

WILLOW ON YELLOWSTONE'S NORTHERN RANGE: EVIDENCE FOR A TROPHIC CASCADE?

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Abstract. Reintroduction of wolves (*Canis lupus*) to Yellowstone National Park in 1995–1996 has been argued to promote a trophic cascade by altering elk (*Cervus elaphus*) density, habitat-selection patterns, and behavior that, in turn, could lead to changes within the plant communities used by elk. We sampled two species of willow (*Salix boothii* and *S. geyeriana*) on the northern winter range to determine whether (1) there was quantitative evidence of increased willow growth following wolf reintroduction, (2) browsing by elk affected willow growth, and (3) any increase in growth observed was greater than that expected by climatic and hydrological factors alone, thereby indicating a trophic cascade caused by wolves. Using stem sectioning techniques to quantify historical growth patterns we found an approximately twofold increase in stem growth-ring area following wolf reintroduction for both species of willow. This increase could not be explained by climate and hydrological factors alone; the presence of wolves on the landscape was a significant predictor of stem growth above and beyond these abiotic factors. Growth-ring area was positively correlated with the previous year's ring area and negatively correlated with the percentage of twigs browsed from the stem during the winter preceding growth, indicating that elk browse impeded stem growth. Our results are consistent with the hypothesis of a behaviorally mediated trophic cascade on Yellowstone's northern winter range following wolf reintroduction. We suggest that the community-altering effects of wolf restoration are an endorsement of ecological-process management in Yellowstone National Park.

Key words: annual ring; elk; predation risk; *Salix*; trophic cascade; willow; wolves; Yellowstone National Park (USA).

INTRODUCTION

Since 1968, the ecological communities of Yellowstone National Park have been managed under a natural-regulation paradigm (Singer et al. 1998, Huff and Varley 1999). Natural regulation also has been described as “ecological-process management” (Boyce 1991) referring to the practice of allowing natural ecological processes to function with minimal human interference. Management of Yellowstone and other national park ecosystems under this paradigm has led to debates over management of park resources (Boyce 1998, Peterson 1999, National Research Council 2002, Wagner 2006). One assertion is that Yellowstone's elk (*Cervus elaphus*) population was limited largely by winter severity, forage production, and density-dependent processes prior to wolf (*Canis lupus*) recovery, and the population was in dynamic equilibrium (Merrill and Boyce 1991, Coughenour and Singer 1996, Singer et al. 1998, Taper and Gogan 2002). However, concerns have been expressed that under natural regulation high herbivore densities have altered plant communities

(Yellowstone National Park 1997, National Research Council 2002). While evidence suggests grassland communities experienced enhanced productivity with herbivory (Frank and McNaughton 1993), some woody plant communities on the northern winter range may be suppressed under high browsing pressure (Singer et al. 1994, Wagner et al. 1995, Kay 1998). For example, based on photographic evidence, the area of willow (*Salix* spp.) communities has declined by ~50–60% since the early 1900s (Chadde and Kay 1991, Soulé et al. 2003) amounting to 0.4–0.8% of the park area (Houston 1982).

Declines in willow on the northern winter range may be attributed to a number of factors, but high ungulate densities, particularly elk, have been cited as the principal cause (Chadde and Kay 1991, Wagner et al. 1995, Kay 1998, Wagner 2006). Alternatively, it has been suggested (Singer 1996) that loss of riparian willow habitat may have occurred following local extirpation of beaver (*Castor canadensis*) populations, and others (Houston 1982, Singer et al. 1994, Romme et al. 1995) have suggested that willow declines may have been a result of plant stress associated with changes in climate and/or hydrology. Indeed, climatic records indicate an increase in mean summer temperature of 0.01°C/yr, a decline in the Palmer drought severity index (representing a trend toward increased aridity) of 0.019/yr and a decline in mean winter precipitation levels of 0.67 mm/yr during

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the past century (Balling et al. 1992). It has further been suggested (Houston 1982, Singer 1996) that most of the decline in willow may have occurred during an extended drought in the 1930s, when elk numbers were unknown, but are believed to be less than at present (Houston 1982). However, there is no direct evidence that links historical climate and/or hydrological changes to declines in willow on the northern winter range.

In addition to allowing ecological processes to regulate populations, the natural-regulation paradigm mandates the restoration ecological processes that have been altered or lost through human actions. In particular, restoration of top predators is necessary for the functioning of trophic relationships (Soulé et al. 2003, Ray et al. 2005). Until the reintroduction of 14 wolves in 1995 (Bangs and Fritts 1996) Yellowstone National Park had been without wolves for ~70 years, their extirpation due to predator-control efforts in early park management (Weaver 1978). By 2002 at least 78 wolves occupied the northern range (Smith et al. 2004b).

Reintroduction of wolves has been hypothesized to promote a trophic cascade by altering prey habitat selection patterns and behavior that, in turn, will lead to changes in plant community structure used by their prey (McLaren and Peterson 1994, Lima 1998, Berger et al. 2001, Smith et al. 2003). Although once thought to be uncommon in terrestrial systems (Strong 1992, Polis and Strong 1996, Lima 1998), recent evidence suggests that trophic cascading of carnivore effects on plants through their prey can be as significant in terrestrial systems as in other systems (Schmitz et al. 2000, Croll et al. 2005). Preliminary evidence indicates that wolves in Yellowstone National Park already may have induced changes in biomass accumulation and persistence of aspen (*Populus tremuloides*), cottonwood (*Populus* spp.; Ripple et al. 2001, Beschta 2003), and willow (*Salix* spp.; Ripple and Beschta 2006).

In this paper, we evaluate the evidence for a trophic cascade among wolves, elk, and willow. If a cascade has occurred since wolf reintroduction, we would expect to find evidence for a decrease in browsing on willow after wolf reintroduction compared to prior to wolf reintroduction, and an increase in willow growth in response to the release in browsing pressure. However, because browsing pressure has not been monitored consistently pre- and post-wolf reintroduction, we address the growth release of willow from browsing only indirectly. As a result, we suggest evidence for a trophic cascade is demonstrated by (1) willow growth increasing when browsing is reduced, (2) willow growth being greater after than before wolf reintroduction, and (3) the increase in willow growth after wolf reintroduction being greater than would be expected by alternative effects of climatic or hydrological factors.

STUDY AREA AND METHODS

This study was conducted on the Yellowstone National Park's northern range (Wyoming, USA;

110°23' W, 44°55' N), a 1526-km² area characterized by low elevation (1500–2000 m) grassland (*Festuca idahoensis*) and sagebrush (*Artemisia* spp.) grasslands fringed by coniferous forests (primarily *Pseudotsuga menzeseii*, *Picea engelmanni*, and *Pinus contorta*) and scattered aspen stands (Despain 1990). Average annual precipitation on the northern range ranges from 25.1 cm (Gardiner, Montana) to 42.2 cm (Tower Falls, Wyoming), with mean daily temperatures in Tower Falls of –10.4°C in January and 14.7°C in July (Western Regional Climate Center, Reno, Nevada, USA).

Sampling sites were located in the Blacktail, Oxbow, Geode, Slough, Lamar, and Soda Butte drainages (Fig. 1) at elevations ranging from 1840 to 2240 m. Drainage bottom vegetation commonly consists of a mixture of sedges and grasses (*Carex* spp., *Deschampsia cespitosa*, *Calamagrostis canadensis*), forbs, and shrubs (see Despain 1990 for a description of vegetation). The drainages range from broad floodplains up to 1 km wide (e.g., Lamar, Slough) to narrow, steep-walled gullies only a few meters wide (e.g., portions of Blacktail, Geode). On the sloped, upper reaches of drainages willow tends to occur only in close proximity (within rooting distance) of the stream, but can be widely distributed across the flat, wetter floodplains. This study focused on the two most common species of willow, *Salix geyeriana* and *S. boothii*, which can grow 4 m tall, although most willow clumps are much shorter due to heavy winter browsing by elk (Singer et al. 1994).

The wolf population has increased steadily since its reintroduction in 1995 with a population in 2002 of ~78 wolves occupying the northern range (Smith et al. 2004b). While individual pack boundaries and sizes are dynamic, there has been a continuous presence of wolves on the northern range since their reintroduction (Smith et al. 2003). Elk numbers prior to wolf reintroduction varied from a low of 3172 in 1968 to a high of 19045 in 1994, and have declined by an average of 4.5% per year from 1995 to 2002 although this includes years of increase and decline in numbers (Fig. 2; Coughenour and Singer 1996, White and Garrott 2005a). During winter, large herds of elk congregate in the valleys and foothills of the northern range (Houston 1982), while during summer elk typically move to higher elevations in the park (Mao et al. 2005). Elk are the principal prey for wolves, constituting 83% of their annual diet (Smith et al. 2004a). Moose (*Alces alces*) numbers on the northern range were at a high in 1970, but following the wildfires of 1988 moose became scarce and do not share winter range with elk on the northern range (Tyers and Irby 1995). Pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) also migrate to winter ranges that usually do not overlap the elk winter range (Barmore 2003).

Site selection and willow sampling

We conducted initial reconnaissance of willow distribution on the northern range from a fixed-wing aircraft

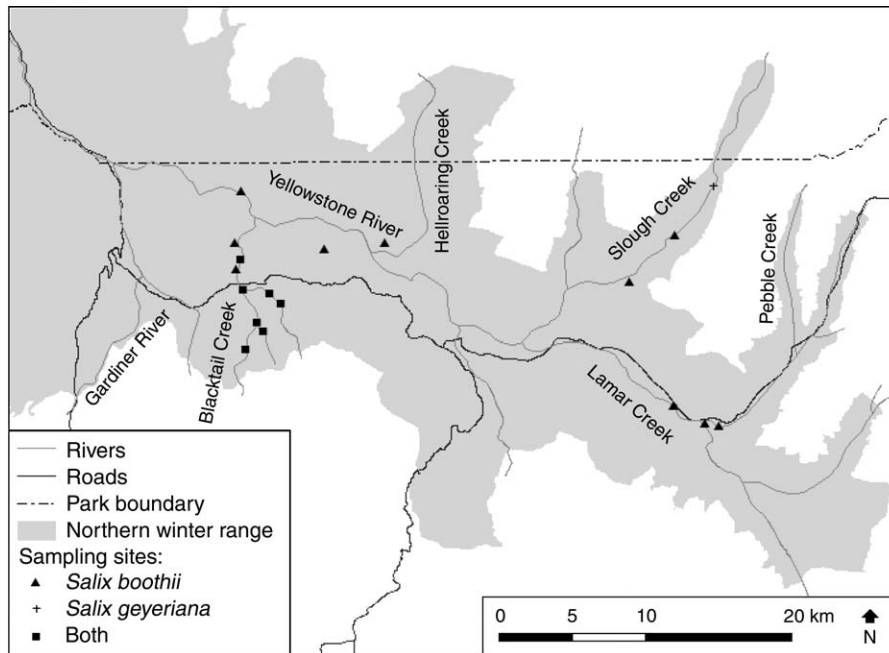


FIG. 1. Location of willow (*Salix boothii* and *S. geyeriana*) study sites on Yellowstone's northern range.

in July 2001 and identified 30 potential sites that appeared to have sufficient *S. boothii* or *S. geyeriana* to sample and that were at least 500 m apart. At each of the 18 sites at which one or both species were found to grow when visited, we established a 25-m transect oriented parallel to the stream passing through the center of the densest willow patches. At 1-m intervals along that transect we selected the closest individual willow clumps for sampling, with an individual willow clump defined as a cluster of stems emerging from the ground in close enough proximity to suggest they originated from the same root system. Within the clumps we selected a representative living stem of average height and recorded the species and stem height from base of stem to tallest point of previous and current-year growth. We recorded percentage of twigs browsed on a stem as an index to browsing pressure by counting the number of browsed and unbrowsed twigs from the previous year's growth (Y_{t-1}), or second year's growth (Y_{t-2}) (Keigley et al. 2003). A 10-cm sample of the basal portion of each stem was cut at ground level, wrapped in protective paper, marked with a unique identification number, and transported to the laboratory for sectioning.

Stem sectioning and growth-ring measurement

The basal end of each stem segment was sanded using fine-grit sandpaper, and the stem was soaked in water for at least 10 minutes, which softened the wood thereby making it easier to section. Stem sections (22–28 μm thick) were cut with a microtome until one complete, evenly cut section was obtained. The section was soaked in distilled water for 2–3 minutes to ensure similar levels

of hydration among all sections prior to mounting the section on a microscope slide. The section was then fixed in one drop of aqueous mounting fluid, covered with a cover slip, and sealed with nail polish. Slides were placed on a backlit stage and photographed with a Nikon digital camera (Nikon Canada, Mississauga, Ontario, Canada) attached to a 20 \times light microscope. A stage micrometer marked to 0.1 mm was placed on top of the

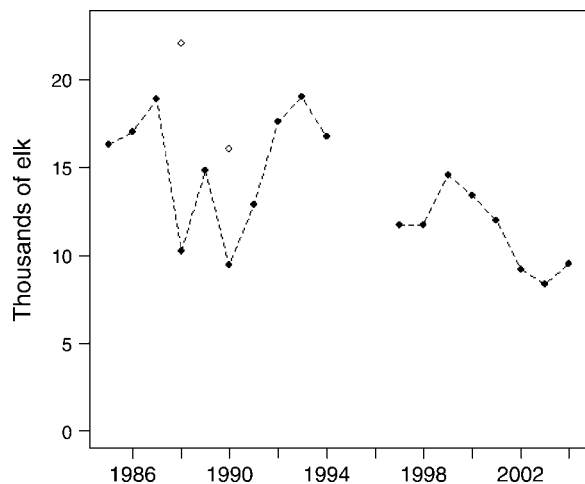


FIG. 2. Elk population counts (solid circles) on the northern winter range of Yellowstone National Park, USA (White and Garrott 2005a). The year corresponds to the December of the winter in which the count took place. No counts took place in the winters of 1995 and 1996. Due to poor survey conditions the counts for 1988 and 1990 are likely underestimates (White and Garrott 2005b); counts adjusted for sightability (open circles) in these winters were estimated by Coughenour and Singer (1996).

TABLE 1. Log likelihood values (LL), Akaike's information criteria scores (AIC), change in AIC score (Δ AIC), and AIC weights (w_i) for the top three of 12 candidate models relating variables to stem ring area of *Salix boothii* and *S. geyeriana* on the northern winter range of Yellowstone National Park, USA.

Model description	LL	AIC	Δ AIC	w_i
<i>Salix boothii</i>				
PYRA, PBRWS	-174.2	358.3	0.0	1.00
PYRA, PBRWS, ELEV	-179.8	371.7	13.4	0.00
PYRA, PBRWS, WSHED	-180.7	373.3	15.0	0.00
<i>Salix geyeriana</i>				
PYRA, PBRWS	-87.0	184.0	0.0	0.49
PYRA, PBRWS, ELEV	-86.2	184.5	0.5	0.38
PYRA, PBRWS, SNOW	-87.4	186.7	2.8	0.12

Note: Variables include the previous year's ring area (PYRA), the percentage of twigs on the stem browsed in the winter preceding growth (PBRWS), elevation (ELEV), watershed area (WSHED), and average snow depth (SNOW). PYRA and PBRWS are stem-level variables; ELEV, WSHED, and SNOW are site-level variables.

section prior to taking the image to provide a scale reference for ring measurements.

Ring widths were digitized from the images using custom software developed for ArcGIS (Environmental Systems Research Institute, Redlands, California, USA). Absolute ring area (square millimeters) of each growth ring was estimated from a minimum of four ring widths taken at approximately equal intervals around the circumference of the ring. When the ring approximated a circle (82% of the samples), their area was calculated based on the ring radius (πr^2) measured from the center to the outer ring edge minus the area of the circle calculated with a radius measured to the inner edge of the ring. When a ring was elliptical (6%), the same approach was used based on the area of an ellipse, πlw , where l is half the diameter of the ellipse along the longest axis, and w is half the diameter of the ellipse along the shortest (perpendicular) axis. Ring areas of irregularly shaped stems (12%) were processed on a case-by-case basis using the previous approach but adding or subtracting an area that corresponded to the deviations of the irregularly shaped ring.

Site and study area variables

Yearly estimates (1989–2001) for two hydrological indices that relate to ground water, the maximum snow depth during the previous winter, which might have mediated browsing pressure, and five climatic factors that might influence growing-season conditions, were used to develop models of annual ring growth. The five climatic variables were the same across all sites within a year (study area variables), but the other variables were calculated on a per site basis (site variables).

Local climate conditions are influenced by elevation (ELEV), which was obtained for each site from a 30-m USGS digital elevation model. Ground water table level is the hydrological variable that may have the most

direct link to willow growth (Singer et al. 2003), but because it is not consistently monitored in our study area, we used watershed area and stream flow rate as proxies. We averaged monthly stream flow rates on the Lamar River gauging station (USGS ID no. 06187950) for May–August of each year. The extent of the watershed above each site (WSHED) was calculated using watershed modeling software (ArcInfo; Environmental Systems Research Institute 2004) and a 30-m USGS digital elevation model.

Weekly estimates of snow depth (SNOW; centimeter) from 1 January to 28 February 1985–2001 were predicted for each site based on elevation, precipitation, topography, and vegetation using the spatial snow model (version 1) of Coughenour and Singer (1996), and the values were averaged to provide an annual estimate of snow depth at each site for each year of the study.

Total annual precipitation (PRECIPA; centimeter), and total growing season precipitation (PRECIPS; May–August) were from the Tower Falls Climatic Station (ID no. 489025). The Palmer drought severity index (PDSI; Wyoming Division 1, NOAA) is based on temperature and precipitation records and indicates prolonged moisture deficiency or excess. The North Pacific index (NPI) was used as an index of climatic conditions because NPI has been found to predict local ecological processes better than local weather variables (see Hallett et al. 2004, Stenseth and Mysterud 2005). Average NPI was calculated for both the growing season (May–August; NPIS) and winter period (September–April; NPIW).

Elk and wolf populations

We used the winter counts of elk on the northern range (ELK; White and Garrott 2005a), with estimates adjusted for sightability for the winters of 1988–1989 and 1990–1991 (Coughenour and Singer 1996), to reflect potential browsing pressure the previous winter (Table 1). The presence or absence of wolves was indicated as a binary variable in our analysis (WOLF): wolves were considered absent until winter 1996. Although wolves were reintroduced in the spring of 1995, the earliest they could have influenced willow browse would have been winter 1995–1996. Thus growth during summer 1996 would be the earliest that release in willow could be expected to occur. Both of these variables are study area variables that do not vary between sites within a year.

Data analysis

We followed a model-selection approach (Burnham and Anderson 2002) using Akaike's information criterion (AIC) to examine evidence that willow growth (ring area) in 2001 was related to browsing pressure (percentage browsed twigs/stem; PBRWS) in the winter preceding ring growth. We used a mixed-effects model with site as a random effect to account for the lack of independence of stems within a site (Pinheiro and Bates

2000). In each model we included ring area from the previous years' growth (PYRA) to account for the fact that previous growth could influence growth the following year. Because we also expected hydrological conditions at a site to influence willow growth we evaluated five combinations of the elevation, watershed area, and snow depth variables (ELEV, WSHED, SNOW, ELEV + WSHED, SNOW + WSHED), with and without PBRWS, resulting in a set of 12 a priori models. Model selection was conducted for the two willow species separately.

To test whether willow growth was greater following wolf reintroduction we compared the mean ring area for each willow species at the same site across the pre- and post-wolf reintroduction periods using a paired *t* test with Bonferroni correction. Ring area was natural log-transformed to create a normal distribution of values.

We also used model selection to compare competing models explaining variation in annual willow growth during 1989–2001 with and without a wolf effect. We first selected the best model for predicting willow growth (annual ring area in each stem) based on climatic condition, winter snow depth, and hydrology and then tested whether the inclusion of the presence of wolves improved the model fit (i.e., lower AIC). We again used a mixed-effects model framework with the random effect of stems nested within sites to account for the fact that rings within stems and stems within sites cannot be considered independent. Furthermore, because annual ring areas within an individual stem were autocorrelated in time (Pearson's *r*, lag = 1; *S. boothii*, 0.707; *S. geeyeriana*, 0.624), we used a first-order autoregressive structure, which assumed an exponential decrease in autocorrelation as lag increases. Model selection was conducted for the two willow species separately.

All statistical analyses were performed in R (R Development Core Team 2004) using the “lme” function in the “nlme” (nonlinear mixed-effects model) library (Pinheiro and Bates 2000). The restricted maximum likelihood estimator (REML) was used in all models.

RESULTS

Annual ring areas were measured on 275 stems of *S. boothii* across 17 sites and 145 stems of *S. geeyeriana* across eight sites (Fig. 1) for a total of 1133 and 815 annual ring measurements, respectively.

Missing previous- and second-year twig browse data at two sites resulted in a reduced sample size for the within-year analysis of ring growth (214 stems of *S. boothii* across 16 sites, and 115 stems of *S. geeyeriana* across seven sites for a total of 980 and 680 annual ring measurements, respectively). Percentage of twigs browsed across sites ranged from 0 to 100% with a median of 100% for both species. In the highest ranked model for each species (Table 1) we found evidence that willow ring growth in 2001 was positively related to ring growth in the previous year (PYRA; *S. boothii*, $\beta = 0.66 \pm 0.051$ [mean \pm SE]; *S. geeyeriana*, $\beta = 0.62 \pm 0.072$)

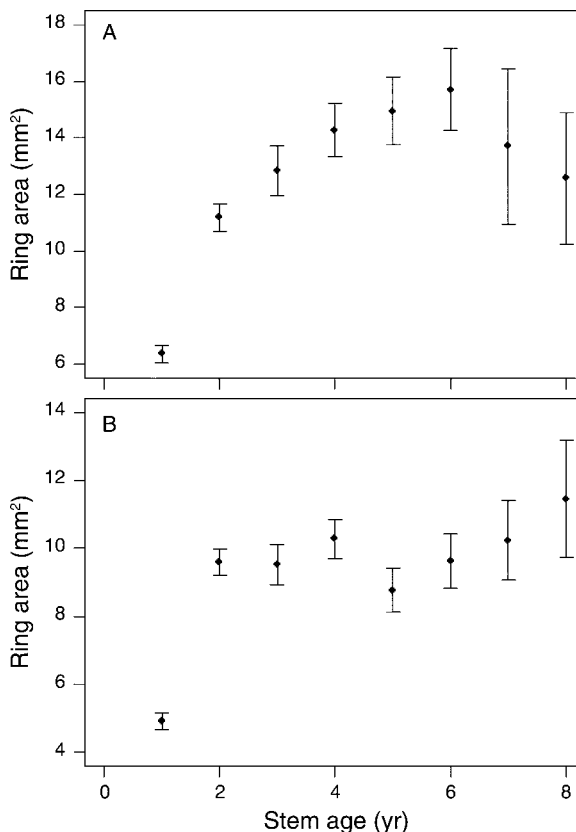


FIG. 3. Annual ring areas (mean \pm SE) for (A) *Salix boothii* stems and (B) *S. geeyeriana* stems, by stem age, from stems collected in 2001 at 17 and eight sampling sites, respectively, on Yellowstone's northern range.

and was inversely related to percentage of twigs browsed on the stem in the winter preceding growth (PBRWS; *S. boothii*, $\beta = -0.22 \pm 0.070$; *S. geeyeriana*, $\beta = -0.42 \pm 0.11$).

Ring counts indicated that the oldest stems we sampled were established in 1989. Because annual ring areas were on average smaller (*t* test with Bonferroni correction, $P < 0.01$ for all comparisons with first-year stem areas) in the first year of growth (Fig. 3) we excluded ring widths representing the year of establishment so this did not confound environmental effects. For both species, mean annual ring area at each site in the six years following wolf reintroduction in 1995 was approximately twofold higher (*S. boothii*, $t = -5.36$, $df = 11$, $P = 0.0002$; *S. geeyeriana*, $t = -3.20$, $df = 6$, $P = 0.02$) than in the four (*S. boothii*) or seven (*S. geeyeriana*) years prior to wolf introduction (Fig. 4).

Of the highest ranking models we evaluated to explain annual variation in willow ring area (Table 2), the model with the most support for *S. boothii* indicated that ring growth was inversely related to elevation (ELEV; $\beta = -0.0017 \pm 0.0004$ [mean \pm SE]) and mean annual precipitation (PRECIPA; $\beta = -0.26 \pm 0.02$), and was positively related to winter NPI (NPIW; $\beta = 0.10 \pm 0.04$)

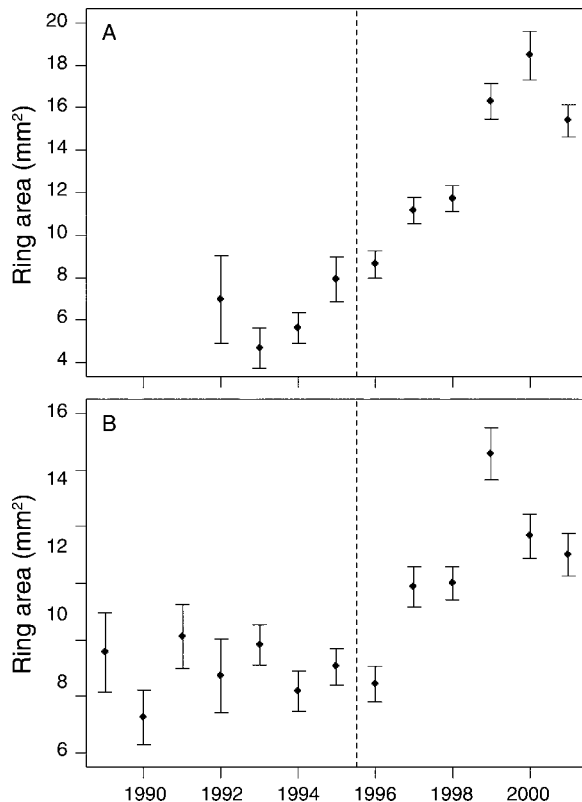


FIG. 4. Annual ring areas (mean \pm SE) for (A) *Salix boothii* stems and (B) *S. geyeriana* stems, by year, collected in 2001 at 17 and eight sampling sites, respectively, on Yellowstone's northern range. The dashed line represents the first winter in which released wolves were present on the northern range following reintroduction.

and wolf presence (WOLF; $\beta = 0.33 \pm 0.066$). For *S. geyeriana* the model with the most support indicated similar relationships with elevation ($\beta = -0.005 \pm 0.0006$), winter NPI ($\beta = 0.09 \pm 0.016$) and wolf presence (WOLF; $\beta = 0.33 \pm 0.066$), but mean annual precipitation was not included in the model (Table 2). Elk population size (ELK) was not present in any of the top models for either species.

DISCUSSION

Our results provide direct evidence that browsing can reduce willow growth. Low levels of browsing have been shown to enhance productivity through stimulation of branching, flowering, and new shoot propagation (Wolff 1978, Elmqvist et al. 1987, Alstad et al. 1999, Singer et al. 2003), but long-term and severe browsing can suppress willow growth, flowering, and seed production (Bryant et al. 1983, Singer et al. 1994, Singer 1996, Case and Kauffman 1997, Brookshire et al. 2002). Browsing may negatively affect growth by reducing root carbon reserves, which would otherwise be used for the production of chemical defenses (tannins) and for future growth (Bryant et al. 1983, Wagner et al. 1995, Peinetti et al. 2001, Brookshire et al. 2002), and prevents plants from growing tall, thereby escaping herbivory. This creates the potential for a positive feedback loop (Romme et al. 1995, Peinetti et al. 2001), whereby browsing ensures plants are short and therefore accessible, while also being more palatable due to reduced chemical defenses (Singer et al. 1994), resulting in continued browsing. The inverse relationship between browsing intensity and stem growth is central to the trophic cascade hypothesis because it establishes the

TABLE 2. Log likelihood values (LL), Akaike's information criteria scores (AIC), change in AIC score (Δ AIC), and AIC weights (w_i) for the top candidate models and two reference models relating variables to annual stem ring area of *Salix boothii* and *S. geyeriana* on Yellowstone's northern range.

Model description	LL	AIC	Δ AIC	w_i
<i>Salix boothii</i>				
ELEV, NPIW, PRECIPA, WOLF	-1055.2	2128.4	0.0	0.53
ELEV, NPIW, PRECIPA, WSHED, WOLF	-1054.6	2129.3	0.8	0.35
ELEV, NPIW, PDSI, WOLF	-1057.3	2132.7	4.3	0.06
ELEV, NPIW, PDSI, WSHED, WOLF	-1056.8	2133.6	5.2	0.04
ELEV, NPIW, PRECIPA	-1061.3	2138.6	10.2	0.00
ELEV, PDSI, ELK	-1078.1	2172.2	43.8	0.00
<i>Salix geyeriana</i>				
ELEV, NPIW, WOLF	-706.0	1428.0	0.0	0.81
ELEV, NPIW, STRFLWS, WOLF	-707.2	1432.5	4.5	0.09
ELEV, NPIW, PRECIPS, WOLF	-707.4	1432.7	4.8	0.08
ELEV, NPIW, PRECIPA, WOLF	-708.7	1435.3	7.3	0.02
ELEV, NPIW	-714.3	1442.5	14.5	0.00
ELEV, NPIW, ELK	-724.6	1465.2	37.2	0.00

Notes: Variables include elevation (ELEV), watershed area (WSHED), mean winter North Pacific index (NPIW), mean annual precipitation (PRECIPA), total growing season precipitation (May–August; PRECIPS), the annual Palmer drought severity index (PDSI), a binary variable representing the presence of wolves on the landscape (WOLF), and the northern range elk population size (ELK). ELEV and WSHED are site-level variables; all the other variables are study area variables that vary between years but not between sites within a year. Only models with a weight ≥ 0.01 are reported for the top models. The reference models include the highest ranked model with the WOLF variable removed, and the highest ranked model that uses the ELK variable, but not the WOLF variable. Variable abbreviations are described in *Methods*.

mechanism by which a trophic cascade occurs: a reduction in browsing intensity can result in increased willow growth, leading to escape from herbivory if plants grow tall.

We also demonstrated an increase in the growth of willow on the northern range that coincides with the reintroduction of wolves. After accounting for climate and hydrology-related factors, the presence of wolves on the northern range was a significant predictor of willow growth in the highest ranked models for both willow species. Wolves may influence willow growth through direct and indirect effects. Although elk densities generally declined after the introduction of wolves (Fig. 2) and there is evidence that wolf predation may have reduced the elk herd (White and Garrott 2005b), elk densities on the northern range ranged from 7.8 to 12.6 elk/km² during this study, densities at least eight times higher than the maximum density White et al. (1998) suggested would be necessary to release aspen from browsing in Banff National Park. We also found little evidence that reduced elk population size was associated with increased willow growth. Instead, we found better evidence for the presence of wolves on the landscape influencing willow growth, implicating indirect rather than direct effects of wolves on elk herbivory on willow.

Indirect (behavioral) effects can occur if elk distribution and/or foraging behavior is altered by predation risk, thereby creating local refugia for willow in which browsing intensity is reduced and plant growth increases. There is evidence suggesting that both of these mechanisms occur on the northern range. Ripple and Beschta (2006) found that increases in willow height pre- and post-wolf reintroduction at 22 riparian sites on the northern range were negatively correlated with percentage of browsed stems, view distances, and impediment distances, and suggest a behaviorally mediated trophic cascade may have been at least partially responsible for this change. Ripple and Beschta (2003) compared browsing rates of cottonwoods on the northern range in stands classified as high or low risk based on wolf detection potential and the presence of barriers to movement that would impede escape. They found that browse rates were lower, and plant heights were taller, at the high-risk sites, and they attribute this to elk avoiding areas where susceptibility of wolves may be greater (Ripple and Beschta 2003). Indeed, wolves appear to be more successful at making kills at hard edges (forest edges and riparian areas; Bergman et al. 2006), in ravines, close to water, and on ice (Kunkel and Pletscher 2000, 2001), probably as a result of decreased speed, maneuverability, and escape routes in these areas (Bergman et al. 2006). There is also evidence that elk alter their habitat selection in response to wolf density (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005). In a study of elk movement on the northern range post-wolf reintroduction, Fortin et al. (2005) demonstrate that habitat selection by elk changed in response to wolf density such that elk used aspen stands in areas of low

wolf density but avoided aspen stands in areas of high wolf density. Elk also appear to reduce their use of their preferred grassland foraging habitat when wolves are present (Creel et al. 2005), which might be a strategy to reduce predation risk.

However, these studies do not clarify whether displacement of elk or changes in feeding behavior are responsible for reduced browsing rates per se. Even if displacement of elk by wolves does not occur or is temporary (Kunkel and Pletscher 2001), predation risk may reduce overall browsing pressure by interrupting feeding or reducing the number or duration of visits made to risky patches. Alternatively, elk may favor the edges of dense aspen or willow stands (White et al. 2003) in risky areas, thereby reducing browse intensity in the center of the patches. While current studies suggest indirect effects may occur (Creel et al. 2005, Fortin et al. 2005, Hebblewhite et al. 2005; see *Results*), a better understanding of how behavioral changes contribute to trophic cascades will require observations that quantify the relationships among predation risk, willow patch residency time and visitation rate, group size, off-take rates, and winter severity. Further, animals are known to alter several behaviors to compensate when factors are limiting. For example, even if increased predation risk reduces willow patch residency time (see Abramsky et al. 2002), this may not result in a reduction in off-take rates if patch visitation rates or feeding rates increase, or if predation risk promotes increased group sizes (Creel and Winnie 2005). Environmental stochasticity is also likely to contribute to these dynamics. Severe winters with deep snow that reduce forage availability may result in high off-take by elk if they become increasingly willing to visit risky habitats to meet their energy requirements. Detailed behavioral studies are needed to characterize the complex interplay among these factors.

Although we have shown that browsing reduces stem growth, we do not have historical data on intensity of browsing at our sites to directly address how wolf reintroduction may have affected willow growth. Nevertheless, the presence of wolves was a significant predictor of willow growth for both species (*S. boothii* and *S. geyeriana*) while elk population size was not. These results best support the hypothesis that a trophic cascade among wolves, elk, and willow is mediated by the indirect effects of wolves on elk on the northern range but provide little mechanistic understanding of what behaviors are important. However, understanding the indirect effects of top carnivores appears to represent an important component of advancing ecosystem conservation and biodiversity maintenance (Berger et al. 2001, Soulé et al. 2003). Our results suggest that predator restoration has resulted in community-altering effects, and in the long-standing debate over Yellowstone's northern range dynamics, the effects of wolf restoration on communities may prove to be an endorsement of the use of ecological process for conservation.

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