2016

Spatio-Temporal Analysis of Ungulate Browsing on Willow (Salix spp.) Communities Within the Northern Range of Yellowstone

Donald L. Belile Jr.

Recommended Citation

Belile, Donald L. Jr., "Spatio-Temporal Analysis of Ungulate Browsing on Willow (Salix spp.) Communities Within the Northern Range of Yellowstone" (2016). *Graduate Student Theses, Dissertations, & Professional Papers*. 10665.
https://scholarworks.umt.edu/etd/10665

SPATIO-TEMPORAL ANALYSIS OF UNGULATE BROWSING ON WILLOW (*Salix* spp.) COMMUNITIES WITHIN THE NORTHERN RANGE OF YELLOWSTONE

By

DONALD LEE BELILE JR.

B.S. Environmental Science, Oglala Lakota College, Kyle, SD, 2010

Thesis Proposal

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Systems Ecology Intercollegiate Program

The University of Montana
Missoula, MT

05/13/2016

Scott Whittenburg, Dean of Graduate School

H. Maurice Valett, Chair
Division of Biological Sciences

Aaron Thomas
Associate Professor of Chemistry

Brady Allred
Assistant Professor of Rangeland Ecology

Table of Contents

Belile, Donald, M.S., Spring 2016 Systems Ecology Intercollegiate Program

“Spatio-Temporal Analysis of Ungulate Browsing on Willow (*Salix* spp.) Communities Within the Northern Range of Yellowstone”

Dr. H. Maurice Valett

ABSTRACT

Spatial and temporal variation in ungulate browsing intensity on willow (*Salix* spp.) communities across Yellowstone’s northern range has been attributed to various biophysical factors including annual cumulative snow depth, elk (*Cervus canadensis*) density, elevation, forage availability, gray wolf (*Canis lupus*) reintroduction, landscape characteristics, and bison (*Bison bison*) browsing and interspecific competition with elk. Past studies have been conducted without a long-term browsing dataset, spatially extensive sampling design, nor inclusion of fine-scale snow characteristics known to affect ungulate mobility, habitat selection, and foraging strategies. This study focused on snow because of its ecological importance and because previous studies have largely failed to include relevant snow characteristics. We applied a non-destructive sampling method by consecutively recording whether stem leaders were browsed between terminal growth scars in order to reconstruct annual winter browsing intensity from 1995 through 2014 with measurements made on an average of 66 plots that spanned Yellowstone’s northern range. I grouped localized sample plots into range units specified as a random effect within a generalized linear mixed model (GLMM). In order to conduct a plot-level analysis of winter browsing intensity, estimates of snow characterisitics (depth, density, and snow water equivalent), were created for January – March of each winter. Snow water equivalents (SWE) at 1-km were derived from two estimates of SWE; 1995-2003 from Daymet and 2004-2014 from SNODAS, and two estimates of 1-km snow depth were derived; 1995-2003 from interpolated NR weather station measurements and 2004-2014 from SNODAS. I downscaled these 1-km estimates based on coefficients derived from ground measurements of snow depth and SWE, which I evaluated as responses to elevation, aspect, and land-cover in generalized linear models. Terrain slope was the only topographic parameter included in GLMM analysis because elevation and aspect were used to generate snow characteristic estimates. I also included annual growing season precipitation from May-July to examine the effect of climate prior to winter browsing. I selected the best best-fit model with the lowest, second order AIC within a hierarchical multi-model structure. The best-fit GLMM identified March snow depth as negatively associated with browsing and singularly the most influential variable on the probability of browsing. Results also showed a negative association between browsing probability and March snow density, a negative association between browsing and terrain slope, and a positive association between browsing and the magnitude of precipitation during the past growing season. In past studies, many have argued for the primacy of top-down influences (predation, fear induced behavioral change), our work suggests that bottom-up forces including the spatial and temporal distribution of snow and its characteristics may be primary determinants of browsing intensity on willow communities across the northern range of Yellowstone.

KEY WORDS

browsing, GLMM, riparian, snow characteristics, topography, willow

CHAPTER 1

History of ungulate browsing

Research is conducted on more natural, functioning ecosystems like Yellowstone National Park’s northern range (NR) in an effort to isolate or remove human impacts. In order to conserve and protect an ecologically intact system, scientists also seek to obtain a deeper understanding of complex issues. This introduction chapter serves to familiarize non-specialist and the public with issues surrounding this thesis topic. In that sense, a holistic philosophy of science may help to understand the background of ungulate browsing on willow (*Salix* spp.) within Yellowstone's northern elk (*Cervus canadensis*) and bison (*Bison bison*) range.

This controversial issue is rooted in a complex history, so a brief historical review is necessary to understand the full context. Since the declaration of The Organic Act of 1916, the NR ecosystem has experienced human-derived change (NPS 2014). Prior to 1930, elk husbandry included winter-feeding and predator control, as a result grey wolves were eliminated by 1930. Following the extirpation of wolves, ungulate populations increased and fear of range deterioration encouraged culling by park officials. By 1960, the elk population was reduced by approximately 75% to approximately 4,000 animals (Eberhardt et al. 2005). Public and political concerns led to the initiation of the Natural Regulation Act of 1969, i.e., allow nature to take its course. In theory, the amount of available forage accessible during winter would provide density control of elk herd size (Singer et al. 1998; Cook et al. 2004; Vucetich et al. 2005). In addition to off-take by carnivores, namely grizzly bears (*Ursus acrtos*), annual elk hunting permits on public and private lands within the northwestern NR outside Yellowstone, also helped keep elk numbers in check (Coughenour and Singer 1996; Smith et al. 2003). Even with these controls, elk numbers continued to escalate until the winter of 1996-1997 when low May-July precipitation, severe weather, gray wolves (*Canis lupus*), and hunter harvest caused a dramatic decline (Fig. 1; Vucetich et al. 2005; Wyman 2013). Additionally, increased bear predation of elk calves and the 100-yr drought that occurred from 2000-2004 have been suggested as factors contributing to the continued elk population decline (Middleton et al. 2013). Hypothetically lower elk numbers have translated to lower browsing intensity in some areas, resulting in taller and thicker willow communities (Ripple et al. 2010).

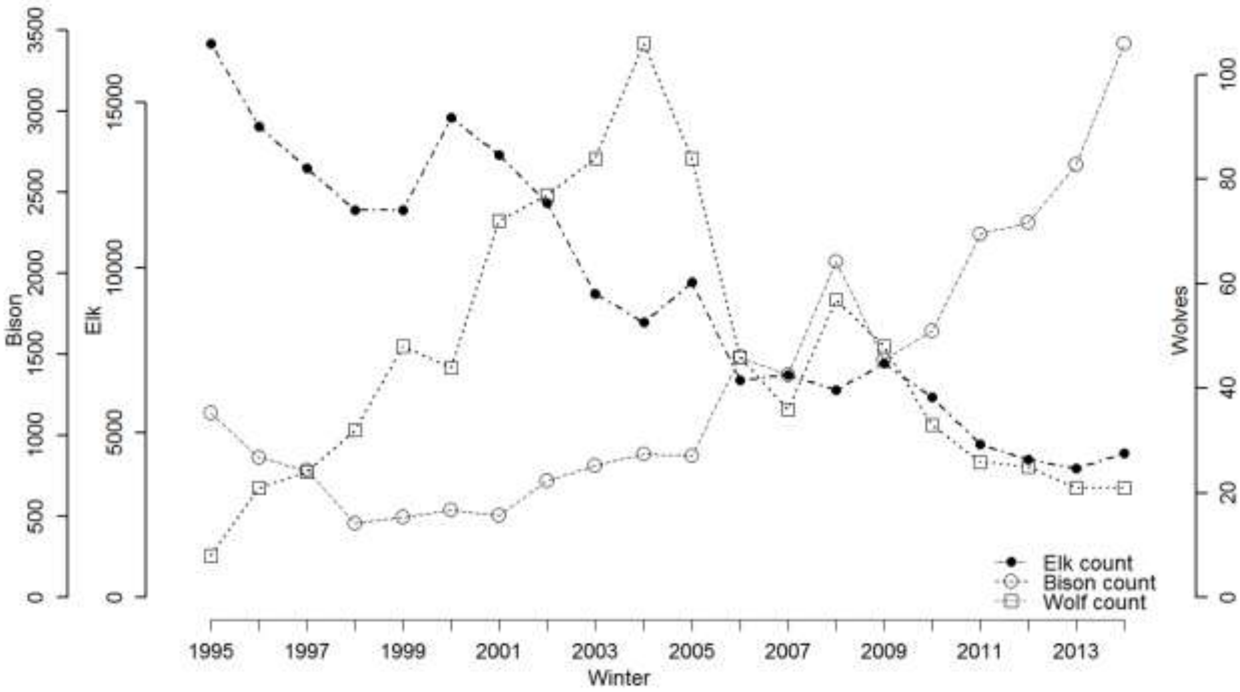

Figure 1: Yellowstone's northern range elk, bison and wolf (yearling to adult age) populations[1] per winter 1995-2014.

[1]Counts obtained through the Yellowstone Center for Resources, Yellowstone National Park (Smith et al. 1995-2014; Blanton 2013; Wyman 2013; [NPS] 2015). Simple imputation was used to estimate the 1996, 1997, and 2014 elk population count (Belile thesis 2016). Note that wolves were not re-introduced to Yellowstone's northern range until mid to late March 1995.

Impact on riparian communities

Research has shown that browsing or herbivory of woody vegetation, can impair growth and reproduction of shrubbery and shrub sized trees (Putman et al. 1989). However, this natural process can also benefit production depending on the timing and browsing intensity, though the balance varies for different browse species under varying water levels (Lay 1965).

When riparian plants are consumed as forage, analysis of elk stomach contents reveals that willow accounted for up to 92% of the riparian vegetation eaten on the NR in the Gallatin Canyon (Creel and Christianson 2009) during winter 2004-2006. Generally, opportunistic elk will browse to supplement their diet especially during the winter season, though they prefer to eat grasses and forbs (Hobbs et al. 1981; Singer et al. 1994). Greater nutrient content of grasses and forbs makes them more desirable than woody browse, such that 83% of the elk winter diet consisted of grasses and forbs, whereas only 8% was sagebrush and woody riparian browse (Singer and Norland 1994).

Willow, the most common woody riparian plant on the NR, is common in riparian zones across the Northern Rocky Mountain Region. Although willows are the dominant woody riparian species, they make up a relatively small portion of the NR vegetation – approximately <1% of vegetation cover ([CUMYNP]; Singer et al. 1994). Though small in extent, these riparian areas provide habitat for birds and other wildlife, maintain bank stability, and sustain nutrient cycles (Berger et al. 2001; Naiman and Decamps 1997). Willow species richness and abundance is interconnected with beaver, which depend on woody riparian vegetation for dam construction and are ecologically indicative of healthy streams. Beaver dam construction alters hydrology, energy flow, and nutrient cycling thereby facilitating species richness (Marshall et al. 2013; Hood and Larson 2014). As with beaver absences in previously occupied NR habitats, willow phenology can be used as an indicator of riparian disturbance ([CUMYNP]; Engstrom et al. 1991; Kay 1997).

Chadde and Kay (1998) reviewed historical photographs of NR willow communities within and outside of ungulate exclosures constructed by the National Park Service. Their photographic review and physical observation of NR willow along transects indicated declines in tall willow communities. Kay (1997) estimated a 95% decline in willow communities with plant heights greater than 2 m since Yellowstone's establishment. A more traditional scientific study was conducted over three summers and four winters, which reported similarly dramatic willow height suppression and lack of recruitment (Singer et al. 1994).

Elk survival and environmental conditions

Coughenour and Singer (1996) investigated the spatial distribution, mortality rates and foraging patterns of elk in response to seasonal weather variables. They discussed the limiting effect of interannual cumulative snow depth on forage availability and elk migrations. Spatial structuring of elk herd densities was hypothesized to follow snow depth, snow crusting, and food availability. They surmised that elk survival was contingent on forage availability and accessibility during summer and winter, i.e., unmet nutritional needs during dry growing seasons in conjunction with deep snow likely induced winter die-offs. Elk herd distributions and snow depth across the NR are primarily dependent on topography (Mao et al. 2005), and willow generally grows in low-lying riparian corridors where there is access to ground water (Chadde and Kay 1998; Bilyeu et al. 2008). This increases the likelihood of browsing on willow and other woody riparian browse species with potential nutritional value.

Wolves and bison as explanatory variables

Where do wolves fit in with woody riparian vegetation? Elevated elk populations in the early 1990's were attributed to ceased culling and the long-term absence of the gray wolf (Singer et al. 1994; Coughenour and Singer 1996). A behaviorally mediated trophic cascade (BMTC) occurs when a predator causes foraging prey to avoid certain areas and provides an opportunity for vegetation to recover (Shmitz et al. 1997). This type of BMTC was hypothesized to occur on the NR involving wolves, elk, and woody riparian vegetation (Ripple and Beschta 2006). After wolves were reintroduced to Yellowstone's NR during the winter of 1995 and 1996, Ripple and Beschta (2004) proposed an 'ecology of fear' brought on by wolf presence. In their view, physical landscape characteristics, e.g., downed trees, steep banks, and gullies could deter elk from browsing due to fear of predation by wolves. Obstacles impede escape from wolves and thereby are conducive to willow growth. They also proposed the likelihood of the obstacles' inherent function as a natural fence to elk, providing the opportunity for willow to attain release height (≥ 2 m). Kauffman et al. (2010) tested this theory by comparing demographic data collected from NR enclosed aspen (*Populus tremuloides*) stands and stands unprotected from browsing. According to their findings, the number of elk on the NR had greater bearing on aspen recovery than either climate or wolves.

Willow, like aspen, has reportedly recovered since introduction of wolf predators in multiple locations within the Yellowstone NR including places along Blacktail Deer Creek and the Lamar River (Ripple and Beschta 2006). However, recent research suggests that recovery is related to direct predation by wolves on elk rather than via a BMTC (Middleton et al. 2013). The importance of elk hunter harvest was emphasized as another factor influencing elk herd size by Vucetich et al. (2005). They modeled elk annual population growth rate in response to interannual elk abundance, intraannual hunter harvest, cumulative annual snowfall, SWE, minimum winter temperature, maximum summer temperature, July precipitation, and annual precipitation. Their analysis of elk population dynamics both pre and post wolf reintroduction in March 1995 identified elk abundance, late winter harvest, annual snowfall, and annual precipitation as the most significant variables affecting elk herd size, suggesting that wolf predation is compensatory alongside more proximate causes (Vucetich et al. 2005).

According to Ripple et al. (2010), interspecific forage competition between elk and bison has likely led to increased browsing on willow. Although bison are predominately grazers, Ripple et al. (2010) suggest that bison both directly browse on woody riparian species and likely cause an indirect effect brought on by interspecific forage competition with elk. Research suggests that wood bison (*Bison athabascae*) will reduce energy expenditure and consume poor quality forage when it is readily available in large quantity (Bergman et al. 2001). Yellowstone bison diet was found to consist of primarily sedges with lesser amounts of rushes and grasses (Meagher 1973). However, in the summer of 2009 Ripple et al. (2010) reported that 87% of willows below 1 m high (reachable height for bison) were browsed at the confluence of Soda Butte Creek and the Lamar River. Painter and Ripple (2012) returned to the Soda Butte and Lamar confluence in summer 2010 and reported that 88% of sampled willow stems less than 1 m high were browsed.

Justification

Despite the emphasis placed on weather to understand ungulate population processes, (Coughenour and Singer 1996; Vucetich et al. 2005), snow depth and snow density have been ignored as factors affecting browsing intensity on willow across the NR. The BMTC hypothesis is further confounded by research of Creel and Christianson (2009) who found that NR browsing increased even in wolf presence when snow was deep and compact, and the effect of snow conditions was stronger than wolf presence. Snow characteristics affect large ungulate habitat selection, forage availability, movement, herd size, and habitat space use (Hobbs et al. 1981; Parker et al. 1984; Delgiudice et al. 2001; Vucetich et al. 2005; Tefler and Kelsall 1984; Kittle et al. 2008, Richard et al. 2014). Parker et al. (1984) studied the energy cost of locomotion for elk in various snow conditions and sloping terrain. They found that both snow depth and snow density limited elk movement by causing increased oxygen intake and energetic expenditure. When snow depth was higher than front knee height the energetic expense of locomotion increased radically. They found that although elk can move when snow depth is as high as their brisket, they must move in leaping gaits. Under these conditions, velocity decreases and the energetic cost increases. Likewise, vertical ascension is inversely correlated with velocity, and elk spend more energy ascending steeper terrain (Parker et al. 1984).

Marshall et al. (2014) considered willow growth and recruitment over time in response to climate, topography, and annual elk population counts. They utilized growth rings of segmented root crowns as dependent variables in a pair of 30-yr spatio-temporal models. According to their analysis, the best model for determining willow establishment included both elk numbers and biophysical factors. Their Bayesian statistical analysis used segmented willow stems as the dependent variable and identified significant effects on growth from elk abundance, hydrology, topography, growing degree-days, and plant age. In their study elk population counts were used as a proxy for top-down trophic effects because they did not directly measure browsing.

Ecosystem dynamics and interactions are complex and multi-dimensional resulting in numerous studies of NR willow and much controversy surrounding the reason for willow recovery. We can hypothesize relationships between elk, wolves, bison, climate, topography, and anthropogenic impacts without narrowing our reasoning. All of these relationships are part of a dynamic system with differential components acting together to determine the intensity of elk browsing on willow. Ripple and Beschta (2006) were not wrong to recognize a possible BMTC effect of wolves on elk foraging patterns and behavior, however, attributing the recovery of willow communities to wolves without considering the bottom-up effects of climate (Robbins 2004; Post et al. 2009) is a problem requiring consideration.

General study design and objectives

Prior to and since wolf reintroduction, studies of browsing on willow were either limited by lack of spatially balanced sampling, failure to include potentially significant variables, or use of auxiliary information to estimate change in, and causes of, riparian shrub herbivory (Singer et al.

1994; Kay 1997; Creel and Christianson 2009; Ripple et al. 2010; Marshall et al. 2014). Accordingly, this research utilized a spatially balanced sample design, investigated effects of interannual and intraannual winter snow conditions and growing season precipitation, and a direct browsing history spanning winters 1995-2014.

We enhanced our spatial understanding of the NR browsing intensity by considering topographic and climatic effects. I included slope but omitted elevation and aspect as covariates because they were used to build spatially explicit and properly scaled measures of snow depth and SWE (i.e., 30-m snow depth model and 10-m SWE model). Accordingly, I investigated the interannual and intraannual variation in winter and summer precipitation events (Vucetich et al. 2005; Marshall et al. 2014). Moreover, winter and summer temperatures were omitted from my analysis because temperature is a covariate included within the Daymet algorithm for SWE and precipitation (Thornton et al. 2014) and within the SNODAS algorithm for SWE and snow depth (NOHRSC 2004).

We recognize the interconnectedness of factors affecting winter browsing and initially intended to include elk, bison, and wolf population counts along with climatic and topographic covariates in order to understand variation in ungulate herbivory on willow communities over space and time. However, because we lacked plot-level spatial resolution of NR elk, bison, and wolf annual population counts, I could not include them with fine scale climatic and topographic variables in my generalized linear mixed model (GLMM) addressing spatially explicit patterns of riparian browsing. Therefore, the focus of my GLMM was the spatial and temporal variation in browsing accounted for by snow characteristics, growing season precipitation, and topography within a random effect, range unit, where a range unit is a combination of sample plots grouped by spatial proximity within the NR.

LITERATURE CITED

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson, 2001. A Mammalian Predator-Prey Imbalance: Grizzly Bear and Wolf Extinction Affect Avian Neotropical Migrants. Ecological Applications 11(4):947-960.

Bergman, C. M., J. M. Fryxell, C. Cormack Gates, and D. Fortin, 2001. Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology 70:289-300.

Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs, 2008. Water Tables Constrain Height Recovery of Willow on Yellowstone's Northern Range. Ecological Applications 18(1):80-92.

Blanton, D., 2013. MEMORANDUM: Abundance and Distribution of Yellowstone Bison.Yellowstone Center for Resources.

Chadde, S. W. and C. E. Kay, 1998. Tall-willow Communities on Yellowstone's Northern Range: A Test of the "Natural Regulation" Paradigm; The Greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press. Chapter 16:231-262.

Creel, S. and D. Christianson, 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. Ecological Society of America 90(9): 2454-2466.

Cook, R. C., J. G. Cook, and L. D. Mech, 2004. Nutritional Condition of Northern Yellowstone Elk. Journal of Mammalogy 85(4):714-722.

Coughenour, M. B. and F. J. Singer, 1996. Elk Population Processes in Yellowstone National Park Under the Policy of Natural Regulation. Ecological Applications 6 (2): 573-593.

[CUMYNP] Committee on Ungulate Management in Yellowstone National Park, 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academy of Sciences.

Delgiudice, G. D., R. A. Moen, F. J. Singer, and M. R. Riggs, 2001. Winter Nutritional Restriction and Simulated Body Condition of Yellowstone Elk and Bison before and after the Fires of 1988. Wildlife Monographs 147:1-60.

Eberhardt, L. L., P. J. White, R. A. Garrot, and D. B. Houston, 2007. A Seventy-Year History of Trends in Yellowstone's Northern Elk Herd. The Journal of Wildlife Management 71 (2):594-602.

Engstrom, D. R., C. Whiloc,, S. C. Fritz, and H. E. Wright, Jr., 1991. Recent environmental changes inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology 5(2):139-174.

Hobbs, T. N., D. L. Baker, J. E. Ellis, and D. M. Swift. 1981. Composition and Quality of Elk Winter Diets in Colorado. The Journal of Wildlife Management 45:156-171.

Hood, G.A. and D.G. Larson, 2014. Beaver-Created Habitat Heterogeneity Influences Aquatic Invertebrate Assemblages in Boreal Canada. Wetlands 34:19-29.

Kauffman, M. J., J. F. Brodie, and E. S. Jules, 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91(9):2742-2755.

Kay, C. E., 1997. Viewpoint: Ungulate herbivory, willows, and political ecology in Yellowstone. Journal of Range Management 50:139-145.

Lay, D.W., 1965. Effects of Periodic Clipping on Yield of Some Common Browse Species. Journal of Range Management 18(4):181-184.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill, 2005. Habitat Selection by Elk before and after Wolf Reintroduction in Yellowstone National Park. The Journal of Wildlife Management 69(4):1691-1707.

Marshall, K. N., D. J. Copper, and N. Thompson Hobbs, 2014. Interactions among hervivory, climate, topography, and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. Journal of Ecology, Accepted 13-Feb-2014; doi: 10.1111/1365-2745.12225.

Marshall, K. N., N. Thompson Hobbs, and D. J. Cooper. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proc R Soc B 280: 20122977. Available at: http://dx.doi.org/10.1098/rspb.2012.2977. Accessed on 10 June 2015.

Meagher, M. M., 1973. The Bison of Yellowstone National Park, National Park Service, Scientific Monograph Series Number 1. Government Printing Office: Washington, DC.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking ani-preditor behavior to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Middleton, A. D., T. A. Morrison, J.K. Fortin, C.T. Robbins, K.M. Proffitt, P.J. White, D.E. McWhirter, T.M. Koel, D.G. Brimeyer, 2013.Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. Proc R Soc B 280: 20130870. Available at: http://dx.doi.org/10.1098/rspb.2013.0870. Accessed on 12 June 2015.

Naiman, J. R., and H. Décamps, 1997. The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics 28:621-658.

[NOHRSC] National Operational Hydrologic Remote Sensing Center, 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, [December-April snow depth and SWE winter 2004-2014]. Boulder, Colorado USA: National Snow and Ice Data Center. Available at URL [http://dx.doi.org/10.7265/N5TB14TC].

[NPS] National Park Service, 2014. Organic Act of 1916. Available at: http://www.nps.gov/grba/parkmgmt/organic-act-of-1916.htm. Accessed on 21 January 2014.

[NPS] National Park Service, 2014. Plants. Available at: http://www.nps.gov/yell/naturescience/plants.htm. Accessed on 21 January 2014.

[NPS] National Park Service, 2015. 2014-2015 Winter Count of Northern Yellowstone Elk. Plants. Available at URL [http://www.nps.gov/yell/naturescience/plants.htm]. Accessed on 6 January 2016.

Richard, J. H., J. Wilmshurst, and S. D. Cote, 2014. The effect of snow use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. Canadian Journal of Zoology. 92:1067-1074.

Painter, L. E. and W. J. Ripple, 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. Forest Ecology and Management 264:150-158.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy Expenditures for Locomotion by Mule Deer and Elk. The Journal of Wildlife Management. 48(2):474-488.

Post, E., et al. 2009. Global Population Dynamics and Hot Spots of Response to Climate Change. BioScience 59(6):489-497.

Putman, R. J., P. J. Edwards, J. C. E. Mann, R. C. How, and S. D. Hill, 1989. Vegetational and Faunal Changes in an Area of Heavily Grazed Woodland Following Relief of Grazing. Biological Conservation 47:13-32.

Ripple, W. J. and R. L. Beschta, 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. Forest Ecology and Management 200:161-181.

Ripple, W. J. and R. L. Beschta, 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96-106.

Ripple W. J., L. E. Painter, R. L. Beschta, and C. Cormack Gates. 2010. Wolves, Elk, Bison, and Secondary Trophic Cascades in Yellowstone National Park. The Open Ecology Journal 3:31-37.

Robbins, J., 2005. Hunting Habits of Wolves Change Ecological Balance in Yellowstone. The New York Times:Environment.

Shmitz, O. J., A. P. Beckerman, and K. M. O'Brien, 1997. Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions. Ecology 78(5): 1388-1399.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley, 1998. Thunder on the Yellowstone Revisited: An Assessment of Management of Native Ungulates. Natural Regulation Wildlife Society Bulletin 26(3):375-390.

Singer, F. J., J. E. Norland, 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. CAN. J. ZOOL. 72:1383-1394.

Singer, F. J., L. C. Mark, and R. C. Cates, 1994. Unglulate herbivory of willow on Yellowstone's northern winter range. Journal of Range Management 47:435-443.

Smith, D. W., R. O. Peterson, D. B. Houston. 2003. Yellowstone after wolves. BioScience 53(4):330-340.

Smith, D., et al. 1995-2014. Yellowstone National Park Wolf Project Annual Report 1995-2014. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR.

Telfer, E. S., J. P. Kelsall, 1984. Adaptation of Some Large North American Mammals for Survival In Snow. Ecology 65(6):1828-1834.

Vucetich, J. A., D. W. Smith, D. R. Stahler, and E. Ranta. 2005. Influence of Harvest, Climate and Wolf Predation on Yellowstone Elk, 1961-2004. Oikos 111(2):259-270.

Wyman, T., 2013. 2012-2013 Annual Winter Trend Count of Northern Yellowstone Elk. Yellowstone Center for Resources, Yellowstone National Park.

Thornton, P E., M. M. Thornton, B. W. Mayer, N. Wilhelmi, Y. Wei, R. Devarakonda, and R.B. Cook, 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. Date accessed: 2014/04/28. Temporal range: 1992/11/01-2013/12/31. Spatial range: N=45.03, S=44.78, E=-109.92, W=-110.861.

CHAPTER 2

Spatio-Temporal Analysis of Ungulate Browsing on Willow (*Salix* spp.) Communities Within the Northern Range of Yellowstone

Donald L. Belile[1], H. Maurice Valett[2]

Authors are [1]Graduate Student, [2]Professor The University of Montana, Missoula, MT 59801.

ABSTRACT

Variation in ungulate browsing intensity on willow (*Salix* spp.) communities across Yellowstone's northern range has been attributed to various biophysical factors including climate, topography, and predators. These studies were conducted without a long-term browsing dataset; they lacked a spatially extensive sampling design, and did not include dynamic snow characteristics known to affect ungulate mobility, habitat selection, and foraging strategies. We therefore focused on snow, an extreme landscape level disturbance that places nutritional stress on ungulates during the winter when most browsing on shrubs occurs. We applied a non-destructive sampling method by consecutively recording whether stem leaders were browsed between terminal growth scars in order to reconstruct annual winter browsing intensity from 1995 through 2014 with measurements made on an average of 66 plots that spanned Yellowstone's northern range. Our best-fit generalized linear mixed model selected according to lowest Akaike information criterion identified March snow depth as negatively associated with browsing and as the singularly most influential variable related to browsing intensity. Our model also included a negative association between browsing and March snow density, a negative association between browsing and terrain slope, and a positive association between browsing and the magnitude of precipitation during the past growing season. Past studies have argued for the primacy of top-down influences like predation and fear-induced behavioral change, our work suggests that bottom-up forces including the spatial and temporal distribution of snow and its characteristics are also strong determinants of browsing intensity on willow communities across Yellowstone's northern range.

KEY WORDS

browsing, GLMM, riparian, snow characteristics, topography, willow

Research was funded primarily by the Yellowstone Ecological Research Center with graduate student support from the Sloan Indigenous Graduate Program, Montana Institute on Ecosystems, Indigenous Research and STEM Education, Hopa Mountain Incorporated.

Correspondence: Donald Belile, Systems Ecology Intercollegiate Graduate Program, The University of Montana, Missoula, MT 59801, USA. Email: donald.belile@umontana.edu; dleebelile@gmail.com.

Current address: Donald Belile, The University of Montana 32 Campus Dr, Missoula, MT 59812.

INTRODUCTION

Elk (*Cervus canadensis*) browsing on willow (*Salix* spp.) communities within Yellowstone's northern range (NR) is a controversial topic and has subsequently motivated numerous studies with conflicting results. While it is clear that browsing has the potential to impair riparian habitat condition, a variety of factors has been identified as primary influences on the magnitude of ungulate browsing. Essentially the controversy surrounds whether top-down trophic cascades (Ripple and Beschta 2004) or bottom-up controls (Creel and Christianson 2009) drive the level of browsing intensity on willow communities on the NR. Riparian community distribution, height suppression, and regeneration have been studied in response to a number of variables including elk densities (Houston 1982; Singer et al. 1994; Marshall et al. 2014), water table elevation (Bilyeu et al. 2008; Johnston et al. 2009), gray wolf (*Canis lupus*) presence (Ripple and Beschta 2006; Middleton et al. 2013), beaver and stream hydrology (Marshall et al. 2013), climate (Singer et al. 1994), interspecific forage competition with other ungulates (Singer and Norland 1994), snowpack (Creel and Christianson 2009), and elevation and browsing pressure (Singer et al. 1994). Recent studies have also highlighted summertime bison (*Bison bison*) browsing on willow communities in the Lamar River valley and Soda Butte Creek confluence area (Ripple et al. 2010; Painter and Ripple 2012).

Prior to NR wolf reintroduction in March 1995, Singer et al. (1994) found a positive correlation between browsing pressure on willow communities and stand elevation. Generally, the tall willow stands were located at higher elevations and experienced less browsing. Leader consumption was greater in suppressed and marginally suppressed willow stands at lower elevations in flatter NR valley bottoms (Singer et al. 1994), which generally have greater densities of wintering ungulates (Bruggeman et al. 2007).

Following gray wolf reintroduction to the NR, partial recovery of willow communities was attributed to a top-down behaviorally mediated trophic cascade (BMTC) – when predators cause foraging prey to avoid certain areas and provide an opportunity for vegetation to recover (Shmitz et al. 1997). On the NR, a BMTC involving wolves, elk, and woody riparian vegetation was hypothesized to explain recovery of woody riparian communities (Ripple and Beschta 2004, 2005, 2006). Predation risk associated with landscape features possibly induced cottonwood (*Populus spp*.), aspen (*Populus tremuloides*), and willow recovery (Ripple and Beschta 2004). Ripple and Beschta (2005) extended the BMTC argument to account for interaction among riparian species including the effects of willow thicket protection of aspen recruitment following wolf reintroduction. Willow and aspen have recovered in some regions of the NR since wolf reintroduction (Ripple and Beschta 2006) and controversy remains about the extent and magnitude of recruitment and the recovery or “release” from browsing pressure and height suppression that is attributable to predator prey interactions.

More recent studies have challenged the BMTC explanation and have provided evidence indicating that factors other than wolves have contributed to willow community dynamics (Creel and Christianson 2009; Kauffman et al. 2010; Middleton et al. 2013, Marshall et al. 2013). For example, browsing was found to increase even in wolf presence when snow levels were deep and compact in the adjacent Gallatin Canyon, and the effect of snow conditions was stronger than wolf presence (Creel and Christianson 2009). Additional and alternate explanations exist for partial recovery of riparian shrubs in the NR (Robbins 2004).

Kauffman et al. (2010) tested the BMTC hypothesis by comparing demographic data collected from NR enclosed and unprotected aspen stands. They determined that the number of elk on the NR had greater bearing on aspen recovery than either climate or wolves (Fig. S1 available online at [insert URL here]). Moreover, they suggested that no aspen recovery had occurred in their NR study plots in contrast to the contentions of Ripple and Betscha (2006). Several studies that followed Kauffman et al. (2010) have suggested a more likely relationship between woody riparian species recovery and reduced elk populations rather than via a BMTC (Middleton et al. 2013). In a related manner, the importance of elk hunter harvest was emphasized by Vucetich et al. (2005) as another factor influencing elk herd size. They modeled elk annual population growth rate in response to interannual elk abundance, intraannual hunter harvest, cumulative annual snowfall, snow water equivalent (SWE), minimum winter temperature, maximum summer temperature, July precipitation, and annual precipitation. Their analysis of elk population dynamics both pre and post wolf reintroduction identified elk abundance, late winter harvest, annual snowfall, and annual precipitation as the most significant variables affecting elk herd size, suggesting that wolf predation is compensatory alongside more proximate causes (Vucetich et al. 2005).

Bison are iconic ungulate species within the NR with the potential to influence elk foraging patterns. Bison are predominately grazers; however, numerous researchers have observed bison browsing on woody riparian species (Meagher 1973; Bergman et al. 2001; Ripple et al. 2010; Painter and Ripple 2012). Interspecific competition between elk and bison can also affect browsing pressure on willow communities especially during mid to late winter when the majority of riparian browsing occurs (Singer et al. 1994; Ripple et al. 2010). Summertime bison browsing on willow < 1 m high has been measured in the Soda Butte and Lamar River confluence area (Ripple et al. 2010; Painter and Ripple 2012), but empirical data for bison browsing that span the 20 yr study period are currently lacking. While bison are relevant browsers, they are also far less abundant than elk (Fig. S1 available online at [insert URL here]). Over the past 20 yrs across the NR, bison populations averaged 1457 ± 956 (SE) while average elk counts (9,221 ± 3962) were 6-fold greater and the maximum ratio of elk:bison density was nearly 19:1 in 1995 ([NPS] 2015, Blanton 2013; Wyman 2013).

Influences of snow on ungulate foraging

Despite potentially large ecological influences on ungulate foraging behavior during the winter when the large majority of browsing occurs, snow characteristics have received surprisingly little attention as determinants of the spatial and temporal variation in ungulate browsing on willow-dominated riparian communities. Snow characteristics greatly influence large ungulate habitat selection, forage availability, movement, herd size, and habitat use (Hobbs et al. 1981; Parker et al. 1984; Delgiudice et al. 2001; Vucetich et al. 2005; Tefler et al. 1978; Olexa and Gogan 2007; Kittle et al. 2008, Richard et al. 2014).

Elk and bison each have unique morphological and behavioral adaptations for coping with snow. Elk are better adapted for locomotion in deeper snow because their mean chest height is 18 cm higher and their foot loading is approximately 50 g cm^{-2} less than bison's (Tefler and Kelsall 1984). As such, elk potentially have the advantage of a greater foraging range and tendency to utilize forage above the snowpack more often than do bison. Alternatively, bison utilize trails between preferred forage patches and they are better adapted for cratering in snow to find forage (Tefler and Kelsall 1984). Sweeney and Sweeney (1984) conducted aerial surveys of elk distribution during four winters in a Colorado mountain valley similar in elevation to the NR. According to their survey, elk began to move into areas with less snow as local depths approached 40 cm. Moreover, they found that elk removed snow with their hooves and muzzles in search of forage only when snow depth was < 40 cm and where preferred forage protruded from the snowpack. Alternatively, when elk were in areas with snow depth > 40 cm they preferentially browsed on shrubs protruding from the snowpack (Sweeney and Sweeney 1984). Similar to elk, bison preferentially select for habitat with shallower snow depth as illustrated by a study of Canadian wood bison in Prince Alberta National Park (Fortin 2000). Coughenour and Singer (1996) studied NR elk survival rates in response to density dependence, July precipitation as a forage production proxy, and cumulative annual snow depths. Their results emphasize the importance of snow depth, including documentation of greater densities of elk in wind swept areas.

In this study, we directly assessed the influence of environmental conditions on ungulate browsing with emphasis on whether snow characteristics are primary drivers. We specifically addressed some of the shortcomings of previous efforts by including direct measures of browsing and fine-scale environmental conditions with extensive and concordant spatial and temporal resolution. Based on studies of the browsing phenology during the winter, elk on the NR generally prefer to browse nutritious leaders from the previous growing season rather than aged woody material from previous years' growth ≥ 1 yr (YERC, unpubl. data). Generally, if a stem's leader is browsed then the next season's growth branches below the last terminal growth scar, making it possible to estimate and age browsing history (Keigley et al. 2003) and applied these methods to record whether or not riparian shrub stems were browsed between outer, annual growth scars. In addition, we made inferences from an extensive and spatially balanced sampling design in relation to the distribution of willow communities across Yellowstone's NR to account for potential sampling biases. Specifically, we investigated relationships between plot level, interannual browsing intensity on willow in response to environmental conditions measured at nearly the same scale, including terrain slope and climatic covariates with emphasis on the role of snow characteristics over a 20 yr record in Yellowstone's NR. Our objectives were: 1) quantify interannual browsing intensity; 2) determine the spatial variation in ungulate browsing accounted for by topographic covariates of aspect, elevation, and slope; 3) address the importance of climatic covariates, namely growing season precipitation and intraannual SWE, snow depth, and snow density; and by so doing elucidate the primary bottom-up factors that influence the spatial and temporal variation in browsing intensity. To do this, we developed a quantitative model using a generalized linear mixed model (GLMM) for spatially explicit statistical analysis and identification of the primary bottom-up drivers of browsing.

METHODS

Study area

The study area was within the Yellowstone National Park portion of the NR (Fig. 1), latitude 44° 46' 58.8" to 45° 1' 58.8"and longitude -110° 51' 39.6" to -109° 55' 12". The NR covers approximately 995 km² of the Lamar River and Yellowstone River watersheds; the remaining 35% (1,530 km²) of the NR extends into Montana public and private lands. The Lamar River valley terrain is generally wide and flat in the eastern NR near the confluence with Soda Butte Creek and becomes increasingly more varied with steeper slopes and narrower riparian areas westward toward the Yellowstone River. The NR elevation within the Yellowstone National Park boundary varies from 1,568 to 3,114 m (USGS) and precipitation, temperature, and snow depth generally vary with changes in elevation (Thornton, et al. 2014; [NOHRSC]; Table 1). However, there is also a strong orographic effect in the northwestern NR within the vicinity of Mammoth Hot Springs' weather station (Houston 1982; Table 1). Elk relocate from higher summer habitat to lower elevation winter habitat and comprise the greatest number of wintering ungulates. Bison inhabit the NR year round and are the second most abundant ungulate population during winter. Other less abundant ungulates include moose (*Alces alces*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*).

Common grasses in the NR include Sandberg's bluegrass (*Poa secunda*), blue-bunch wheatgrass (*Pseudoroegneria specata),* Idaho fescue (*Festuca idahensis*), and prairie junegrass (*Koeleria macrantha)* (NPS 2014). A wide variety of forbs also occurs, including northern bedstraw (*Galium boreale*), wild iris (*Dietes iridioides*), balsamroot (*Balsamorhiza sagittata*), and bitterroot (*Lewisia rediviva*) (NPS 2014). Sagebrush (*Artemisia tridentata*) dominates the xeric Lamar River valley landscape that is also intersected by mesic riparian corridors. Willow and aspen (*Populous tremuloids*) are dispersed along the corridors, within drainages, and in areas with access to ground water. Less dispersed along riparian zones are cottonwood (*Populous* spp.), alder (*Alnus rhombifolia*), and water birch (*Betula occidentalis*). Higher elevation coniferous forests include lodge pole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*).

Sampling methods

In 2001, a NR-wide sampling design was created to select a spatially balanced sample of woody riparian plots ranging in elevation from 1,688 m to 2,255 m. Plots averaged 100 m^2 in size and at least one stem was measured from an average of 11 plants per plot (range = 2-20). Browsing history data was collected during late summer and fall sample seasons of 2002, 2006, 2010, and 2014 (n = 86, 82, 66, and 69 plots, respectively). In these plots, we applied in-situ, nondestructive browsing history methodology similar to Keigley et al.'s (2003) for reconstruction of ungulate browsing history spanning 20 yrs (1995-2014).

Plot selection. A GIS overlain with streamside or floodplain riparian areas was derived from 1-m resolution, 4-band multispectral imagery to identify all possible woody riparian areas as potential plot sites. Images were collected in 1994 and 1995 using an Airborne Data Acquisition and Registration (ADAR) 5500 camera. Many of the plots were located on top of existing riparian vegetation plots set up originally in 1994, 1995, 1997, 1999, and 2002. Selected plots were at least 300 m apart, except when plots were traditional plots from prior research. New study plots were established within riparian woody vegetation covering 900 m^2 and buffered on two or more sides by 15 m. In light of the above criteria, a randomly selected quadrant was chosen to locate the plot within the 900 m^2 area. Approximately 10% of plots were excluded because of extant grizzly bear closures or other logistical constraints. A total of 86 study plots were established in 2002 and employed for a spatially explicit assessment of browsing history over time.

Browsing history. During warm season sample collection (2002, 2006, 2010, and 2014), we recorded ungulate browsing history using a non-destructive form of the technique previously applied by Keigley et al. (2003) where browsing was identified by branching below the terminal growth scar. For a given plant, one stem was analyzed for browsing history in 2002, 2006, and 2010 seasons and for two stems in the 2014 season; in all field seasons the vast majority of mean plant height within plots was < 2 m (Fig. S2 available online at [insert URL here]). The stem's primary leader between growth rings was recorded as one (browsed) or zero (non-browsed) (Fig. S3 available online at [insert URL here]). Careful attention and training was conducted to reduce the rare bias that occurs when elk remove more than the most recent growth. Furthermore, we tested the method-associated biases with destructive sampling in riparian areas outside of Yellowstone National Park to reduce or eliminate error in the date (yr) that browsing occurred. During training outside the Park, we physically segmented stems and matched inner growth rings with the outer growth scars from leader tip to stem base. In the field, we non-destructively observed and recorded browsing history between outer growth scars. During our statistical analysis, no distinction was made between elk and bison browsing due to consistently lower bison population size over the majority of the 20 yr study period. Moreover, despite a relatively high bison population in 2010-2014 bison had a lower influence on browsing intensity in comparison to elk browsing over the 5 yr study period in which the difference in ungulate browsing was recorded (Fig. S1 and Fig. S4 available online at [insert URL here]). Elk and bison browsing were grouped as total ungulate browsing for the 20 yr analysis with the understanding that the majority of browsing is attributable to elk. This inference is based on previous research and ecological knowledge in conjunction with field observations (Singer et al. 1994; Ripple et al. 2010; YERC unpubl. data).

Stem selection process. Prior to the 2014 field season, field technicians visually selected a single willow stem that appeared representative of browsing for the entire plant. In summer 2014, we repeated the collection protocol with addition of a randomization process for stem selection. Instead of selecting a single stem, we selected the thickest base stem by observing the plant base and randomly selecting a stem from the plant's crown edge associated with that base. Older, taller stems are typically found near the center of willow plants and likely yield the oldest age with most complete browsing history. However, center stems are often mechanically shielded from browsing (Keigley et al. 2013). We tested this possible source of bias by randomly selecting a stem from the outer crown edge of plants with more than one base stem.

We used stratified simple random selection without replacement (Valentine et al. 2009) to ensure an unbiased, representative sample from the outer crown. First, we visually separated the plant crown into quadrants. From each quadrant, a single stem was selected that appeared representative. We then selected a single stem at random using a random number generator. We selected the stem from quadrant one if the random number was ≤ 0.25, the stem from quadrant two if the random number was > 0.25 and ≤ 0.50, etc. We compared the 2009 estimate of mean NR browsing between the 2010 and 2014 collection years. Comparison was derived from alignment of only plots with data from both collection years. Global mean browsing for the NR during winter 2010 was 39% as estimated from the 2010 dataset; and the corresponding value derived from the summer 2014 protocol was 37%. This finding suggests that documenting browsing history using our randomized stem selection agrees well with past techniques.

Most willow communities were populated exclusively by willow, although there were plots with lesser amounts of aspen, cottonwood, and alder. Prior to analysis, we removed alder from the browse history dataset because the outer growth scar was not discernible in most cases.

Aspen and cottonwood comprised a relatively small portion (≤ 8%) of total sample size (Table S1 available online at [insert URL here]), and were included in the final browsing history dataset and not differentiated from willow.

Quantifying browsing intensity

To quantify the annual intensity of browsing at the plot level, we calculated a proportion of stems browsed per number of sampled stems in each plot ($\bar{y} = n / N$) where N is the number of plants sampled. This pooled sequence of categorical Bernoulli trials (Gotelli and Ellison 2013) per plot renders an annual mean proportion of stems browsed per plot. For each year's browsing estimate, we used data sets derived from the most recent survey to maximize accuracy of assessment. Each dataset captured four yrs of browsing history with the exception of the 2002 dataset, which includes an eight yr history. In addition, the 2014 survey included nine original plots not assessed in 2010 within which browsing was recorded back to 2006. These sites were supplemented into the 2010 dataset to increase the sample size in 2007-2010. From these browsing histories, we generated an annual, overall mean and 95% confidence intervals (CIs) for the NR with a one yr off set, e.g., 2013 growth was browsed during winter 2014.

Topographic and climatic covariates

Topography. To address the influences of topography, slope and aspect were derived separately from a 10-m elevation dataset ([USGS]). ArcGIS automated Spatial Analyst tools ([ESRI]) were applied to calculate 10 m slope and aspect parameters. Slope was then used as an independent parameter in our statistical analysis of browsing (see below). Elevation and aspect were not in included in the GLMM analysis because they were used in conjunction with a 30-m land-cover (forested/non-forested; [USGS]) geospatial layer (raster) to develop a maximum-likelihood based snow depth model and SWE model for downscaling purposes (see below).

Climate. Daily snow depth (mm) estimates were extracted from 1-km Snow Data Assimilation System (SNODAS; [NOHRSC]; Clow et al. 2012) raster dataset estimates and mean monthly snow depth (m) were calculated for January-March 2004-2014. However, SNODAS data were not available prior to 2004 (Risch and Frank 2006) so we developed a novel method based on snow depth measurements taken by YERC and a combination of regression analysis and generalized linear model coefficient estimation to generate downscaled estimates of January-March snow depth and SWE for winter 1995-2014. These estimates were then used to calculate snow density over the same period.

We used normally distributed snow depth and SWE measurements collected from a 600-m grid network (Fig. S5 and S6 available online at [insert URL here]) to estimate coefficients for the change in snow depth per unit change in elevation, elevation-derived aspect, and land-cover ([USGS]). We applied snow depth coefficient estimates to elevation, aspect and land-cover rasters to build a continuous 30-m snow depth model necessary to downscale 1-km inverse distance weighted (IDW; Blanchet, J. and M. Lehning 2010) snow depth (1995-2003) and 1-km SNODAS snow depth (2004-2014) to 30-m resolution. IDW was used instead of other interpolation methods because distance was the primary source of variation between weather stations, which were generally aligned in the east-west direction. Furthermore, there was no need to assess the covariance structure of the weather stations to derive an estimation interval, such as is possible with kriging. To address the coherence between IDW and SNODAS data sources, we first addressed similarity in snow depth measures based on the 1-km data ($r^2 = 0.38$, residual SE = 0.25, n = 2376) over the 2004-2014 time period; after applying the snow model to each source over the same time period estimates were correlated at the 30-m scale ($r^2 = 0.79$, residual SE = 0.07, n = 2376). Likewise, we applied estimated SWE coefficients to the elevation raster (only variable significant at the 5% level) and used the 10-m SWE model to downscale 1-km Daymet SWE estimates (1995-2003) and 1-km SNODAS SWE estimates (2004-2014) to a 10-m resolution. After we applied the SWE model to both raw Daymet SWE (2004-2014) and raw SNODAS SWE (2004-2014) their correlation improved from $r^2 = 0.19$ (residual SE = 74, n = 2310) to $r^2 = 0.80$ (residual SE = 33, n = 2310). We then calculated mean monthly snow density ($kg \cdot m^{-3}$) by dividing monthly SWE ($kg \cdot m^{-2}$) by each month's mean snow depth (m). Further description of snow depth and SWE modeling methods can be found in the appendix (available online at [insert URL here]). In order to illustrate the spatial distribution of snow depth and snow density we used ordinary kriging of the overall study period mean values at established study plots.

We limited our winter analysis period to January-March because coefficients used to generate snow depth and SWE estimates were based on snow measurements taken in January-March. This period is when ungulates are most concentrated on the NR and when nearly all browsing occurs (Singer et al. 1994; YERC unpubl. data). Growing season precipitation ($mm \cdot day^{-1}$) estimates were extracted from 1-km Daymet rasters (Thornton et al. 2014) using plot coordinates. Precipitation was averaged for May-July using a one-year offset, e.g. 2003 growing season precipitation was aligned with winter 2004. Growing season precipitation functions as a proxy for potential browse and forage production available for winter use. During wet growing seasons (May-July), willow growth is enhanced by water availability and lower evaporative loss (Kabenge and Irmak 2012).

Data analysis

Exploratory data analysis showed multicollinearity between December through March snow depths (r = 0.91 – 0.98; Table S3 available online at [insert URL here]), with lowest correlations between December snow depths and snow depths in all other months (r = 0.91 – 0.94). Also evident were high levels of correlation between snow densities for all months (r = 0.60-0.96) with lowest in December (r = 0.60-0.7). Further examination of boxplot graphs for monthly snow characteristics in all years indicated that there were consistently lower snow depths in December and that the distributions of December snow densities were inconsistent with all other months in winters 1995-2004 (Table S3 and Fig. S7 available online at [insert URL here]). Generally, snow accumulates and depth increases through February and there is a slight decline in snow depth in March, likely due to settling and snow compaction (Dibb and Fahnestock 2004). As such, snow density increases throughout the winter with the highest densities occurring in March. December snow characteristics were removed from further analysis because they are inconsistent with other months and because browsing generally takes place in mid to late winter (Singer et al. 1994; Ripple et al. 2010). Further analysis and explanation for exclusion of December snow characteristics can be found in the appendix (available online at [insert URL here]).

As an initial set of predictor variables, we identified range unit (see below), slope, January-March snow depth, January-March snow density, January-March SWE, and mean growing season (May-July) precipitation as independent variables to be used to address the proportion of browsed stems across time and space within the NR. Slope was included in the analysis as a control variable that limits ungulate mobility during the winter by increasing energy expenditure (Parker et al. 1984). Whereas, growing season precipitation was included for its functional effect on willow growth (Kabenge, I. and S. Irmak, 2012), where higher growing season precipitation increases caloric content and nutrition gained when willow is supplemental to ungulate diets (Christianson and Creel 2007; Christianson and Creel 2009). In order to remove the influence of multicollinearity in potential snow characteristics before deciding which to include as predictor variables, we applied R car package's (Fox et al. 2015; RStudio Team 2015) variance inflation factor (VIF) with a conservative threshold value of 5 (r = 0.8; Dormann et al. 2013). We populated a full GLM with browsing in response to SWE, snow depth, and snow density covariates for all months (January-March) and iteratively eliminated the highly correlated covariates using VIF (Dormann et al. 2013; Zuur et al. 2010). After a complete VIF analysis, only March snow depth and March snow density remained (Table S4 available online at [insert URL here]), were poorly correlated (r = 0.15), and were the only measures of snow characteristics employed in further analysis. In order to be certain that we were not missing an ecologically significant signal by failure to consider the January-March mean snow depth and January-March mean snow density, we ran a second VIF analysis with winter means and March characteristics (Table S5 available online at [insert URL here]). March snow depth and snow density passed this VIF analysis as well, from which we infer that March snow characteristics represent interannual winter snow conditions and are well suited as covariates capable of capturing the variability in browsing attributable to winter snow conditions. Henceforth, we infer that reference to March snow characteristics implies general winter snow characteristics.

We applied the lme4 package (Bates et al. 2015; RStudio Team 2015) statistics to develop and assess GLMMs. The random effect in all GLMMs was range unit (n = 7; Table S2 available online at [insert URL here]). Generally, study plots were clustered into groupings we called range units based on proximity to each other to form the random effect. We also derived range unit to account for spatial autocorrelation of predictor variables within closely associated plots and maximize variability in browsing between range units (Fig. S8 available online at [insert URL here]). Plots grouped into the Corridor range unit include seven plots with similar elevations that occur along NR migration corridors (Bruggeman et al. 2007). There are two Corridor plots along Gardiner River, two along Yellowstone River, and three along Hellroaring Creek (Fig. 1). Accounting for the spatial random effect addressed by range unit with a GLMM was relevant because it provides a more accurate approximation of response variance per parameter variance than the conventional GLM.

All models were fitted using a Laplace approximation, binomial distribution, and a logistic link function (Bolker 2007, Bolker et al., 2008, Bolker 2014). We used the method of lowest AICc (second order AIC) model selection within a hierarchical multi-model structure (Burnham and Anderson 2001) to identify the best model for assessing ungulate browsing intensity across the NR. Our multi-model framework consisted of 11 a priori candidate models (Chamberlin 1965), which were constructed based on previous research and ecological knowledge (Houston 1982; Singer and Norland 1994; Singer et al. 1994; Coughenour and Singer 1996; Bilyeu et al. 2008; Creel and Christianson 2009; Marshall et al. 2013; Marshall et al. 2014). We considered March snow depth, March snow density, growing season precipitation, and slope as explanatory variables. No polynomial transformations were used because our goal was to generalize the associative effects of our explanatory variables on the probability of browsing. We did however consider various term combinations and interactive terms, such as snow depth:snow density, snow depth:precipitation, and snow depth:slope. We calculated GLMM AICc, delta AICc, and AICc weights for all candidate models as described by Burnham and Anderson (2001). Only the top four models were considered for further analysis. Pearson's and predicted residuals were assessed for model fitting, and deviance residuals per range unit also helped verify that the random effect structure of the best GLMM had approximated normality (Fig. S9 and S10 available online at [insert URL here]).

We applied the R ‘effects package’ (R Studio Team 2015) to generate interpretable magnitude of effect displays for each parameter’s coefficient estimate in relation to the binomial response (Fox 2003). With the effects package each predictor variable’s extent of influence is displayed on the x-axis and the associated, relevant probability of browsing is on the y-axis (Fox and Hong 2010). The relative strength of a variable’s effect is distinguishable on the y-axis, where a stronger effect is designated by tick marks that are closer together and thus illustrating a greater change in the probability of browsing per variable unit change. As such, if the effect’s strength changes over the span of x-axis values the distance between the y-axis tick marks automatically lengthens or shortens accordingly. This automated probability based graphing utility supported an unbiased identification of response thresholds.

RESULTS

From winter 1995-2014 the overall mean proportion of stems browsed on the NR was 0.62, the minimum was 0.34 in 2011, and the maximum was 0.81 in 2006 (Fig. 2). Our 20-yr record suggests three distinct phases of browsing intensity including 1) a period of high intensity from 1995-2006, 2) a declining phase from 2006- 2011, and 3) a recovery phase from 2011-2014 wherein browsing progressively increased. Proportion of stems browsed was above the overall study period mean from 1995-2006 until a dramatic decline of 0.18 occurred in in 2007. From 2007-2011 annual mean browsing continued to decline at an average rate of 4% annually. Beginning in winter 2012, browsing intensity increased at an average annual rate of 7% until the end of the study record (2014) when browsing equaled the study period mean (0.62).

The annual global mean of March snow depth and snow density for the 20 yr study period illustrates the interannual change in snow characteristics (Fig. 3). Over the 20-yr study, interannual mean March snow depth at established study plots varied from 0.06 – 0.29 m with average depth generally declining from 1995 to 2004 and increasing again thereafter to 2010 and returning to typical average depth by the end of the study period (Fig 3). While mean depths ranged from 0.06 to 0.29 m, maximal values in areas containing study plots varied from 0.53 – 1.60 m over the 20-yr record (data not shown). Interannual mean snow density at study plots varied from 177 – 398 kg · m^{-3} with the minimum average occurring in 1995 and the maximum average in 1996. Following winter 1996 there was a general decline in snow densities through 2002 and a general increase from 2003 to 2007 before a return to near typical averages between 2008 and 2014 (Fig. 3). Maximal annual snow densities in areas containing study plots varied from 291 – 892 kg · m^{-3} over the 20-yr record (data not shown). Annual means of snow characteristics were not correlated ($r^2 = 0.15$, $P < 0.001$) though both were positively correlated with elevation. Spatial distribution of snow characteristics (Fig. 4) illustrates the positive association between snow depth and elevation ($r^2 = 0.44$, P = < 0.001) and the positive association between snow density and elevation ($r^2 = 0.52$, P = < 0.001).

Over the 20 yr analysis mean growing season precipitation (May-July) at established study plots ranged from 0.98 to 2.19 mm · day^{-1} with an overall mean of 1.66 mm · day^{-1} (standard deviation = 0.38 mm · day^{-1}). Maximal precipitation values at study plots ranged from 1.35 to 2.69 mm · day^{-1}. Slopes for the browsing plots averaged 3.4% because most of the places we studied were flat, with the exception of two extreme slopes (20% and 26%). Histograms and boxplots showing the 20 yr distribution of variable values at established study plots can be found in the appendix (Fig. S11 and S12 available online at [insert URL here]).

Ecological implications of GLMM results

March snow depth occurred in each of the top four GLMMs selected via lowest AIC_c whereas March snow density occurred in two models and both slope and precipitation occurred in three models (Table 2). All four predictor variables occurred in GLMM No. 1, providing the greatest number of parameters (K^A). Despite the fact that GLMM No. 1 had the greatest K^A, it was identified as the best-fit GLMM (henceforth GLMM) based on ΔAIC_c assessment (Table 2).

The four predictor variables identified by the GLMM represent bottom-up influences that have affected browsing intensity over the 20 yr record addressed here. Proportion of stems browsed was significantly related to two snow characteristics (Table 3; Fig. 5). March snow depth was negatively (-1.393) and significantly ($P < 0.001$, Table 3) associated with the probability of browsing. When March snow depth is > 0.4 m the probability of browsing is less than 50%. Further, the close spacing among tick marks between 0 and ca. 0.4 m depth suggests that changing snow depths in this range had strong influences on browsing probability, while beyond this range distance between tick marks on both the x-axis and y-axis become wider suggesting that the effect is lessoning. During the study period 94% of established study plots (n = 1241) had March snow depth < 0.4 m. In addition to the negative relationship between snow depth, the probability of browsing was negatively (-0.0008, Table 3) and significantly ($P < 0.001$) associated with March snow density, and according to the effects graph the significant influence began as values approached 200 $kg \cdot m^{-3}$ (Fig. 5 b.). Nearly 79% of study plot occurrences (n = 1051) had March snow density > 200 $kg \cdot m^{-3}$ of which only about 5% had densities above 600 $kg \cdot m^{-3}$ (Fig. 5 b.). An important feature of the effect graph is that snow density's effect is less pronounced than snow depth and browsing probability remains above 50% until snow densities surpass 750 $kg \cdot m^{-3}$. Terrain slope was also negatively (-0.016, Table 3) and significantly ($P < 0.001$) related to browsing probability and unlike the snow characteristics, this effect was most pronounced across only a minor portion (terrain slope < 5%, n = 978) of the entire range of terrain slopes encountered by the model (Fig. 5 c.). In contrast to the influences of snow characteristics and topography, increased growing season precipitation positively (+ 0.36, Table 3) and significantly ($P < 0.001$) enhanced the probability of browsing intensity. This positive association was consistent across nearly the entire range of growing season precipitation (Fig. 5 d.).

The relative influences of the four predictor variables are illustrated both by the magnitude of the parameter coefficient estimates (Table 3) and by the magnitude of effect per change in predictor variables (Fig. 5). While our GLMM indicates that all predictor variable are statistically significant, terrain slope only varies spatially, while snow depth, snow density and growing season precipitation are both spatially and temporally stochastic. With this perspective two features of snow cover during winter in combination with precipitation during the growing season, and how these are distributed across the NR's topography, serve as spatially and temporally significant bottom-up features influencing the probability of ungulate browsing on willow communities.

DISCUSSION

Bottom-up influences ranging from water availability to promote browse and forage growth, steepness of terrain in which browsing occurs, and characteristics of winter snow conditions including snow depth and snow density significantly influence browsing on willow as assessed by a 20 yr history robustly gathered from a spatially explicit design in Yellowstone's NR. These relationships likely reflect winter trade-offs between ungulate energy expenditure and caloric intake. Similar to other animals, ungulates will seek to optimize their fitness by adapting behavioral strategies to maximize energy intake per time spent foraging (Pyke 1984). Significant factors identified in this study and their degree of relative influence on ungulate browsing intensity on willow communities within the NR contributes to our interpretation of seasonal foraging strategies adapted by large ungulates.

The importance of the previous spring and summer on ungulate behavior during the winter is illustrated by the coherent variation in growing season precipitation and browsing intensity throughout winters 1995-2014 within the NR. Our results indicate that browsing frequency increases as net primary productivity of willow shoots is bolstered by increasing growing season precipitation. Although willow depend on snowmelt run-off for recruitment (Changwoo et al. 2007) and elevated water table levels for sustained growth during the growing season (Johnston et al. 2009), increasing precipitation augments water availability, decreases water stress (Kabenge, I. and S. Irmak, 2012), and indirectly influences water table elevation. In turn, enhanced stem growth increases caloric content and increases the nutritional gain per time spent browsing, features beneficial to ungulates. Additionally, our data suggest that in winters following dry growing seasons, e.g., 2000-2005, with low primary production of preferred forage, browse can become supplemental to ungulate diets (Christianson and Creel 2007; Christianson and Creel 2009).

According to our results, NR willow communities along hillslope seeps and streams are less likely to be browsed then are communities along waterways on low gradient terrain. This inverse association between the proportion of stems browsed and terrain slope is probably related to the trade-off between ungulate energy expenditure and caloric intake. Regardless of weight the energetic efficiency of upslope locomotion for elk is 36-56%, relative to a theoretical 100% energetic efficiency during horizontal movement (Parker et al. 1984). During winter condition, ungulate nutritional gain from browsing is likely less than the caloric cost of the upslope climb because ungulate locomotion on a 25% slope increases exponentially as a function of sinking depth (Parker et al. 1984).

By far the most influential of all features identified by our GLMM, March snow depth is a strong indicator of interannual winter (i.e., January-March) effects on NR ungulate browsing intensities. Elk and bison fitness is adversely affected when snow depth is high (Tefler and Kelsall 1984) and sinking depth of 0.32 m nearly doubles energy expenditure associated with locomotion, which in turn affects ungulate foraging behavior by limiting mobility (Parker et al. 1984). Elk typically maximize energy intake per time spent foraging by selection of convenient browse protruding above the snowpack when snow depth is > 0.4 m (Tefler and Kelsall 1984), whereas bison are better equipped to dig craters with their horns in order to access forage under the snowpack (Tefler and Kelsall 1984).

However, increasing snow depth can be argued to alter ungulate behavior in ways that generate contradictory predictions for propensity to browse woody vegetation. Snow depth may influence browsing in one of two potential ways, 1) decreased rates of browsing due to limited mobility and space use, or 2) increased browsing due to convenience of secondary riparian resources when snow depth and density limit access to grasses. Our data suggest that when March snow depth is > 0.4 m the probability of browsing is less than 50%. This threshold identified by our model agrees with studies addressing the influence of snow depth on ungulate locomotion and forage selection. At approximately 0.32 m, there exists a trade-off between energy expenditure during movement required for foraging per energy gained (Parker et al. 1984; Bourgoin et al. 2008). A decline in the probability of browsing may reflect ungulate reduction in global activity and allocation of calories to thermal regulation (Bourgoin et al. 2008) and localized patch foraging (Tefler and Kelsall 1984). Alternatively, animals may choose to migrate to lower elevation habitats with less snow (Sweeney and Sweeney 1984) as snow depth nears a critical depth of 0.46 m (Parker et al. 1984) or into wind swept areas (Coughenour and Singer

1996). A migratory response could happen earlier in the season, in which case, elk may have relocated to outside Yellowstone Park boundaries thereby reducing the browsing intensity on NR willow communities. On the other hand, if elk have moved into wind swept areas where NR willow communities occur then our results accurately reflect increased probability of browsing. In a similar way, snow density can influence the energetic cost of locomotion and increase browsing by limiting access to preferred forage under the snowpack (Tefler and Kelsall 1984; Parker et al. 1984).

What is not so clear is why our model indicates a greater probability of browsing when March snow depth is < 0.4 m. When initially considered this may seem contrary to increased browsing when snow depth is > 0.4 m as identified by Tefler and Kelsall (1984). An explanation for this is that Yellowstone willow produce less chemical defense compounds to herbivory, such as tannins and phenolics, than willow in Rocky Mountain National Park (Singer et al. 1998). Following a comparative analysis of willow (*Salix* spp.) responses to experimental clipping in both National Parks, Singer et al. (1998) hypothesized that Yellowstone willow were less resistant to browsing because of the composite effects of herbivory and a drier climate, effects that are enhanced by low water tables related to the limited presence of beaver ponds (Singer et al. 1998). Accordingly, Yellowstone willow palatability may translate to greater browsing probability at lower snow depths when ungulates are present on the NR.

Alternatively, predator presence during foraging is another likely factor that affects foraging behavior causing ungulates to allocate more time to predator surveillance than to foraging (Christianson and Creel 2007; Kittle et al. 2008). Risk of wolf predation is likely amplified when deep snow limits movement, in which case it is more beneficial to remain sedentary and safe within the herd than to forage. This scenario supports the BMTC hypothesis within the context of snow conditions. Together, deep snow in March 1995 and coincident wolf reintroduction, plus deep snow in winter 1996 and 1997, likely contributed to willow growth to release height (> 2 m) in specific areas (Ripple and Beschta 2004, 2005, 2006). However, at the scale of the NR, browsing intensity was above the study mean proportion during all winters from 1995-1997. The greater rates of browsing during that time likely reflect intense pressure due to high elk populations despite challenging abiotic conditions; elk abundance exceeded 11,000 animals (1998 count) in all years (Blanton 2013).

After browsing proportion reached its lowest value in 2011 (0.34, Fig. 2), and the first time since 2006, the proportion of stems browsed equaled the mean value derived from the entire study period (0.62, Fig. 2) in 2014, even though elk abundance was under 5,000 animals in 2014 (Fig. S1 available online at [insert URL here]). An alternative hypothesis to explain the increased browsing intensity is that 2014 mean March snow depth was 0.13 cm (± 0.21 [SE]) which was similar to the study period mean 0.14 cm (± 0.17), while mean March snow density was 336 $kg \cdot m^{-3}$ (± 178 $kg \cdot m^{-3}$) which was slightly greater than the study period mean of 301 $kg \cdot m^{-3}$ (± 163 $kg \cdot m^{-3}$). According to our results, the 2014 snow depth translates to a browsing probability of approximately 0.57 and the mean snow density translates to a browsing probability of approximately 0.6. In which case, freedom of mobility and limited forage access could have induced greater browsing intensity.

INTERPRETATION

Daily Daymet and SNODAS climatic covariate estimates can be utilized as an inexpensive decision support tool to estimate the interannual spatial variation in potential for bottom-up influences to alter browsing intensity. Results indicate that snow is an important and relevant explanatory variable to consider among the suite of top-down and bottom-up influences.

Reflection on the proportion of leaders browsed under previous winter conditions concomitant with respective ungulate population densities should provide future insights into the multivaritate causal relationships influencing ungulate browsing. Fore-casting probable future browsing intensity in response to differential elk and bison densities needs to embrace issues of climate change that may manifest through snow and moisture parameters addressed here to assist wildlife managers in determining interannual and intraannual carrying capacity.

ACKNOWLEDGEMENTS

Special thanks to Jeffrey Henry and Tonya Belile for their dedicated field work and data entry during 2014. We likewise owe thanks to Yellowstone Ecological Research Center interns and staff for collection and logging of field data. We appreciate the statistical review provided by Alan Swanson, Brian Steele, and David Affleck. Special thanks to Aaron Thomas and Brady Allred for their guidance.

FUTURE WORK

Researchers can take annual browse measurements over a period of four yrs and compare the results to a browsing history corresponding history taken on the fourth yr. In this way the browsing estimation presented here can be further validated. In addition to browsing history collection within established NR plots, collection of browsing history from plots within the NR outside of Yellowstone Park boundaries could provide insight into the browsing impact of elk densities along the Gardinar and Yellowstone Rivers. Furthermore, GPS marked, fine resolution, snow characteristic estimates can be derived and sharpened from annual snow course measurements of snow depth and snow density throughout January-March over the four yr study period.

Validation of interannual browsing across the entire northern range, within and outside Yellowstone Park, can be accomplished by collection of data from a spatially balanced portion of the established plots throughout January-March. Collection of this monthly winter estimate over the four yr study period would increase the accuracy of intraannual and interannual ungulate browsing estimates in response to topography and snow conditions. Additionally, care can be taken to distinguish elk browsing form bison browsing by recording the number of rings within the browsed stem tip cross-section.

LITERATURE CITED

Agresti, A., 1992. A Survey of Exact Inference for Contingency Tables. Statistical Science 7(1):131-153.

Agresti, A., 2002. Categorical Data Analysis; Second Edition. Wiley Science 5 and 266 p.

Bates, D., et al., 2015. Linear Mixed-Effects Models using 'Eigen' and S4. R package version 1.1-9.

Bergman, C. M., J. M. Fryxell, C. Cormack Gates, and D. Fortin, 2001. Ungulate foraging strategies: energy maximizing or time minimizing? Journal of Animal Ecology 70:289-300.

Beyer, et al., 2007. WILLOW ON YELLOWSTONE'S NORTHERN RANGE: EVIDENCE FOR A TROPHIC CASCADE? Ecologicala Applications 17(6):1563-1571.

Bilyeu, D. M., D. J. Cooper, and N. T. Hobbs, 2008. Water Tables Constrain Height Recovery of Willow on Yellowstone’s Northern Range. Ecological Applications 18(1):80-92.

Blanton, D., 2013. MEMORANDUM: Abundance and Distribution of Yellowstone Bison.Yellowstone Center for Resources.

Blanchet, J. and M. Lehning, 2010. Mapping snow depth return levels: smooth spatial modeling versus station interpolation.

Brennan, A. B., P. C. Cross, M. Higgs, J. P. Beckmann, R. W. Klaver, B. M. Scurlock, and S. Creel, 2013. Inferential consequences of modeling rather than measuring snow accumulation in studies of animal ecology. Ecological Applications 23(3):643-653.

Bruggeman, J. E., Garrott, R. A., White, P. J., Watson, F. G. R., & Wallen, R. (2007). Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. Ecological Applications, 17(5), 1411-1423.

Bolker, B. M., 2007. Ecological Models and Data in R. PRINCETON UNIVERSITY PRESS, 348 p.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. Henry, H. Stevens, and Jada Simone S. White, 2008. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24(3): 127-135.

Bolker, B. M., 2014. Linear mixed-effects models using Eigen and S4. Contact LME4 Authors lme4-authors@lists.r-forge.r-project.org.

Bourgoin, G., et al., 2008. Determinants of seasonal variation in activity patterns mouflon. Can. J. Zool. 86:1410-1418.

Burnham K. P., and D. R. Anderson, 2001. Kullback-Leibler information as a basis for strong inference ecological studies. Wildlife Research 28:111-119.

Burnham K. P., and D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed.). Springer. 66 p.

Chamberlin, T. C., 1965. The Method of Multiple Working Hypotheses. Science 148(3671):754-759.

Christianson, D. and S. Creel, 2007. A Review of Environmental Factors Affecting Elk Winter Diets. Journal of Wildlife Management 71(1):164–176.

Christianson, D. and S. Creel, 2009. Effects of Grass and Browse Consumption on the Winter Mass Dynamics of Elk. Oecologia 158(4):603-613.

Changwoo, A., et al. 2007. Developing a dynamic model to predict the recruitment and early survival of black willow (Salix nigra) in response to different hydrologic conditions. Ecological Modelling 204:315-325.

Coughenour, M. B. and F. J. Singer, 1996. Elk Population Processes in Yellowstone National Park Under the Policy of Natural Regulation. Ecological Applications 6 (2): 573-593.

Clow, D. W., L. Nanus, K. L. Verdin, and J. Schmidt, 2012. Evaluation of SNODAS snow depth and snow water equivalent estimates for the Colorado Rocky Mountains, USA. Hydrological Processes. DOI: 10.1002/hyp.

Creel, S. and D. Christianson, 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. Ecological Society of America 90(9): 2454-2466.

Delgiudice, G. D., R. A. Moen, F. J. Singer, and M. R. Riggs, 2001. Winter Nutritional Restriction and Simulated Body Condition of Yellowstone Elk and Bison before and after the Fires of 1988. Wildlife Monographs 147:1-60.

Dibb, J. E. and M. Fahnestock, 2004. Snow accumulation, surface height change, and firn densification at Summit, Greenland: Insights from 2 years of in situ observation. Journal of Geophysical Reasearch 109 doi:10.1029/2003JD004300.

Dormann, C. F., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46.

[ESRI] Environmental Systems Research Institute, 2014. ArcGIS Desktop: Release 10.2.1. Redland, CA.

Fox, J. 2003. Effect Displays in R for Generalised Linear Models. Journal of Statistical Software 8(15) 1-9.

Fox, J. and J. Hong, 2010. Effect Displays in R for Multinomial and Proportional-Odds Logit Models: Extensions to the effects Package. Journal of Statistical Software 32(1):1-24.

Fox, J., et al., 2015. Companion to Applied Regression. R package version 2.0-26.

Gotelli, N. J. and A. M. Ellison, 2013. A Primer of Ecological Statistics; Second Edition. Sinauer Associates, Inc. 28 p.

Hobbs, T. N., D. L. Baker, J. E. Ellis, and D. M. Swift, 1981. Composition and Quality of Elk Winter Diets in Colorado. The Journal of Wildlife Management 45:156-171.

Houston, D. B.. 1982. The northern Yellowstone elk: ecology and management. Macmillan New York.

Johnston, D. B., D. J. Cooper, and N. Thompson Hobbs, 2009. Relationships between groundwater use, water table, and recovery of willow on Yellowstone's northern range.Ecosphere 2(2):1-11.

Kabenge, I. and S. Irmak, 2012. Evaporative losses from a common reed-dominated peachleaf willow and cottonwood riparian plant community. Water Resources Research 48, W09513, doi:10.1029/2012WR011902.

Kauffman, M. J., J. F. Brodie, and E. S. Jules, 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91(9):2742-2755.

Keigley, R. B., M. R. Frisina, and C. Fager, 2003. A Method for Determining the Onset Year of Intense Browsing. Journal of Range Management 56(1):33-38.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr, 2008. The scale-dependent impact of wolf predation on resource selection by three sympatric ungulates. Oecologia 157:163-175.

Larter, N.C., A. R. E. Sinclair, T. Ellsworth, J. Nishi, and C. C. Gates, 2000. Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. Animal Conservation 4:299-309.

Lay, D.W., 1965. Effects of Periodic Clipping on Yield of Some Common Browse Species. Journal of Range Management 18(4):181-184.

Marshall, K. N., D. J. Copper, and N. Thompson Hobbs, 2014. Interactions among hervivory, climate, topography, and plant age shape riparian willow dynamics in northern Yellowstone National Park, USA. Journal of Ecology, Accept*e*d 13-Feb-2014; doi: 10.1111/1365-2745.12225.

Marshall, K. N., N. Thompson Hobbs, and D. J. Cooper, 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proc R Soc B 280: 20122977. Available at URL [http://dx.doi.org/10.1098/rspb.2012.2977]. Accessed on 10 June 2015.

Meagher, M. M., 1973. The Bison of Yellowstone National Park, National Park Service, Scientific Monograph Series Number 1. Government Printing Office: Washington, DC.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White, 2013. Linking ani-preditor behavior to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecology Letters 16:1023-1030.

Milsom T. P., S. D. Langton, W. K. Parkin, S. Peel, J. D. Bishop, J. D. Hart, and N. P. Moore, 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. Journal of Applied Ecology 37:706-727.

[NOHRSC] National Operational Hydrologic Remote Sensing Center, 2004. Snow Data Assimilation System (SNODAS) Data Products at NSIDC, [December-April snow depth and SWE winter 2004-2014]. Boulder, Colorado USA: National Snow and Ice Data Center. Available at URL [http://dx.doi.org/10.7265/N5TB14TC].

[NPS] National Park Service, 2014. Plants. Available at URL [http://www.nps.gov/yell/naturescience/plants.htm]. Accessed on 21 January 2014.

[NPS] National Park Service, 2015. 2014-2015 Winter Count of Northern Yellowstone Elk. Plants. Available at URL [http://www.nps.gov/yell/naturescience/plants.htm]. Accessed on 6 January 2016.

Olexa, E. M. and P. J. P. Gogan. Spatial Population Structure of Yellowstone Bison. The Journal of Wildlife Management 71(5):1531-1538.

Painter, L. E. and W. J. Ripple, 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. Forest Ecology and Management 264:150-158.

Parker, K. L., C. T. Robbins, and T. A. Hanley, 1984. Energy Expenditures for Locomotion by Mule Deer and Elk. The Journal of Wildlife Management. 48(2):474-488.

Pettitt, A. N., 1979. A non-parametric approach to the change point problem. Journal of the Royal Statistical Society Series C, Applied Statistics 28, 126-135.

Pyke, G. H., 1984. OPTIMAL FORAGING THEORY: A CRITICAL REVIEW. Ann. Rev. Ecol. Syst. 115:523-75.

RStudio Team, 2015. RStudio: Integrated Development for R. RStudio, Inc., Bostion, MA http://www.rstudio.com.

Richard, J. H., J. Wilmshurst, and S. D. Cote, 2014. The effect of snow use of an alpine ungulate: recently fallen snow tells more than cumulative snow depth. Canadian Journal of Zoology. 92:1067-1074.

Ripple, W. J. and R. L. Beschta, 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystyms? BioScience 54(8):755-766.

Ripple, W. J. and R. L. Beschta, 2005. WILLOW THICKETS PROTECT YOUNG ASPEN FROM ELK BROWSING AFTER WOLF REINTRODUCTION. Western North American Naturalist 65(1):118-122.

Ripple, W. J. and R. L. Beschta, 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management 230:96-106.

Ripple W. J., L. E. Painter, R. L. Beschta, and C. Cormack Gates, 2010. Wolves, Elk, Bison, and Secondary Trophic Cascades in Yellowstone National Park. The Open Ecology Journal 3:31-37.

Risch A. C. and D. A. Frank, 2006. Carbon Dioxide Fluxes in a Spatially and Temporally Heterogeneous Temperate Grassland. Oecologia 147(2):291-302.

Robbins, J., 2005. Hunting Habits of Wolves Change Ecological Balance in Yellowstone. The New York Times:Environment.

Shmitz, O. J., A. P. Beckerman, and K. M. O'Brien, 1997. Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions. Ecology 78(5): 1388-1399.

Singer, F. J., J. E. Norland, 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. CAN. J. ZOOL. 72:1383-1394.

Singer, F. J., et al., 1998. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin 26(3):419-428.

Singer, F. J., L. C. Mark, and R. C. Cates, 1994. Unglulate herbivory of willow on Yellowstone's northern winter range. Journal of Range Management 47:435-443.

Sweemey, J. M., J. R. Sweeney, 1984. Snow Depths Influencing Winter Movements of Elk. Journal of Mammalogy. 65(3):524-526.

Telfer, E. S., 1978. Cervid Distribution, Browse and Snow Cover in Alberta. Journal of Wildlife Management 42:652-361.

Telfer, E. S., J. P. Kelsall, 1984. Adaptation of Some Large North American Mammals for Survival In Snow. Ecology 65(6):1828-1834.

Thornton, P E., M. M. Thornton, B. W. Mayer, N. Wilhelmi, Y. Wei, R. Devarakonda, and R.B. Cook, 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. Date accessed: 2014/04/28. Temporal range: 1992/11/01-2013/12/31. Spatial range: N=45.03, S=44.78, E=-109.92, W=-110.861.

Valentine, H. T, D. L. R. Affleck, and T. G. Gregoire, 2009. Systematic sampling of discrete and continuous populations: sample selection and the choice of estimator. Canadian Journal of Forest Research 39:1061-1068.

[USGS] United States Geological Survey. The National Map Viewer. (Digital Elevation Data) Available at URL [http://viewer.nationalmap.gov/viewer/]. Accessed December 2013.

[USGS] United States Geological Survey, 2011. National Land Cover Database. Available at URL [http://www.mrlc.gov/nlcd2011.php]. Accessed December 2013.

Smith, D., et al. 1995-2014. Yellowstone National Park Wolf Project Annual Report 1995-2014. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR.

Vucetich, J. A., D. W. Smith, D. R. Stahler, and E. Ranta, 2005. Influence of Harvest, Climate and Wolf Predation on Yellowstone Elk, 1961-2004. Oikos 111(2):259-270.

Wyman, T., 2013. 2012-2013 Annual Winter Trend Count of Northern Yellowstone Elk. Yellowstone Center for Resources, Yellowstone National Park.

[WRCC] Western Regional Climate Center, 2014. Climate Summaries. Available at: http://www.wrcc.dri.edu/. Accessed 15 December 2014.

Zuur, A. F., E. N. leno, and C. S. Elphick, 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14.

LIST OF MANUSCRIPT TABLES AND FIGURES

List of Tables:

Table 1: Mean daily precipitation (May-July), mean annual temperature, mean daily snow depth (January-March), and elevation at NR weather stations from 1983-2012.

Table 2: Top four GLMMs with relevant independent variables – random effect, March snow depth (m), March snow density (kg · m^{-3}), growing season precipitation (mm · day^{-1}), and terrain slope percent. Model assessment values – No. of parameters K^A, second order Akaike information criterion (AICc), delta AICc (ΔAIC = AICi – minimum AICc), and AICc weight (Wt).

Table 3: GLMM fixed effect parameters – March snow depth (m), March snow density (kg · m^{-3}), growing season precipitation (mm · day^{-1}), and terrain slope percent – and their associated conditional mean coefficient estimate (Estimate), standard error of the mean (SE), lower and upper bound of the 95% CI, F-statistic (F-value), and significance statistic (P-value).

List of Figures:

Figure 1: Study area map showing the locations of study plots (black diamonds, n=86), waterways and weather stations (stars, n=3) within Yellowstone's NR.

Figure 2: Annual means (± 95% CI) of the proportion of stems browsed by ungulates within Yellowstone's NR willow communities per winter 1995-2014. Dotted line represents the overall, study period mean.

Figure 3: Yellowstone's NR mean snow depth (open circles) and snow density (closed triangles) at existing study plots (n = 10 to 86 plots per year) derived from NR snow depth and SWE model at 30-m resolution from 1995-2014. Data are means ± 95% CIs.

Figure 4: Maps display study period (1995-2014) mean snow depth (a.) and mean snow density (b.) distributions across Yellowstone's NR as calculated by ordinary Kriging of the study plot means. Note the broad range of snow conditions existing among the established study plots (black dots).

Figure 5: R effects package display to illustrate the magnitude of effect and effect direction for NR browsing probability in response to March snow depth (a.), March snow density (b.), terrain slope (c.), and growing season precipitation (d.). Gray area represents 95% CIs. Tick marks represent study plot occurrences.

Table 1: Mean daily precipitation (May-July), mean annual temperature, mean daily snow depth (January-March), and elevation at NR weather stations from 1983-2012.

Station	Precip. (mm · day^{-1})	Temp. (˚F)	Depth (cm)	Elev. (m)
Mammoth	1.5 ± 3.6	40 ± 20	15 ± 12	1,913
Tower	1.5 ± 3.5	36 ± 24	43 ± 15	1,910
Cooke City	2.3 ± 4.9	34 ± 21	85 ± 26	2,302

Table 2: Top four GLMMs with relevant independent variables – random effect, March snow depth (m), March snow density (kg · m^{-3}), growing season precipitation (mm · day^{-1}), and terrain slope percent. Model assessment values – No. of parameters K^A, second order Akaike information criterion (AICc), delta AICc (ΔAIC = AICi – minimum AICc), and AICc weight (Wt).

No.	GLMM	K^A	AICc	ΔAICc	Wt
1	range unit + depth + density + slope + precip.	6	7540.06	0	1
2	range unit + depth + slope + precip.	5	7567.59	27.52	0
3	range unit + depth + precip.	4	7578.10	38.03	0
4	range unit + depth + density + slope	5	7586.18	46.12	0

Table 3: GLMM fixed effect parameters – March snow depth (m), March snow density (kg · m^{-3}), growing season precipitation (mm · day^{-1}), and terrain slope percent – and their associated conditional mean coefficient estimate (Estimate), standard error of the mean (SE), lower and upper bound of the 95% CI, F-statistic (F-value), and significance statistic (P-value).

Parameter	Estimate	SE	Lower	Upper	F-value	P-
snow depth	-1.393	0.131	-1.652	-1.139	112.1	< 0.001
snow density	-0.0008	0.0002	-0.001	-0.0005	27.7	< 0.001
slope	-0.016	0.004	-0.025	-0.008	16.0	< 0.001
precipitation	+0.358	0.052	+0.257	+0.460	48.0	< 0.001

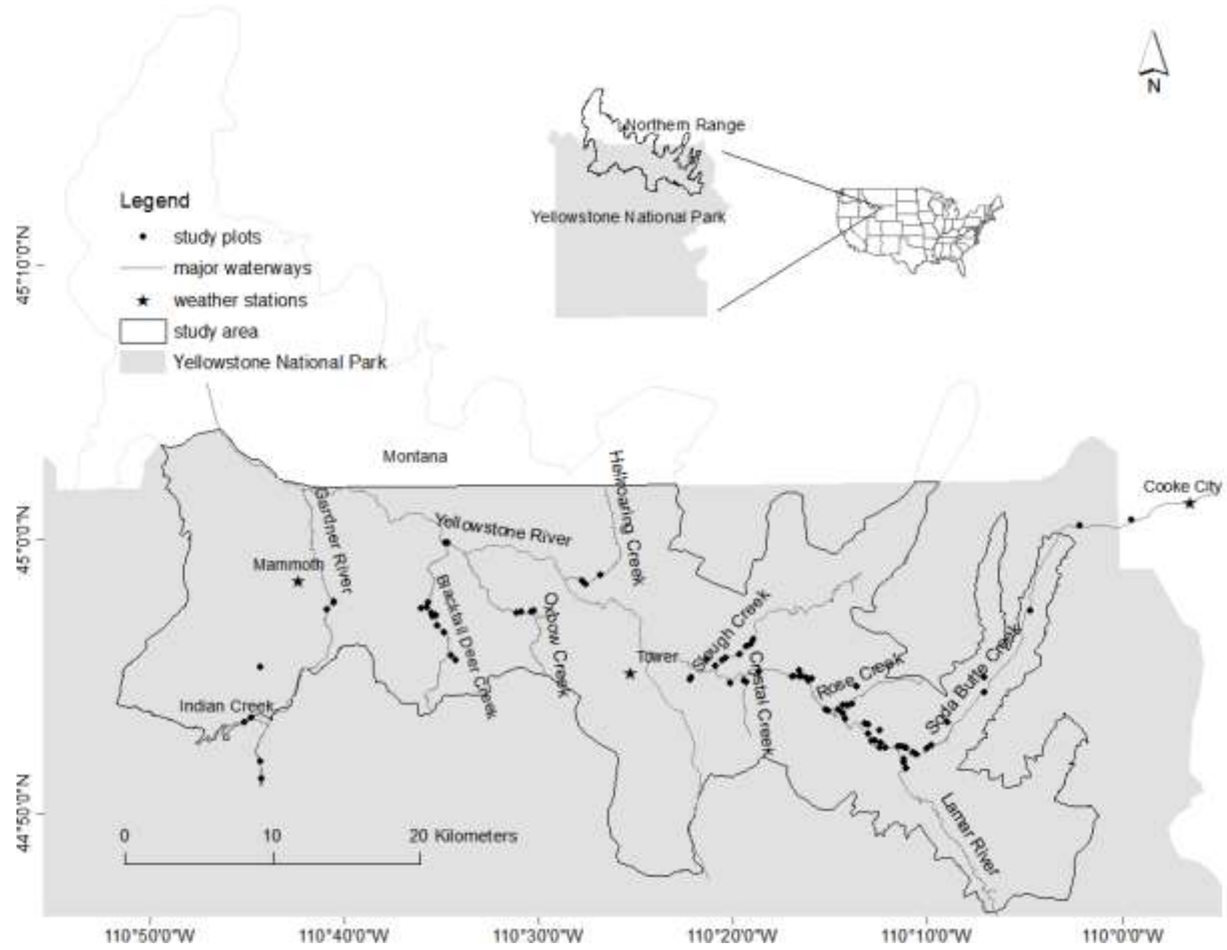

Figure 1: Study area map showing the locations of study plots (black diamonds, n=86), waterways and weather stations (stars, n=3) within Yellowstone's NR.

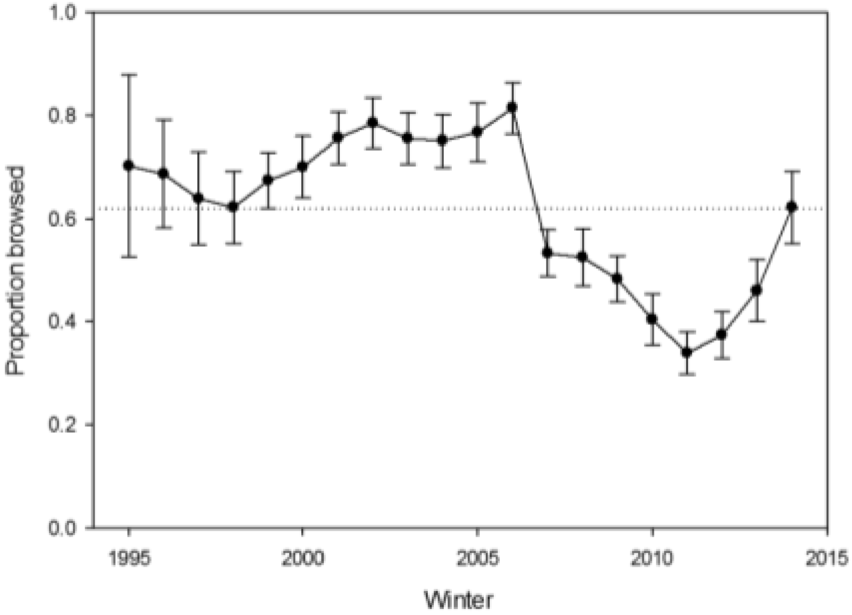

Figure 2: Annual means (± 95% CI) of the proportion of stems browsed by ungulates within Yellowstone's NR willow communities per winter 1995-2014. Dotted line represents the overall, study period mean.

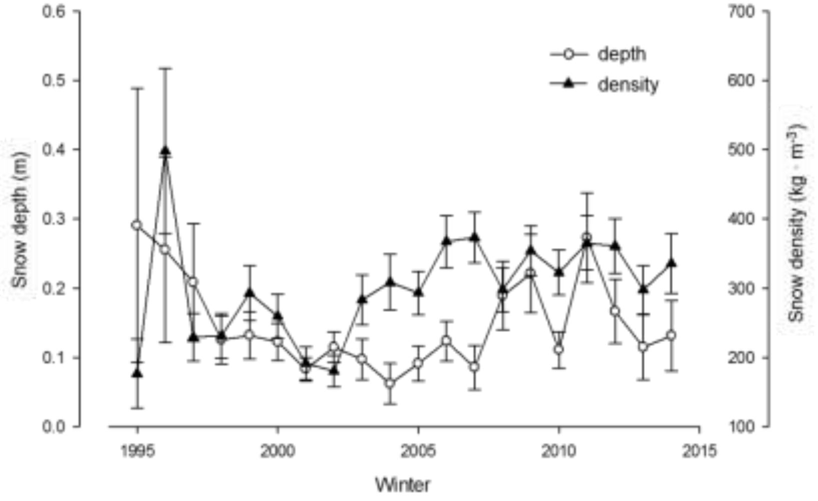

Figure 3: Yellowstone's NR mean snow depth (open circles) and snow density (closed triangles) at existing study plots (n = 10 to 86 plots per yr) derived from NR snow depth and SWE model at 30-m resolution from 1995-2014. Data are means ± 95% CIs.

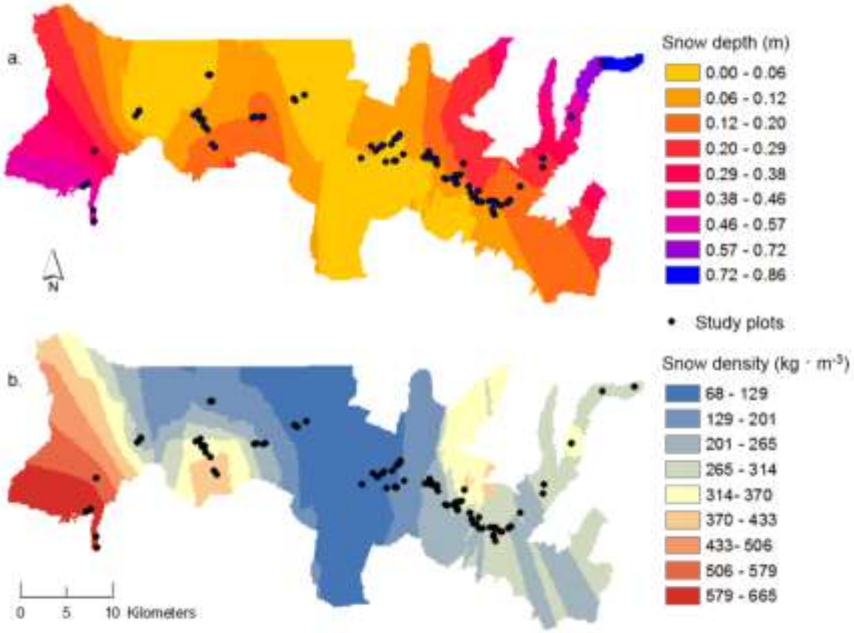

Figure 4: Maps display study period (1995-2014) mean snow depth (a.) and mean snow density (b.) distributions across Yellowstone's NR as calculated by ordinary kriging of the study plot means. Note the broad range of snow conditions existing among the established study plots (black dots).

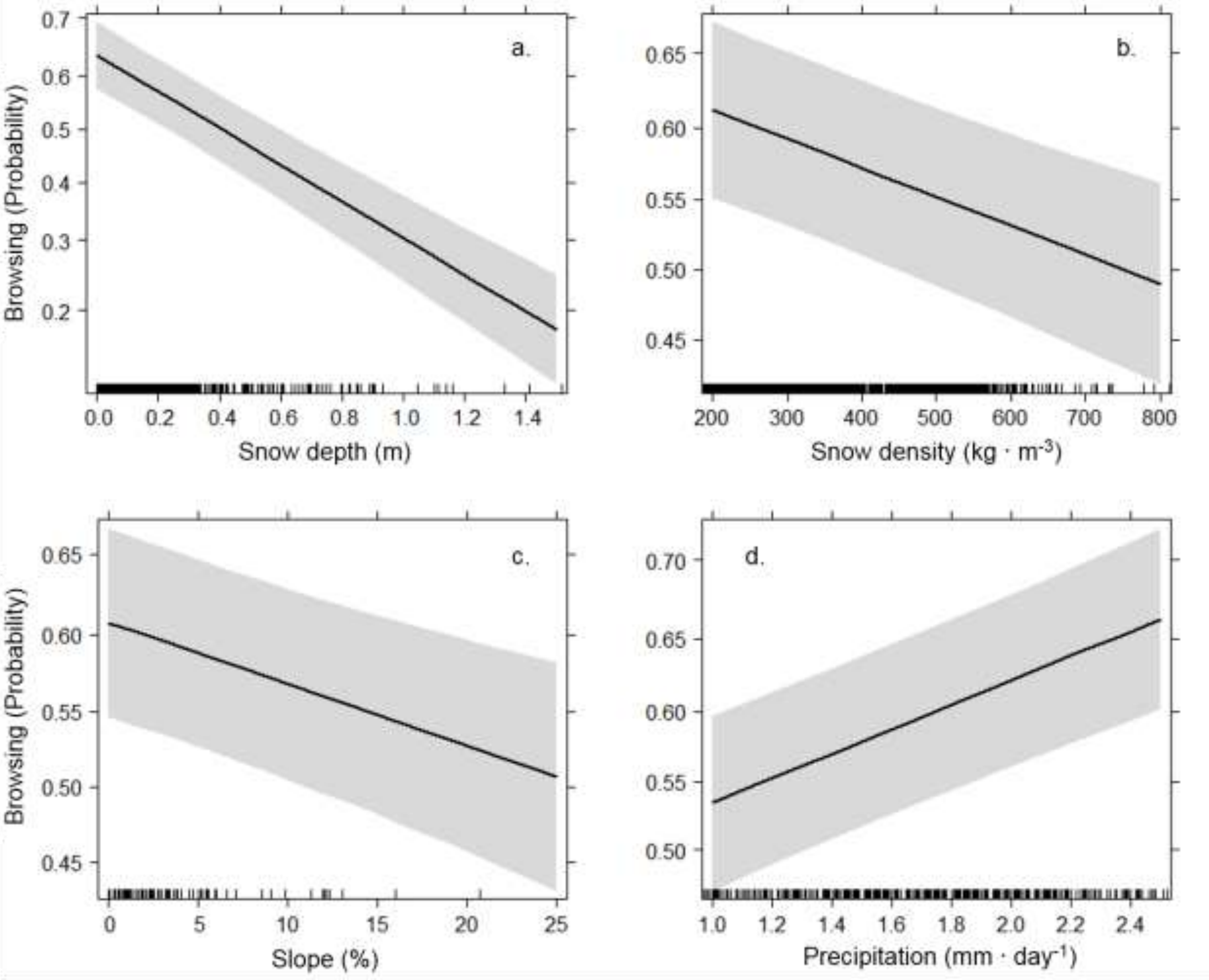

Figure 5: R effects package display to illustrate the magnitude of effect and effect direction for NR browsing probability in response to March snow depth (a.), March snow density (b.), terrain slope (c.), and growing season precipitation (d.). Gray area represents 95% CIs. Tick marks represent study plot occurrences.

APPENDICES

Table S1: species' plant count and approximate percent of total sample size each collection year (2002, 2006, 2010, and 2014).

year	species	plant count	% of total
2002	Willow	916	93%
2002	Cottonwood	23	2%
2002	Aspen	46	5%
2006	Willow	843	91 %
2006	Cottonwood	39	4 %
2006	Aspen	41	4 %
2010	Willow	685	88 %
2010	Cottonwood	19	2 %
2010	Aspen	23	3 %
2014	Willow	725	89 %
2014	Cottonwood	10	1 %
2014	Aspen	30	4 %

Table S2: list of the 7 range units, No. of plots and No. of sampled stems from 1995-2014 on the NR of Yellowstone.

Range unit	Name	plots	samples
Blacktail	Blacktail Deer Creek & Oxbow Creek sites	249	2883
Corridor	Hellroaring Creek & canyon corridor sites	114	888
Indian	Indian Creek & Swan Lake	55	730
Lamar 1	Lamar River Valley & Soda Butte confluence sites	301	3294
Lamar 2	Lamar River Valley & Rose Creek sites	268	2442
Slough	Slough & Crystal Creeks	219	2437
Soda Butte	Soda Butte Creek	118	1153

Table S3: Summary table for monthly snow characteristics' Pearson r.

Snow depth					Snow density				
month	Dec.	Jan.	Feb.	March	month	Dec.	Jan.	Feb.	March
December	.	0.94	0.94	0.91	December	.	0.7	0.68	0.6
January	0.94	.	0.98	0.97	January	0.7	.	0.96	0.88
February	0.94	0.98	.	0.97	February	0.68	0.96	.	0.92
March	0.91	0.97	0.97	.	March	0.6	0.88	0.92	.

Table S4: complete VIF analysis of monthly snow characteristics.

	Feb. SWE	March SWE	Feb. depth	Jan. depth	Feb. density	Jan. SWE	Jan. density	March depth	March density
VIF 1	616.1	239.8	281.2	210	74.2	361.5	54.7	158.3	19.7
VIF 2	-	162.7	91.6	137.5	46.7	127.2	41.7	133.2	17.9
VIF 3	-	-	90.2	82.5	46.5	16.3	35.2	52	13.6
VIF 4	-	-	-	43.6	37.4	15.7	30.8	35.6	12.4
VIF 5	-	-	-	-	37.2	12.5	30.2	10.2	11.5
VIF 6	-	-	-	-	-	12.3	10	9.9	8.9
VIF 7	-	-	-	-	-	-	9.2	1.2	8.9
VIF 8	-	-	-	-	-	-	-	1.2	1.2

Table S5: VIF analysis table for March characteristics and mean January-March snow characteristics.

	Ȳ depth	Ȳ density	March depth	March density
VIF 1	120.5	31.2	120.1	30.8
VIF 2		29	1.3	28.1
VIF 3			1.2	1.2

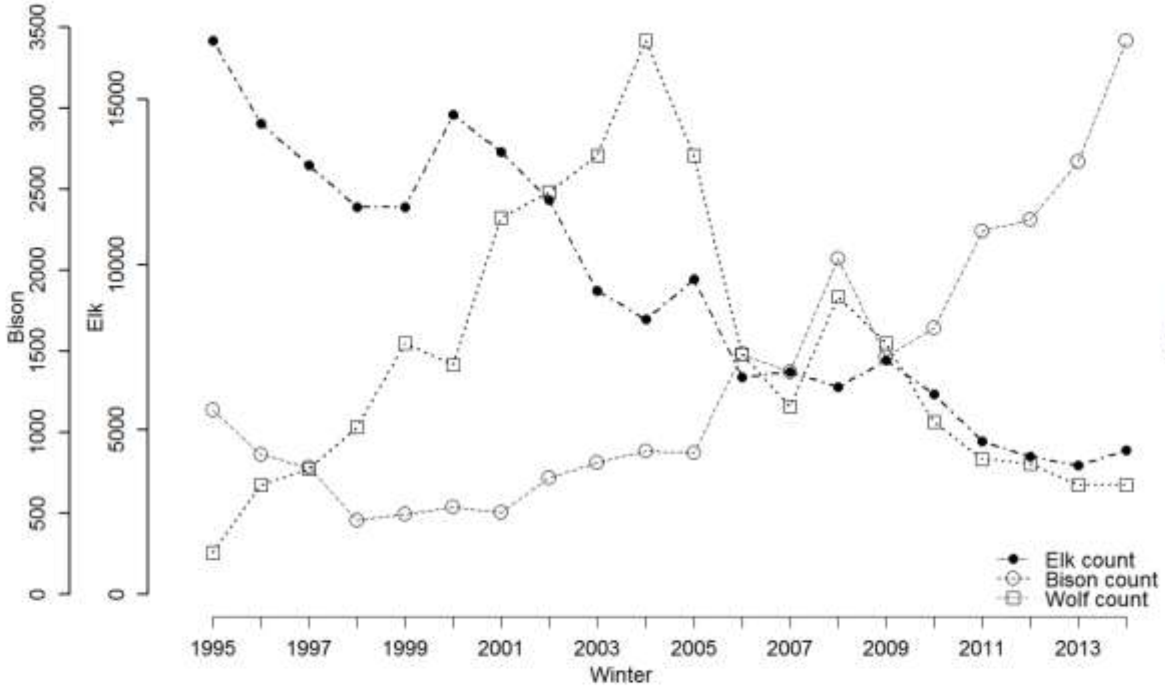

Figure S1: Yellowstone's northern range elk, bison and wolf (yearling to adult age) populations[1] per winter 1995-2014.

[1] Counts obtained through the Yellowstone Center for Resources, Yellowstone National Park (Smith et al. 1995-2014; Blanton 2013; Wyman 2013; [NPS] 2015). Simple imputation was used to estimate the 1996, 1997, and 2014 elk population count (Belile thesis 2016). Note that wolves were not re-introduced to Yellowstone's northern range until mid to late March.

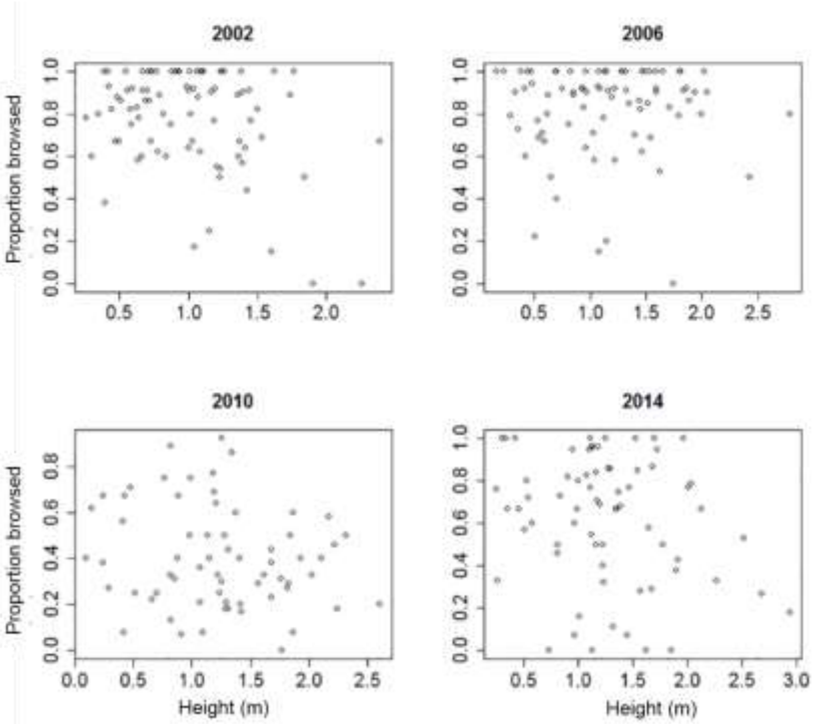

Figure S2: Illustrates the mean proportion of stems browsed per average plant height within plots for each field season.

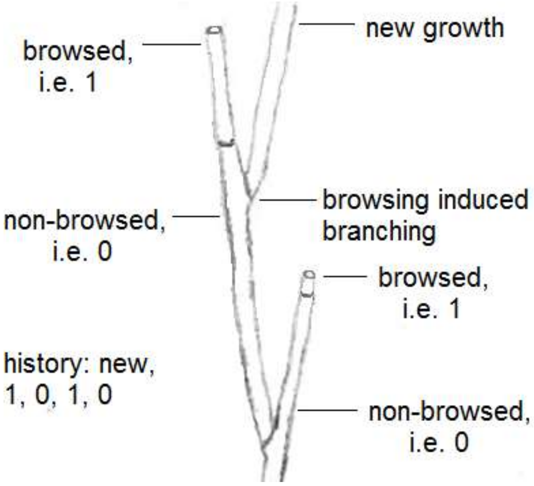

Figure S3: Illustration of stem browsing history, i.e. non-browsed and browsed leaders and subsequent branching below terminal growth scar.

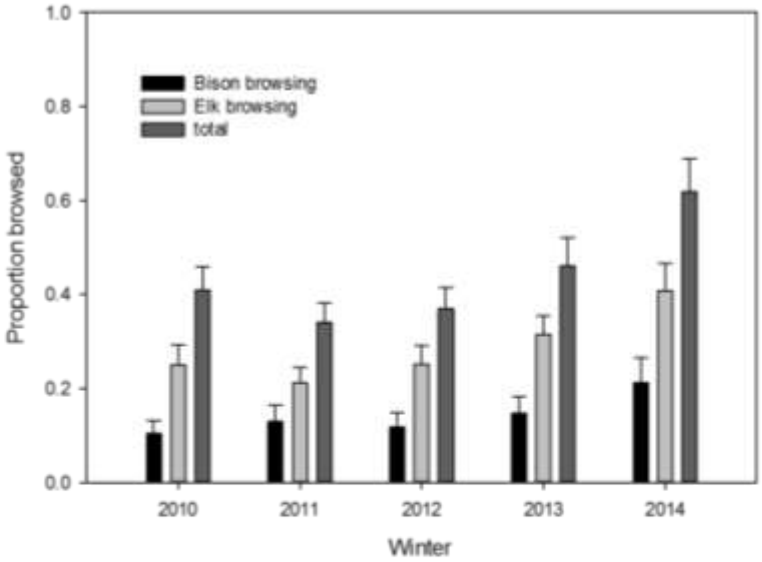

Figure S4: Total annual mean proportion of stems browsed within willow communities by ungulates per winter 2010-2014, mean proportion browsed by elk per winter 2010-2014, and mean proportion browsed by bison per winter 2010-2014 on the NR of Yellowstone. Means have 95% CIs.

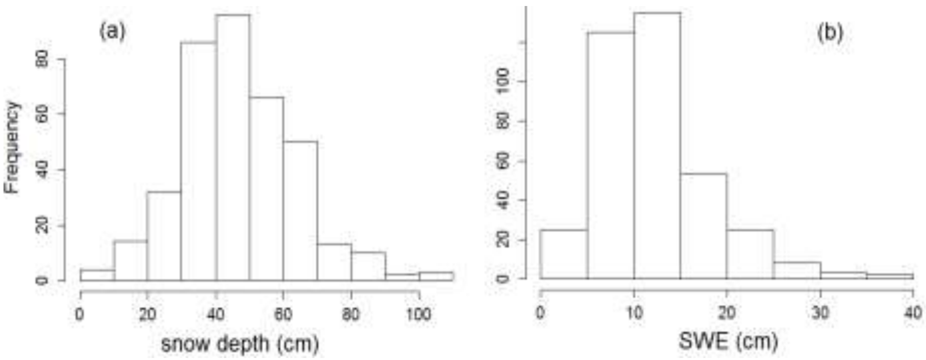

Figure S5: histograms represent the distribution of 1993 NR snow depth (a) and SWE (b) measurements.

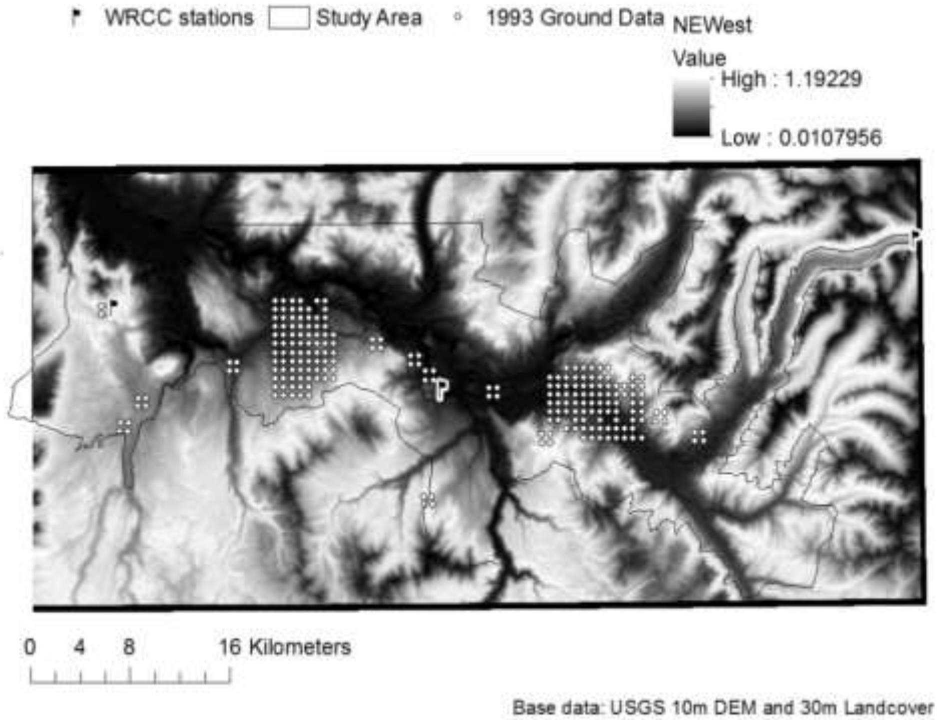

Figure S6: map showing 1993 NR snow measurement locations and NEWest snow depth model.

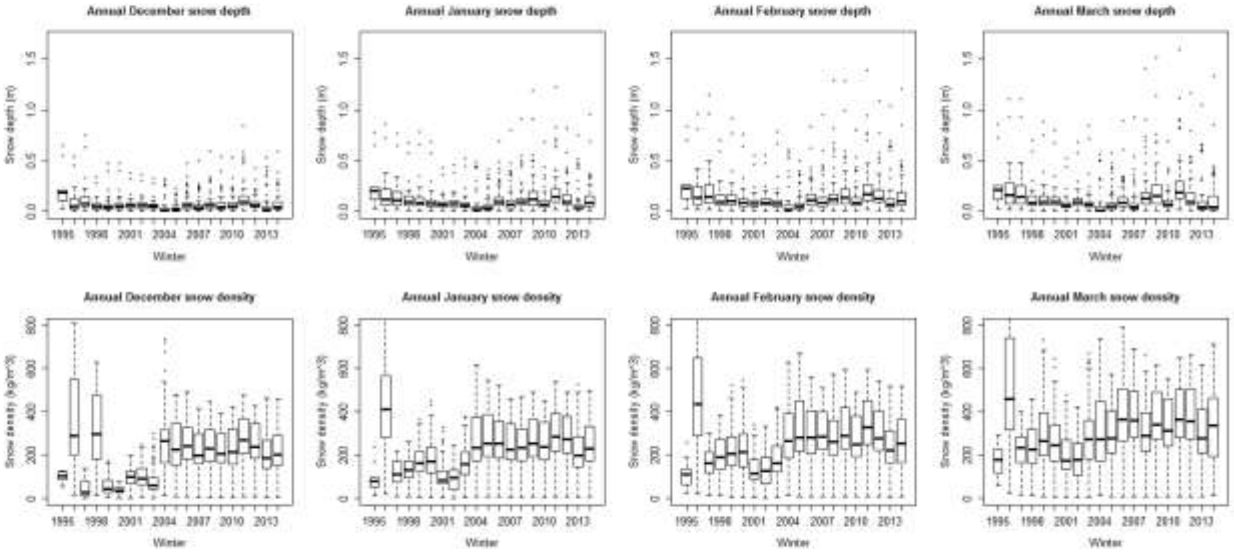

Figure S7: Separate boxplot graphs illustrate monthly snow depth and snow density distributions from 1995 through 2014 on the NR.

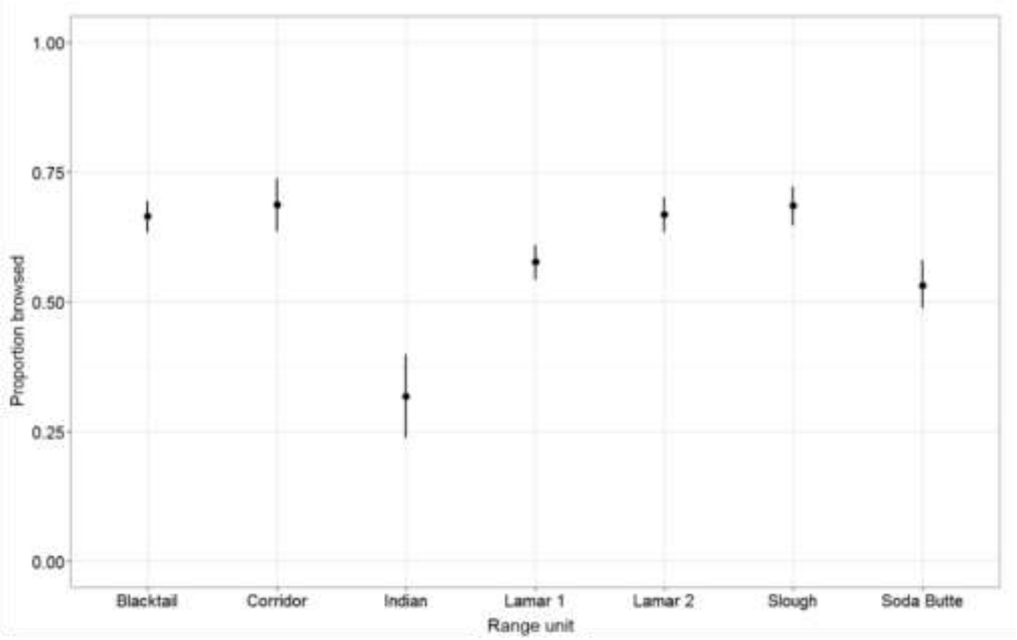

Figure S8: Variation in mean proportion of leaders browsed (± 95% CI) per range unit winter 1995-2014 within NR of Yellowstone.

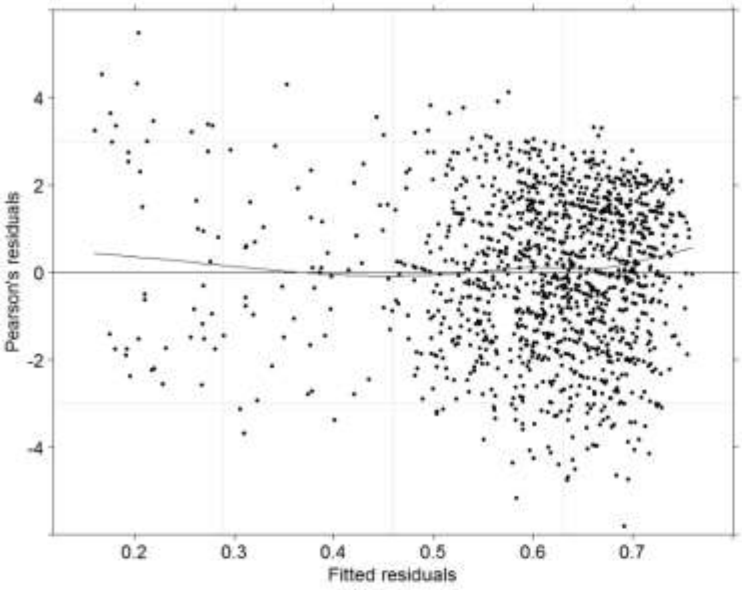

Figure S9: Pearson's residuals for GLMM plotted against the models predicted residuals to assess model fitting to the proportion of stems browsed across the NR of Yellowstone.

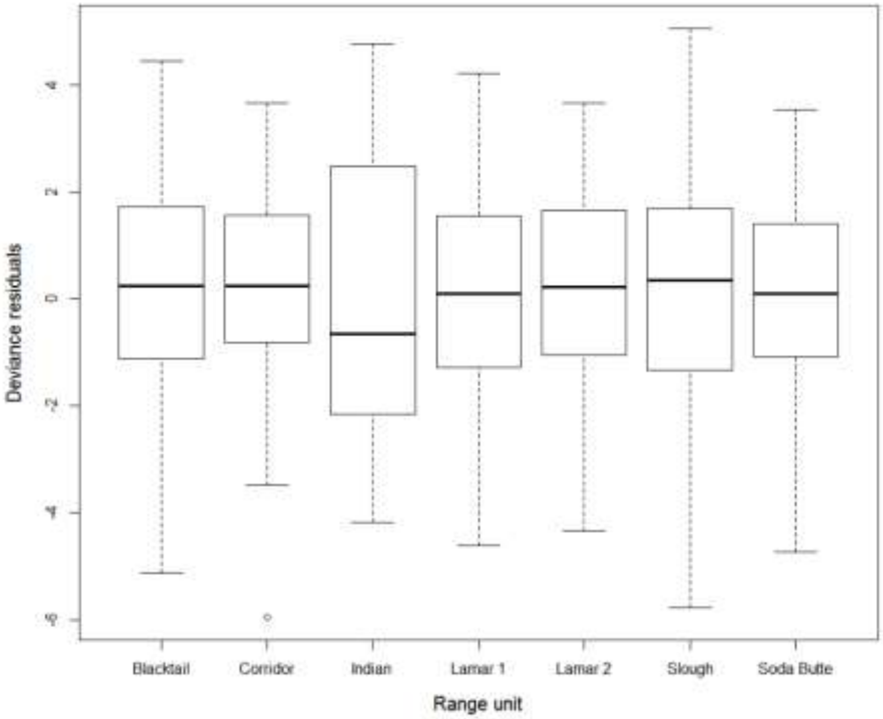

Figure S10: illustrates GLMM deviance residuals for the annual NR proportion browsed per range unit winter 1995-2014.

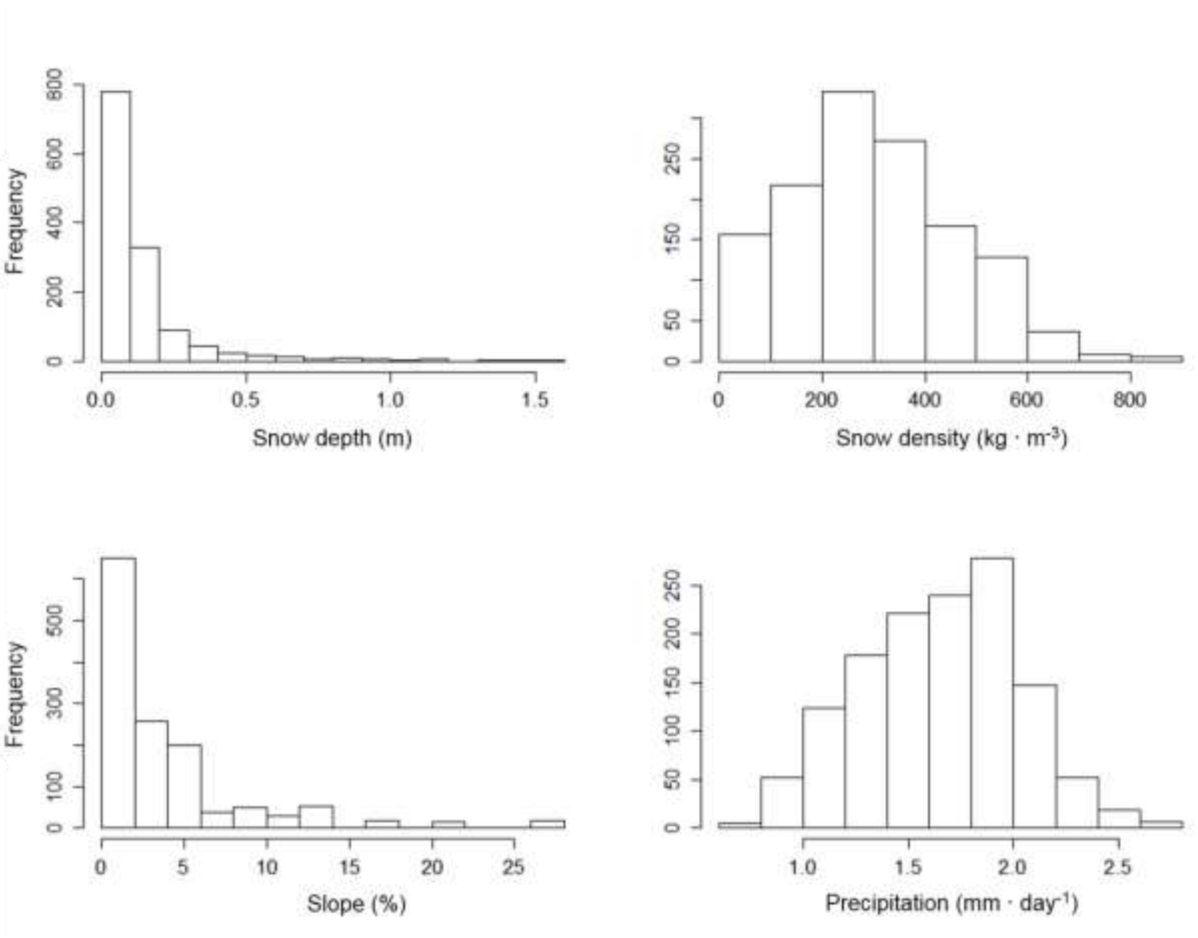

Figure S11: Frequency histograms show distributions of March snow depth, March snow density, growing season precipitation and terrain slope for the 20 yr study period within Yellowstone's NR.

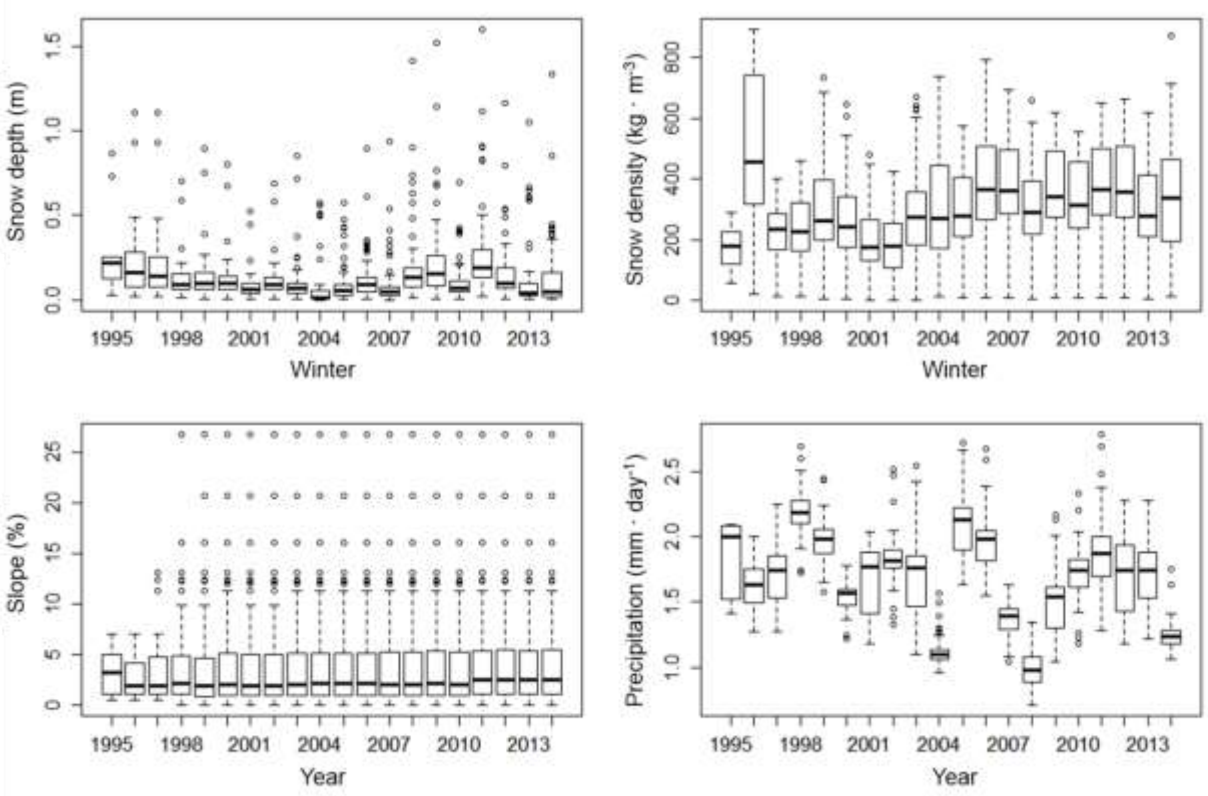

Figure S12: Boxplots show interannual distributions of March snow depth, March snow density, growing season precipitation and terrain slope for the 20 yr study period within Yellowstone's NR.

Total ungulate browsing justification

Bison browsing was only recorded by the field season team in 2014, as such, bison browsing data could only account for bison browsing back to winter 2010 for three primary reasons. Foremost the 2014 team realized the potential bias resulting from apparent bison browsing history from older stems that could have been broken by bison or by some other means, i.e. frayed, torn stems with multiple growth rings could have been aged bison browsing or aged broken stems, which looked very similar. The second reason is that when building the browsing history dataset, 2010 is the separate field seasons' data overlap year. Third, bison browsing prior to 2010 comprised an unknown proportion of total browsing history extending back to 1995. Moreover, elk and bison browsing trends with total browsing for the recorded history (Fig. S4). Further, the data collected by the 2010 field team indicated that the overall NR mean proportion of leaders browsed by elk was 0.39, while the total estimate based on data collected by the 2014 team was 0.41 of which elk browsing accounted for only 0.25. In light of these uncertainties, the conservative decision was to use total ungulate browsing data as the response in the GLMM for all years 1995-2014.

Plot count and plant identification

The Yellowstone Ecological Research Center (YERC) in Bozeman, MT collected field data on the NR during late summer and autumn of 2002, 2006, and 2010. The three sample periods included 86 original sites in 2002, 82 in 2006, and 66 in 2010. The reason for the difference in site numbers between 2002 and 2006 was that plots 85 and 87 were not relocated, plot 36 had eroded, prairie rose was measured at plot 55 in 2002, and no willow presence was noted at plot 27. The difference between 2006 and 2010 was due to non-relocation of 15 plots, dead plants at plot 28, and plant absence at plot 37. Summer 2014, my team collected data from 72 sites. Near the Soda Butte and Lamar River confluence plots 9, 14, and 16 had completely eroded. All plants at plot 33 and 45 were either dead or eroded; mortality was likely due exclusively or in combination to drought, low water levels, and/or browsing. Plants at plots 26, 29, 61, & 83 were entirely gone, including dead bases. Plots 57 and 72 were not done because they were not done in 2010.

Summer 2014, we re-located the plot coordinates of 81 plots (excluding plots 57, 72 and those omitted in 2010) previously marked by YERC. We attempted to relocate every plant measured in 2010 or 2006 using 2006 plant coordinates, plot sketches, and photographs. Approximately 35% of the plants measured in 2006 were positively identified as the same plants from 2002 and 51% were probably the same plant. In 2010, 22% were positively the same plant as in 2006 and 72% of identifications were probable. Summer 2014, 21% of plants were positively identified as the same plants from either 2010 or 2006 field seasons. Relocation of 41% of plants was likely, based on 2014 plant waypoint occurrence within a 2m buffer derived from 2006 plant coordinates. We marked each plant and plot corner to 100% accuracy using a Garmin Dakota 10, and recorded video of each plant and plot corner. We also noted each plot's species composition and abundance of all woody vegetation (e.g., willow, aspen, cottonwood, and alder). Visual estimation of ground cover was done using a plot’s edge meter tape for reference.

Browsing history taken within winter 2000 and 2014

YERC collected browsing data (n = 1776 sampled stems) in winter 2000 from 14 transects during January-April. Winter willow phenology is especially important because snow characteristics have been the most ignored factor affecting browsing intensity on willow across the NR (YERC, unpubl. data). The winter 2000 transect data indicated that the proportion of leaders browsed increased from 0.11 in December to 0.58 by end of April at an average rate of 0.09 per month, with the greatest increase of 0.16 in March (YERC, unpublished data, 2000). In winter 2014, 13 of the original 14 transects were resampled (n = 6131 sample stems) during November and January-April. Winter 2014 browsing data indicated that the proportion of leaders browsed increased from 0.22 in November to 0.51 by end of April at an average rate of 0.05 per month, with the greatest increase of 0.12 in March (YERC, unpublished data, 2014).

Snow characteristics modeling

First, we used the regression coefficients between 1-km IDW (inverse distance weighted) interpolation snow depth (m) estimates (Blanchet, J. and M. Lehning, 2010) and SNODAS snow depth (m) estimates to correlate them 1:1 for 2004-2014 winters, their correlation was $r^2 = 0.43$. Specifically, using linear modeling, we regressed December-April monthly mean IDW depths (values from each study plot; 4,126 values total) against December-April monthly mean raw SNODAS depths (values from each study plot; 4,126 values total) to estimate regression slope and intercept coefficients; the r^2 was 0.43. We multiplied the original IDW grids by the regression slope coefficient (0.91) and added the intercept coefficient (0.17) prior to study plot level, raster sampling and again regressing the modified IDW depths against SNODAS depths. Modified IDW snow depth and raw SNODAS snow depths remained correlated with an r^2 of 0.43, however, their new regression slope was 1.0051 and the new intercept was -0.0004. Using the slope-intercept coefficients, we generated regression corrected IDW snow depth estimates for the 1995-2003 period. Specifically, we sampled interpolated IDW depth values for each month (December-April) and modified them by the IDW~SNODAS regression slope (0.91) and intercept (0.17).

Second, we used ground data and maximum likelihood to estimate snow depth coefficients for continuous 10 -m elevation and 10-m aspect gridded geospatial layers (rasters) and a 30-m classified land-cover raster. We used the normally distributed 1993 NR snow depths (Fig. S6) as our response in a GLM (generalized linear model) with Gaussian family and identity link function. Through winters 1993-1995 ground snow depth measurements (n = 1544) were collected seven days per month, on average, during January-March. In 1993, 448 snow depth measurements were collected from a 600-m grid network (Fig. S6). We held back 10% of the

1993 data for validation and used the remaining for GLM coefficient generation. We included classified elevation (5 classes) and cosine of aspect (northness), however according to lowest AIC and the greatest ANOVA F-statistic and the lowest χ^2 significance P-value statistic the best-fitted model included elevation (m), aspect (degrees), and land-cover. Resulting χ^2 significance P-values for elevation, aspect, and land-cover (non-forested) coefficient estimates were < 0.001.

Third, we rescaled the elevation raster and aspect raster using Rescale by Function tool [ESRI]; we set the distribution for both aspect and elevation to Gaussian. For elevation, we left the upper and lower thresholds to default of the elevation raster and used the difference between highest elevation (3,360.77 m) and lowest elevation (1,568.13 m) to set rescale from range 1 to 1,793 m. We rescaled aspect in the same manner leaving upper and lower thresholds to default of the aspect raster and rescaled from 1 to 360. We then multiplied the rescaled elevation and aspect rasters by their respective GLM coefficients. It is important to ignore the negative sign (-) in front of the aspect and land-cover coefficients. For land-cover, we simply reclassified the non-forest class (p-value < 0.001) by corresponding coefficient and reclassified forest class (no p-value) to zero, so forest cells within the land-cover raster would not affect the final coefficient model. Finally, we used raster calculator to generate the final snow coefficient raster, i.e. (elevation + aspect + landcover)/100 = snow depth model (NEWest; Fig. S4) at 30-m resolution.

We validated NEWest downscaled daily IDW interpolation estimates corresponding to the day of point measurements using the 10% hold-out data from 1993 and all 1994 and all 1995 depth measurements. After application of 30-m NEWest to 1-km IDW snow depth estimates, the correlation between downscaled IDW snow depth at measurement point coordinates was r^2 = 0.39, which means that our model accounts for 39% of the variation in snow depth. We also compared downscaled IDW snow depths and downscaled SNODAS snow depths for January-

March 2004-2014. The correlation between raw 1-km IDW snow depth estimates and raw 1-km SNODAS snow depth estimates before application of 30-m NEWest was $r^2 = 0.38$, and after application of NEWest to both estimates they were correlated with $r^2 = 0.79$.

Moreover, we used the same probability based method to downscale 1-km SNODAS SWE (kg/m^2) and 1-km Daymet SWE (kg/m^2) to a 10-m resolution based on SWE measurements that were approximately normally distributed with a right skew (Fig. S6). At nearly every point that YERC took ground measurements of snow depth, technicians also measured SWE. First, we regressed 1-km Daymet SWE against 1-km SNODAS SWE for January-March 2004-2014, their r^2 was 0.19. We used the linear regression slope-intercept to align them 1:1 before applying the SWE coefficient model (SWEest). SWEest was the product of the rescaled 10-m elevation raster multiplied by the GLM coefficient for elevation. The reason for only using elevation was that the best GLM, according to AIC and χ^2 p-value, for SWE coefficient estimation only included elevation. As a result, we generated SWEest at a 10-m resolution. Our only validation of SWEest was the comparison of downscaled 10-m Daymet SWE with downscaled 10-m SNODAS SWE after application of SWEest. Recall that the correlation between raw Daymet SWE and raw SNODAS SWE for 2004-2014 was $r^2 = 0.19$. After application of SWEest to both 1-km estimates, the correlation improved to $r^2 = 0.80$. Because both Daymet SWE and SNODAS SWE have been validated and used in published research we accepted downscaled SWE estimates as valid.

Analysis of December and March snow characteristics

Statistical and graphical observations, in conjunction with the within winter browsing observations in winters 2000 and 2014, which indicated monthly increases in browsing with the highest increase in March, warranted further exploratory analysis of December and March snow characteristics to determine if December inclusion was justified. Comparison between December and March snow depths and snow densities (data not shown) in winter 2000 indicated high correlation for snow depths ($r^2 = 0.99$) and snow densities ($r^2 = 0.92$), whereas in 2014 correlation was high for snow depth ($r^2 = 0.92$) and less synchronous for snow densities ($r^2 = 0.78$). Comparison of December snow depth and snow density in winter 2000 with December depth and density in 2014 revealed very low correlation for snow depths ($r^2 = 0.01$) and zero correlation for snow densities ($r^2 = 0.00$). Comparison of March snow depth and snow density in winter 2000 with March depth and density in 2014 revealed zero correlation for snow depths ($r^2 = 0.00$) and snow densities ($r^2 = 0.00$). A closer inspection showed that winter 2000 mean December snow depth was 0.07 m and mean density was 36.7 kg·m^{-3}, whereas winter 2014 mean December snow depth was 0.08 and mean density was 207.6 kg·m^{-3}. A closer inspection of March in winter 2000 showed mean March snow depth was 0.12 m and mean density was 260 kg·m^{-3}, whereas winter 2014 mean March snow depth was 0.13 and mean density was 336 kg·m^{-3}. To summarize, we observed the highest rate of browsing in March during two winters with very different snow depths and densities, lower in winter 2000 and higher in 2014 for both characteristics. Consideration of these correlations, during two winters when we do have within winter browsing data, alongside the study period correlations for December and March snow depths and snow densities ($r^2 = 0.91$ and $r^2 = 0.6$ respectively; Table S3) suggests that December snow depth and snow density are confounding covariate candidates. Hence, we infer that inclusion of December characteristics in the GLMM analysis could lead to confusing or wrong ecological interpretation. December snow characteristics were excluded from further analysis because they are poor indicators of overall winter snow conditions (Fig. S7), and there is no definitive way to determine what portion of December browsing identified during the two winter phenology seasons was actually attributable to browsing that occurred during the growing season and fall.

GLMM residual deviance analysis

We checked dispersion of residuals for GLMM No. 1 with Pearson's χ^2 statistic (Bolker et al. 2008), which is calculated by dividing the sum of a model's Pearson's residuals squared by the model's residual deviance; value > 1 = over-dispersion. Our well-fitting model GLMM No. 1 was under-dispersed. Moreover, we performed model validation for GLMM No. 1 via a 10-fold cross-validation (Agresti 2002). We randomly shuffled the dataset and used 90% for training and 10% to test the model's validity. Pearson's χ^2 dispersion value (Bolker et al. 2008) for the trained GLMM and the test GLMM were calculated and compared to check for over-dispersion; neither training nor test GLMMs were over-dispersed for GLMM No. 1, here forth GLMM.

In addition, we also plotted our GLMM's dependent Pearson's residuals ($r_{Pi} = (y_i - u_i) * \surd$ $(w_i / V(u_i)$: where Pearson's residual = $\surd$ ith contribution to Pearson's chi-square) against predicted residuals ($r_i = y_i - u_i$: where y_i=ith response and u_i = corresponding predicted mean) to assess model fit (Fig. S9). Residuals were plotted about a theoretical mean of zero; convergence of values close to zero implied a well-fitting model (Agresti 1992). For GLMM, the mean of Pearson's residuals was 0.06, the median was 0.18, the 25th percentile was -1.21 and the 75th percentile was 1.33. Clustered residuals about the lower y-axis single digits, suggested that our final GLMM was well fitted for corresponding response and predictor variables.