0.0359	0.0246	299	0.1457
Elk	0.0320	0.0246	299	0.1939
Frenchy	0.3259	0.0246	299	<.0001
Grizzly	0.0670	0.0246	299	0.0069
Hart’s	0.0286	0.0246	299	0.2459
Hellroaring	0.2766	0.0246	299	<.0001
Holeman’s	0.1584	0.0246	299	<.0001
Lake Abundance	0.0266	0.0246	299	0.2797
Lake Creek	0.0339	0.0246	299	0.1690
Stillwater	0.1143	0.0246	299	<.0001

Table D2: Estimated marginal mean slopes for average willow canopy trends over time (1981-2019) for each southern Absaroka-Beartooth Wilderness study meadow.

Meadow	Year trend	SE	df	p-value
Beaver	0.561	0.0969	39	<.0001
Bull Moose	0.381	0.0969	39	0.0003
Christenson’s	0.459	0.0969	39	<.0001
East Fork	0.792	0.0969	39	<.0001
Elk	0.653	0.0969	39	<.0001
Frenchy	0.862	0.0969	39	<.0001
Grizzly	0.315	0.0969	39	0.0024
Harts	0.282	0.0969	39	0.0060
Hellroaring	0.672	0.0969	39	<.0001
Holeman’s	0.393	0.0969	39	0.0002
Lake Abundance	0.391	0.0969	39	0.0002
Lake Creek	1.043	0.0969	39	<.0001
Stillwater	0.581	0.0969	39	<.0001

Table D3: Results of an estimated marginal means test for significant change over time (1987-2021) of average moose observed per transect within each road section.

Road Section	Slope	df	p-value
Section 1	0.000000	125	1.0000
Section 2	-0.003903	125	0.0525
Section 3	0.000134	125	0.9466
Section 4	0.009276	125	<.0001
Section 5	-0.010103	125	<.0001

Table D4: Results of an estimated marginal means test comparing differences in trends of average moose observed per transect over time (1987-2021) for each road section.

Contrasts	Estimate	df	p-value
Section 1 - Section 2	0.003903	125	0.6390
Section 1 - Section 3	-0.000134	125	1.0000
Section 1 - Section 4	-0.009276	125	0.0112
Section 1 - Section 5	0.010103	125	0.0043
Section 2 - Section 3	-0.004036	125	0.6086
Section 2 - Section 4	-0.013178	125	0.0001
Section 2 - Section 5	0.006201	125	0.1869
Section 3 - Section 4	-0.009142	125	0.0130
Section 3 - Section 5	0.010237	125	0.0037
Section 4 - Section 5	0.019379	125	<.0001

Table D5: Estimated marginal means (slopes) of willow height from 1987-2021 for each sampling location (Slough Cr Cabin, Bannock, Lost Creek, and Soda Butte).

Location	Year Trend	SE	df	p-value
Slough Cr Cabin	6.49	0.189	3935	<0.0001
Bannock	1.65	0.155	3935	<0.0001
Lost Creek	3.38	0.266	3935	<0.0001
Soda Butte	2.27	0.190	3935	<0.0001

Table D6: Estimated marginal mean slopes of willow height over time (1987-2021) for 6 willow and 1 birch species (Geyer, Barclay, Booth, Drummond, Farr, Wolf, and Bog Birch).

Species	Year Trend	SE	df	p-value
SAGE	6.70	0.342	3935	<0.0001
BEGL	2.40	0.361	3935	<0.0001
SABA	3.32	0.443	3935	<0.0001
SABO	3.23	0.134	3935	<0.0001
SADR	2.94	0.189	3935	<0.0001
SAFA	3.04	0.246	3935	<0.0001
SAWO	2.50	0.224	3935	<0.0001

Table D7: Estimated marginal mean slopes of moose browsing (%twigs browsed) from 1987-2021 for each sampling location (Slough Cr Cabin, Bannock, Lost Creek, and Soda Butte).

Location	Year Trend	SE	df	p-value
Bannock	-1.297	0.0414	3935	<0.0001
Lost Creek	-0.786	0.0713	3935	<0.0001
Slough Cr Cabin	-0.936	0.0506	3935	<0.0001
Soda Butte	-1.107	0.0509	3935	<0.0001

Table D8: Estimated marginal mean slopes of moose browsing (%twigs browsed) from 1987-2021 for 6 willow and 1 birch species (Geyer, Barclay, Booth, Drummond, Farr, Wolf, and Bog Birch).

Species	Year Trend	SE	df	p-value
BEGL	-0.824	0.0966	3935	<0.0001
SABA	-1.186	0.1188	3935	<0.0001
SABO	-1.130	0.0359	3935	<0.0001
SADR	-1.087	0.0507	3935	<0.0001
SAFA	-0.621	0.0658	3935	<0.0001
SAGE	-1.347	0.0917	3935	<0.0001
SAWO	-1.028	0.0599	3935	<0.0001

Table D9: Estimated marginal mean trends of average willow height as a function of browsing for each location.

Location	Trend	SE	df	p-value
Bannock	-0.435	0.0999	3935	<0.0001
Lost Creek	-1.462	0.2050	3935	<0.0001
Slough Cr Cabin	-2.322	0.1249	3935	<0.0001
Soda Butte	-0.965	0.1318	3935	<0.0001

Table D10: Pairwise comparison of estimated marginal means of browsing effects on willow height (cm) for each location.

Pairwise Comparisons (location)	Estimate	SE	df	p-value
Bannock - Lost Creek	1.027	0.209	3935	<0.0001
Bannock - Slough Cr Cabin	1.887	0.148	3935	<0.0001
Bannock - Soda Butte	0.530	0.163	3935	0.0064
Lost Creek - Slough Cr Cabin	0.859	0.225	3935	0.0008
Lost Creek - Soda Butte	-0.497	0.237	3935	0.1552
Slough Cr Cabin - Soda Butte	-1.356	0.185	3935	<0.0001

Table D11: Estimated marginal means of willow height (cm) as a function of browsing pressure (% twigs browsed) for each willow species.

Species	Trend	SE	df	p-value
BEGL	-0.847	0.2302	3935	0.0002
SABA	-0.927	0.3015	3935	0.0021
SABO	-1.150	0.0865	3935	<.0001
SADR	-0.957	0.1217	3935	<.0001
SAFA	-1.023	0.2094	3935	<.0001
SAGE	-3.063	0.2251	3935	<.0001
SAWO	-1.106	0.1518	3935	<.0001

Table D12: Pairwise comparison of estimated marginal means of willow height as a function of browsing pressure for each willow species.

Pairwise Comparisons (Species)	Estimate	SE	df	p-value
BEGL - SABA	0.0795	0.384	3935	1.0000
BEGL - SABO	0.3032	0.237	3935	0.8608
BEGL - SADR	0.1096	0.250	3935	0.9995
BEGL - SAFA	0.1753	0.302	3935	0.9973
BEGL - SAGE	2.2159	0.324	3935	<.0001
BEGL - SAWO	0.2584	0.260	3935	0.9555
SABA - SABO	0.2237	0.314	3935	0.9920
SABA - SADR	0.0301	0.322	3935	1.0000
SABA - SAFA	0.0957	0.347	3935	1.0000
SABA - SAGE	2.1363	0.386	3935	<.0001
SABA - SAWO	0.1788	0.346	3935	0.9986
SABO - SADR	-0.1936	0.141	3935	0.8178
SABO - SAFA	-0.1279	0.223	3935	0.9975
SABO - SAGE	1.9127	0.239	3935	<.0001
SABO - SAWO	-0.0448	0.166	3935	1.0000
SADR - SAFA	0.0657	0.235	3935	1.0000
SADR - SAGE	2.1063	0.244	3935	<.0001
SADR - SAWO	0.1488	0.185	3935	0.9845
SAFA - SAGE	2.0406	0.315	3935	<.0001
SAFA - SAWO	0.0831	0.257	3935	0.9999
SAGE - SAWO	-1.9575	0.264	3935	<.0001

APPENDIX E

PHOTOGRAPHS OF THE SLOUGH CREEK EXCLOSURE

Figure E1: Exclosure camera point 1; 1962. Photo: USFS historic files.

Figure E2: Exclosure camera point 1; 1986. Photo: Steve Chadde, Charles Kay (1986)

Figure E3: Exclosure camera point 1; 2009. Photo: Dan Tyers, USFS

Figure E4: Exclosure camera point 1; 2020

Figure E5: Exclosure camera point 3; 1962. Photo: USFS Historic Files

Figure E6: Exclosure camera point 3; 1986. Photo: Steve Chadde, Charles Kay (1986)

Figure E7: Exclosure camera point 3; 2009. Photo: Dan Tyers, USFS

Figure E8: Exclosure camera point 3; 2020