

Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem

William J. Ripple*, Robert L. Beschta

College of Forestry, Oregon State University, Corvallis, OR 97331, United States

Received 14 November 2005; received in revised form 14 April 2006; accepted 17 April 2006

Abstract

After an absence of approximately 70 years, gray wolves (*Canis lupus*) were re-introduced into Yellowstone National Park in the mid-1990s. We studied the potential influence of wolf/ungulate interactions upon willow (*Salix* spp.) growth in the valleys of the Gallatin and Lamar Rivers, as well as Slough and Soda Butte Creeks, in the northern Yellowstone ecosystem. When we compared willow heights from photographs taken prior to 1998 (willows <2 m tall) with those taken in 2004, we found an increase in willow height for 22 of 42 sites within the study area. Based on comparisons of the chronosequence photos, since wolf introduction none of the 16 upland riparian sites showed an increase in willow height, while 22 of 26 of the valley-bottom riparian sites had willow height increases. In 2004, willow height exhibited a strong inverse relationship with the percentage of browsed stems ($r = -0.81, p < 0.01, n = 42$). Results of regressions for valley-bottom sites indicated that view distance, impediment distance, and the number of bison (*Bison bison*) flops were inversely related to willow height ($p \leq 0.02$). Increased willow heights were not significantly ($p = 0.18$) related to patterns of moisture availability. Willow height increases documented in this study appear to have been at least partially due to behaviorally mediated trophic cascades involving wolves and ungulates, via a mechanism of predation risk. While willow release (i.e., increased height growth) within the study area is in a very early stage, results suggest potentially important indirect effects of a top carnivore in a terrestrial food chain that may aid in the restoration of riparian species and the preservation of biodiversity.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Wolves; Elk; Willow; Trophic cascades; Predation risk

1. Introduction

Patterns of herbivory by wild ungulates can affect plant structure, succession, productivity, and species composition (McLaren and Peterson, 1994; Larsen and Ripple, 2003). Thus, vegetation communities can be profoundly altered (by ungulates) when large carnivores are removed from ecosystems (Waller and Alverson, 1997; White et al., 1998; Ripple and Larsen, 2000; Russell et al., 2001; Beschta, 2003, 2005; Rooney and Waller, 2003). Even so, vegetation structure changes following the loss or return of large carnivores have seldom been documented and are currently not widely understood due to the long-term absence of such predators throughout much of the United States (Ray et al., 2005). For example, gray wolves (*Canis lupus*), once widely distributed across the conterminous 48 United States, were systematically

extirpated from most of the nation by the 1930s (Paquet and Carbyn, 2003). Only in recent years have wolves returned to some of their former range in the Great Lakes region, the northern Rocky Mountains, and the Southwest.

Wolves can clearly influence the size of ungulate populations through direct mortality (lethal effects), which, in turn, can affect herbivory pressure on plants (McLaren and Peterson, 1994; Messier, 1994; Berger et al., 2001a; Ripple and Beschta, 2005b). Thus, when a top trophic level predator interacts with the next lower level herbivore and this interaction alters or influences vegetation, a “trophic cascade” occurs. Another mechanism associated with trophic cascades is predation risk (non-lethal effects), whereby ungulates, under the risk of predation, alter their foraging patterns (Lima and Dill, 1990) vigilance, or movements in a “landscape of fear” (Laundré et al., 2001; Hernández and Laundré, 2005). Changes in prey behavior due to the presence of predators are referred to as behaviorally mediated trophic cascades (Beckerman et al., 1997; Lima, 1998), in that herbivores balance needs for both safety and forage as described by optimal foraging theory

* Corresponding author. Tel.: +1 541 737 3056; fax: +1 541 737 3049.

E-mail address: bill.ripple@oregonstate.edu (W.J. Ripple).

(MacArthur and Pianka, 1966; Brown et al., 1999; Berger et al., 2001b). Importantly, predation risk effects on plants may be equal to, or even higher than, cascading effects resulting from changes in predator or prey populations (Schmitz et al., 1997; Werner and Peacor, 2003). Furthermore, recent research assessing predation risk in carnivore/ungulate systems concludes that changes in patterns of herbivory might be affected by terrain conditions such as topographic position, landforms, view available to ungulates, or escape terrain (Lingle, 2002; White et al., 2003; Ripple and Beschta, 2004b; Fortin et al., 2005). Because of their potential to ultimately affect a wide range of ecosystem functions and processes, Soulé et al. (2005) consider wolves to represent a subset of carnivores characterized as “strongly interacting species”.

Since wolf re-introductions in Yellowstone National Park (YNP) in the mid-1990s, elk (*Cervus elaphus*) appear to be avoiding browsing certain riparian areas and increasing their use of upland habitats (higher ground hypothesis). Ripple and Beschta (2003, 2004a) hypothesized that the use of higher ground by elk was a risk-sensitive foraging strategy to avoid wolf encounters, detect wolves, escape from wolves, and/or evade wolves by hiding in nearby upland conifer forests. In recent years, willows (*Salix* spp.) along valley-bottom floodplains have been increasing in height at potentially high risk sites, i.e., sites with limited visibility (for seeing approaching wolves) and/or terrain features that could impede ungulate escape from attack, such as below high terraces, along steep streambanks, and near gullies (Ripple and Beschta, 2003, 2004b). While vigilance levels of elk and bison (*Bison bison*) have generally increased since the re-introduction of wolves in YNP (Laundré et al., 2001; Childress and Lung, 2003), researchers are just beginning to obtain information about the anti-predator tactics of ungulates regarding their use of habitat (Bergman, 2003; Fortin et al., 2005; Mao et al., 2005) and foraging patterns (Ripple et al., 2001; Ripple and Beschta, 2003, 2005b; Fortin et al., 2004). Landscape features can affect the susceptibility of ungulates to predation by wolves (Hebblewhite et al., 2005).

Given that a growth response of riparian woody browse species is underway within winter ranges that are inside or bordering northern YNP subsequent to wolf re-introduction (Ripple and Beschta, 2003, 2004b, 2005a), we undertook this study to better understand factors that could potentially influence the willow growth response. Our objectives were: (1) to assess changes in willow height since wolf re-introduction with time-series photographs; (2) to quantify variables associated with risk-sensitive foraging by ungulates in the presence of wolves; and (3) to test a set of a priori hypotheses regarding willow heights and risk-sensitive foraging. These a priori hypotheses include the following: (1) willow height will be inversely related to the percentage of willow stems browsed; (2) willows will be taller at valley-bottom riparian sites than at upland riparian sites (higher ground hypothesis); and (3) willows will be taller at sites where visibility is limited and escape impediments are close. We also collected data on other non-hypothesized factors that could influence elk browsing and/or willow growth including road and conifer distances, bison, moisture, and climatic influences.

2. Study area

This research was conducted within the upper Gallatin elk winter range (180–250 km²) near the northwest corner of YNP (Edwards, 1941; Allen, 1970) and the northern Yellowstone elk winter range (~1500 km²) largely located in the northeastern corner of YNP (YNP, 1997; Barmore, 2003); both are located within the northern Yellowstone ecosystem. See Ripple and Beschta (2003, 2004b) for maps of both winter range study areas. The upland vegetation of both winter ranges is comprised of steppe and shrub-steppe, grading into conifers at increasing elevation above the valley floor (Lovaas, 1970; Houston, 1982). The shrub-steppe community is dominated by big sagebrush (*Artemisia tridentata*), while Douglas-fir (*Pseudotsuga menziesii*) and Lodgepole pine (*Pinus contorta*) are the primary conifer species (Despain, 1990). Scattered communities of aspen (*Populus tremuloides*) and willows are common in upland riparian settings, with willows and cottonwoods (*Populus* spp.) occurring along valley-bottom riparian systems. In winter, cold temperatures and snow force elk to move from high mountain summer ranges to the lower-elevation winter ranges that are the focus of this study.

Following the removal of wolves in the early 1900s, woody browse species on both winter ranges have been suppressed from long-term browsing by wild ungulates, principally elk (NRC, 2002). To help understand the potential effects of ungulate browsing, in 1957 the Park Service installed fenced exclosures at Tower Junction, Mammoth, and the Lamar Valley in the northern elk winter range. Height measurements from 1958 to 1989 (Singer, 1996; Barmore, 2003), a period of over three decades, indicate willows outside exclosures never exceeded 70 cm in height, while those inside (initially 40–60 cm in height) increased in height by over 600%. Additional evidence indicating the extent to which riparian willows have been suppressed by browsing following the elimination of wolves is found in the Gallatin elk winter range. There, willows largely “died out” after the 1930s due to heavy browsing pressure from elk, whereas willows protected from browsing maintained dense, vigorous stands (Peek et al., 1967; Patten, 1968; Lovaas, 1970; Ripple and Beschta, 2004b).

Field sites for this study lay within the upper Gallatin River valley in the Gallatin winter range, as well as the Lamar River, Soda Butte Creek, and Slough Creek valleys in the northern Yellowstone winter range. Riparian areas located >20 m in elevation above each of the river valley bottoms were classified as upland sites, while those ≤20 m above these four main streams were considered lowland or valley-bottom sites. We chose 20 m since it was typically the minimum elevation above the rivers where a clear view of the valley bottom could be obtained (e.g., elk could see approaching wolves on the valley bottom). Willows in upland riparian areas were typically growing along small perennial tributaries to the Gallatin and Lamar Rivers.

After approximately seven decades of absence, wolves returned to the Gallatin Range in the mid-1990s. Beginning with 3 wolves in 1996, wolf numbers have ranged from 8 to 13 individuals since 1997 (Smith et al., 2003). Since 1995, elk

censuses have indicated an average of 1050 elk in the Gallatin winter range, or approximately 5 elk/km². Bison are not found in the upper Gallatin basin. During the winter of 1995–1996, the northern winter range in YNP was a primary release point for 31 wolves; by 2003, nearly 100 gray wolves inhabited this area (Smith et al., 2004). From 1998 to 2002, the number of elk in the northern winter range averaged 12,700 or about 8–9 elk/km² (Vucetich et al., 2005; White and Garrott, 2005). According to census reports, in 2003 there were 9220 elk (6.1 elk/km²), and in 2004 there were 8340 elk (5.6 elk/km²) in the northern range. An estimated 1000–1500 bison (P.J. White, personal communication) currently reside in the northern range throughout the year, focusing their winter foraging along the Lamar River valley bottom and along open hillslopes adjacent to the Yellowstone River near Gardner, Montana.

3. Methods

To characterize willow conditions before the re-introduction of wolves, we searched for photographs taken during a 20-year period (1977–1997). For the purposes of this study, we considered photos taken through the summer of 1997 to represent pre-wolf conditions even though the wolf re-introduction was completed in 1996. We assumed this lag time for wolves to functionally colonize the winter ranges and for elk to develop potential risk-sensitive foraging strategies (Ripple and Beschta, 2004b). We obtained a total of 42 photographs taken between 1977 and 1997, in which willows were visible in the field of view, including 8 sites in the Gallatin elk winter range and 34 sites on the northern elk winter range. In 2004, we re-photographed each pre-1998 scene, located the tallest willow patch visible in each of the 2004 photos, and then measured the heights of the five tallest willow plants within each selected patch. Since we did not have field measurements of willow height for the pre-1998 photos, we used the measured willow heights for the tallest willows evident in the 2004 photos as a basis for ocularly estimating willow heights in the pre-1998 photos. We categorized the height of the tallest willows in each historical and current photograph into one of four general height classes: <1, 1–2, 2–3, and 3–4 m. We restricted our analysis to the tallest individual willows, to help evaluate any early release from browsing and height growth following wolf re-introduction and not to estimate the population of willow heights.

For each willow whose height was measured in 2004, we used “plant architecture” assessment techniques (Keigley et al., 2003; Ripple and Beschta, 2003) to evaluate plant height and browsing history during previous years. Since browsing usually removes the terminal bud of a stem, causing growth to emerge from a lateral bud, the stems grow in a zigzag pattern, leaving behind stubs identifying annual segments. We thus measured whether browsing had occurred and the height for each annual terminal bud scar along a stem. The occurrence/absence of browsing and bud scar heights could be typically evaluated for approximately the last 5 years on a given stem. In addition, we examined the two tallest leaders in each of four quadrants on each willow crown to determine the percentage of

stems browsed the previous winter. Tall willow species sampled include booth willow (*S. boothii*), geyer willow (*S. geyeriana*), whiplash willow (*S. lasiandra*), coyote willow (*S. exigua*), and bebb willow (*S. bebbiana*).

We characterized predation risk using both viewshed and escape terrain variables. From the center of each sampled willow patch, we used a hand-held laser rangefinder to determine the distance to which the view was obstructed, up to a maximum of 900 m, in each of the four 90° quadrants. View distance was defined as the minimum distance to where most of the view in a given quadrant was obstructed by terrain (ridge, top of terrace) or forest cover (Bowyer et al., 1999). For the purposes of this study, willows were not included as obstructions to view since leaves are off in the winter and this study was mainly focused on the winter behavior of ungulates, when browsing of woody plants normally occurs. We also used the rangefinder to determine the distance to any escape impediments, up to a maximum of 250 m. An escape impediment was defined as any terrain feature or object that could slow fleeing ungulates. Escape impediments included stream cutbanks, gullies, roads, cliffs, and woody debris ≥ 0.3 m tall or ≥ 0.3 m deep (Ripple and Beschta, 2004b), as well as rocky surfaces.

For each sampled willow patch we recorded its elevation above the valley-bottom using a global positioning system. We determined distances to the nearest conifer forest and nearest road, using the hand-held rangefinder and digital planimetric maps. To index the extent of bison use and the potential effects of bison herbivory, we counted bison flocs (fecal droppings) in a 10 m \times 10 m plot located at each sampled willow patch. Since measured willows were typically growing on alluvial surfaces close to a stream, we recorded the height of each willow’s root collar relative to the adjacent stream’s water surface (an index of accessibility to shallow groundwater) during summertime periods.

Univariate regression analysis was undertaken to test for the effect of visibility and escape impediments in a priori models for the response variable of willow height. We also tested for significance of the non-hypothesized covariates of distance to nearest road, distance to nearest forest cover, density of bison flocs, and height of willow root collars above surface water.

Multivariate linear regression was conducted using all impediment and visibility variables as input into a stepwise model, with willow height in 2004 as the response variable. These variables were measured in each of four quadrants, consisting of a 90° arc pointed outward from the measured willow, to encompass the potential total 360° field of view. We used four viewshed variables as input to the stepwise regression including: (1) the shortest distance in any quadrant to which the view was obstructed; (2) the average of the two shortest quadrant distances to an obstructed view; (3) the average of the three shortest distances to an obstructed view; and (4) the average of the four shortest distances to an obstructed view. We also characterized two impediment variables including: (1) distance to the nearest impediment and (2) the average distance to the two nearest impediments.

To help assess weather/climatic variables that might influence the availability of soil moisture and hence willow growth in recent years, we acquired a historical time series of snow depth and streamflow for the Gallatin and northern winter ranges from the nearest snow courses and stream gauges. We obtained maximum annual snowpack depths (as an index of soil moisture availability) for the Twenty-One Mile Snow Course (NRCS #11E06) in the upper Gallatin basin and the Northeast Entrance (NRCS #10D07) Snow Course in the northern range. Snowpack depths can also be an important factor affecting seasonal elk migrations (deep snow forcing animals to lower elevations) and predation rates (NRC, 2002; Smith et al., 2003). We used streamflow data for the Gallatin River near Gateway (USGS #060435) and the Lamar River near Tower Falls (USGS #061880) to evaluate temporal patterns of: (1) annual peakflows (important for overbank flows, channel changes, and willow seedling establishment) and (2) July flows (important for maintaining riparian water tables during a period of generally high transpiration demands by riparian plant communities).

4. Results

All willows were <2 m tall in the 42 photographs taken during the pre-wolf period of 1977–1997 (Table 1). Following wolf re-introduction, none of the photo sites comprising upland riparian areas showed an increase in willow height (e.g., Table 1 and Fig. 1). Of the 26 valley-bottom riparian sites, only four did not show an increase in willow height, and all of these sites occurred in a relatively broad portion of the Lamar Valley. Of the 22 valley-bottom sites where willows had increased in height by 2004 (e.g., Fig. 2), 10 had attained a height of 2–3 m and 8 had attained a height of 3–4 m (Table 1). In 2004, willow heights were inversely related to the percentage of willow stems browsed ($r = -0.81$, $p < 0.01$, $n = 42$).

Table 1

Summary of willow height classes from 42 photo locations in the upper Gallatin and northern Yellowstone winter ranges during two periods: (1) when wolves were absent in these ecosystems (photographs from 1977 to 1997) and (2) after they had been re-established (photographs from 2004)

Willow height Height classes (m)	Number of willow sites	
	Wolves absent	Wolves present
Upland riparian sites		
0–1 m	8	8
1–2 m	8	8
2–3 m	–	–
3–4 m	–	–
Total	16	16
Valley-bottom riparian sites		
0–1 m	13	4
1–2 m	13	4
2–3 m	–	8
3–4 m	–	10
Total	26	26

Willows did not increase in height at any of the upland riparian sites (i.e., sites >20 m above the valley-bottom), but increased in height at 22 of 26 valley-bottom riparian sites.

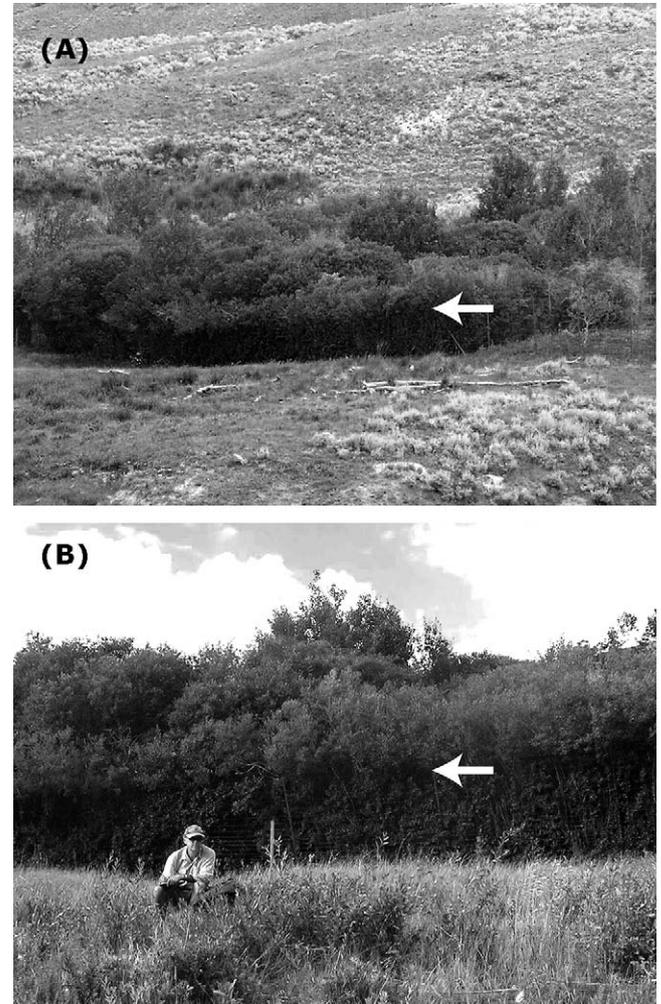


Fig. 1. Upland willow enclosure located above the Lamar Valley photographed in 2004. Photo (A) shows a landscape view the enclosure with 3–4 m high willow within the fenced area, while photo (B) is a close-up photograph of the same enclosure showing suppressed willow (<1 m tall) outside the fence near the subject. The white arrows point to the 2-m high browse line above the fence on the edge of the enclosure.

For willows <2 m in height in 2004, the percentage browsing was relatively high ($\geq 95\%$) and remained unchanged from 2002. For willows that had a height of >2 m by 2004, average browsing levels decreased from $\geq 65\%$ in 1999 to $\leq 6\%$ in 2003 (Fig. 3A). In general, as browsing levels decreased, mean willow height increased annually since 1999 (Fig. 3B).

In 2004, the percentage of stems browsed in upland riparian areas ($\bar{x} = 94\%$) was significantly greater ($p < 0.01$) than for valley-bottom riparian areas ($\bar{x} = 49\%$). Thus, upland willow heights ($\bar{x} = 93$ cm) remained significantly shorter ($p < 0.01$; Table 2) than those of valley-bottom willows ($\bar{x} = 231$ cm). Since many of the upland riparian sites were relatively confined by adjacent hillslopes, view distances from willow communities along these riparian areas were significantly less ($p \leq 0.01$) relative to the valley-bottom sites. There were no significant differences ($p \geq 0.26$) in impediment distances for riparian sites in uplands versus those located in valley bottoms.

The heights of willow root collars above the water surface at upland riparian sites ($\bar{x} = 31$ cm) were significantly less

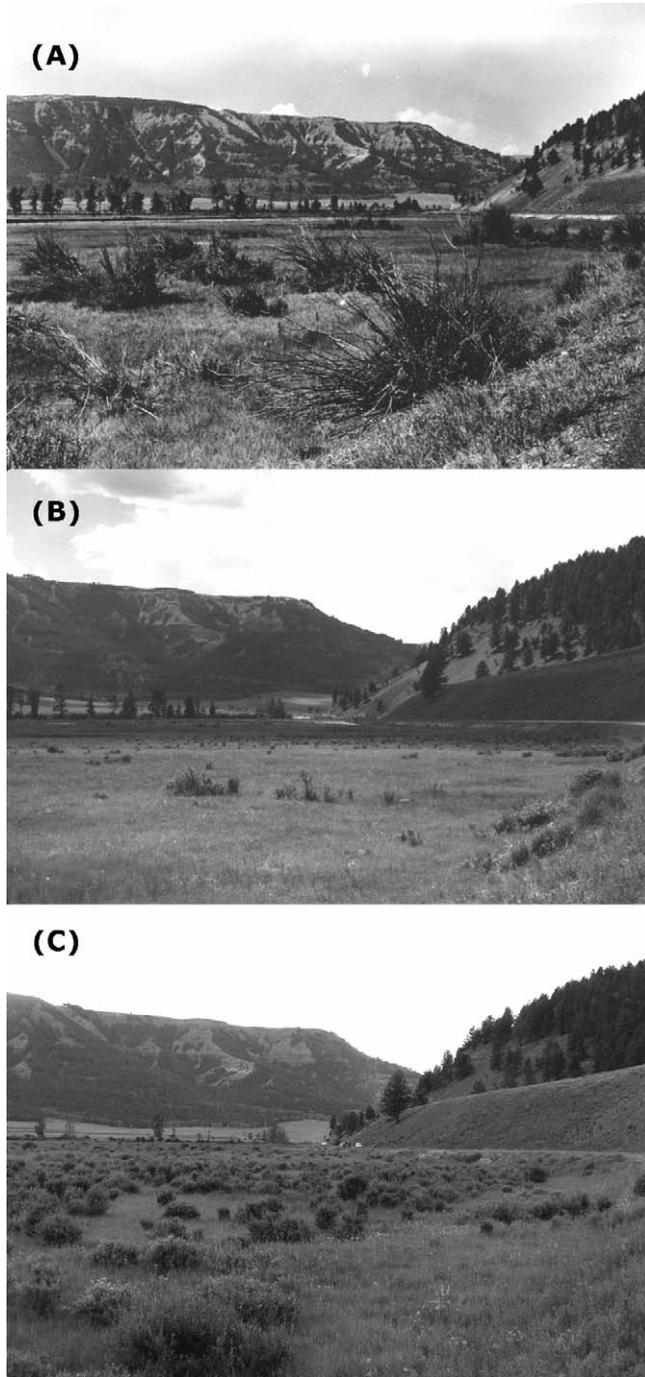


Fig. 2. Chronosequence of a valley-bottom site in the northern range showing long-term browsing suppression of willow plants when wolves were absent (A, 1949; B, 1988) and the recent increase in willow numbers and heights (C, 2004), following the re-introduction of wolves in the winter of 1995–1996. Photo credits: (A, Yellowstone National Park; B and C, Kay).

($p = 0.03$) than for valley-bottom riparian sites ($\bar{x} = 96$ cm). The distance to the nearest road for upland sites ($\bar{x} = 922$ m) was significantly farther ($p = 0.03$) than for valley-bottom sites ($\bar{x} = 460$ m). There were no significant differences ($p = 0.18$) between uplands and valley-bottom sites in distance to the nearest conifer forest cover or in the density of buffalo flocks ($p = 0.94$).

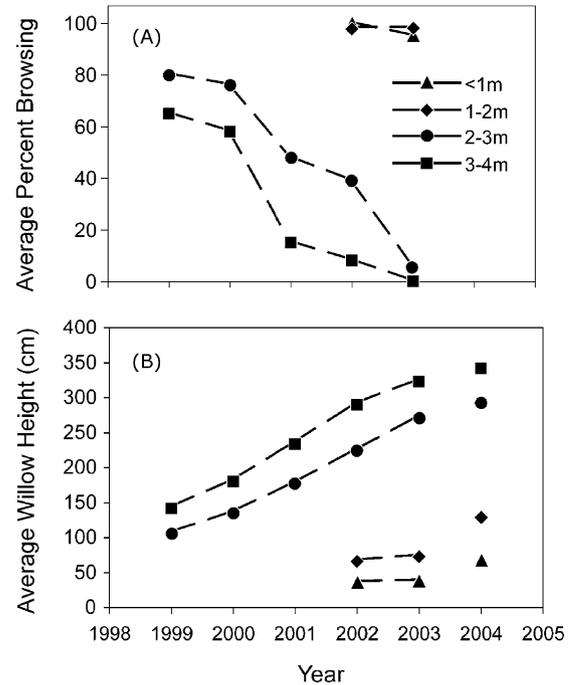


Fig. 3. Percentage of willow leaders browsed (A) and willow heights for recent years (B) based on plant architecture measurements. Note: Willow heights for 2004 were measured in the summer of 2004 and thus have not experienced elk herbivory.

Since upland riparian sites had not shown increases in willow height between the two photo periods (Table 1), we considered only valley-bottom riparian sites for stepwise regression analysis. Results of univariate regressions for the 26 valley-bottom sites (Table 3) showed that willow height was significantly correlated ($p \leq 0.02$) with both view distance and impediment distance variables. The correlation coefficients

Table 2
Descriptive statistics from August 2004 field measurements for site variables at 16 upland riparian sites (≥ 20 m above the valley-bottom) and 26 valley-bottom riparian sites (< 20 m above the valley-bottom)

Variable	Upland sites			Valley-bottom sites			p-Value
	Average	S.D.	n	Average	S.D.	n	
2004 willow height (cm)	93	31	16	231	103	26	<0.01
2003 browsing (%)	94	10	16	49	45	26	<0.01
View distance (m)							
One quadrant	56	49	16	238	305	26	<0.01
Two quadrants	71	61	16	281	316	26	<0.01
Three quadrants	131	125	16	365	304	26	<0.01
Four quadrants	190	181	16	453	282	26	<0.01
Impediment distance (m)							
One quadrant	38	69	11	13	10	26	0.26
Two quadrants	25	54	9	15	11	26	0.58
Root collar height (m)	31	19	16	96	41	25	<0.01
Road distance (m)	922	536	16	460	786	26	0.03
Forest distance (m)	509	274	16	641	356	26	0.18
Bison flocks (#/100 m ²)	1.9	2.9	16	1.8	3.2	26	0.94

p-Values from two-tailed, two-sample t-tests were used to test for statistically significant differences (i.e., $p < 0.5$) in upland vs. valley-bottom variables.

Table 3
Results of simple linear correlations between willow heights in 2004 and environmental variables at valley-bottom riparian sites ($n = 26$) in northern Yellowstone ecosystems

Variables	r	p -Value
Hypothesized		
Average view distance (m)		
One quadrant	-0.46	0.02
Two quadrants	-0.52	<0.01
Three quadrants	-0.60	<0.01
Four quadrants	-0.61	<0.01
Average impediment distance (m)		
One impediment	-0.52	<0.01
Two impediments	-0.61	<0.01
Non-hypothesized		
Root collar height (m)	-0.28	0.18
Road distance (m)	0.00	0.86
Forest distance (m)	-0.25	0.23
Bison flops (#/100 m ²)	-0.57	<0.01

between willow height and mean view distance were greater for data from three or four quadrants in comparison to data from one or two quadrants (Table 3). Likewise, the correlation coefficient for the average of the nearest two impediments was higher than when data from a single impediment was used. Results of the stepwise regression included two explanatory variables (Fig. 4): (1) logarithm of mean distance to the first two impediments ($p < 0.01$) and (2) mean view distance in three quadrants ($p < 0.01$), with an adjusted r^2 of 0.57 ($p < 0.01$). Whereas willow height was inversely related ($p < 0.01$) to the density of bison flops, the remaining non-hypothesized variables showed no significant relationships ($p \geq 0.18$) with willow height (Table 3).

Above-average snowfall depths occurred in both winter ranges for the years 1997 and 1999, followed by below-average years since 1999 (Fig. 5A). Relatively high annual peakflows occurred in 1996 and 1997, followed by peakflows fluctuating around the long-term average (Fig. 5B). July streamflows were generally above average for 1996–1999, below average from

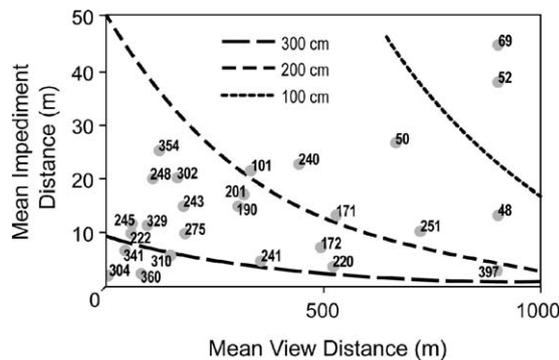


Fig. 4. Relationship between willow heights for valley-bottom riparian sites relative to (1) impediment distance and (2) viewshed distance; curvilinear lines are isopleths of willow heights for valley-bottom sites calculated from the regression equation: willow height (cm) = -58.8 (impediment distance, m) + (-0.162) (viewsed distance, m) + 431 ; ($r^2 = 0.57$, $n = 26$). Numbers indicate actual willow heights (cm) in 2004 associated with each data point.

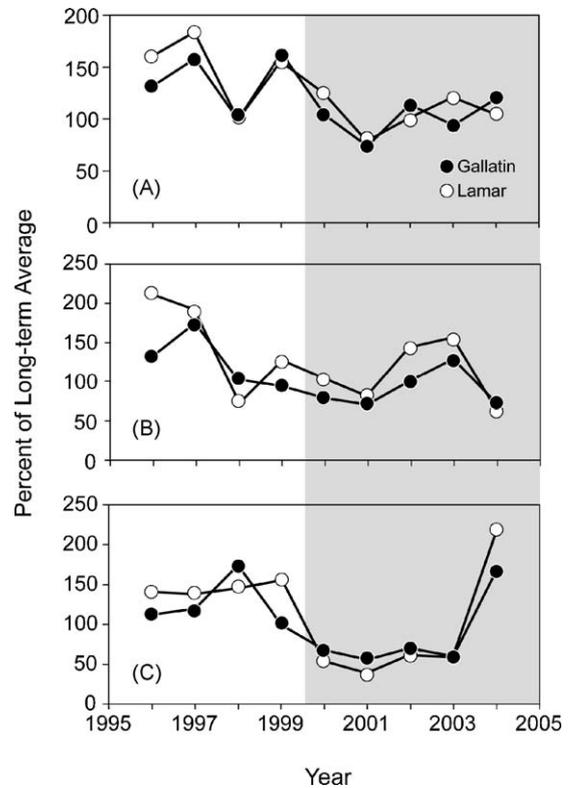


Fig. 5. Percentage of long-term annual maximum snowpack depth (A), peak-flow (B), and July streamflow (C) over the period 1996–2004 for stations in the upper Gallatin basin (closed circles) and the northern Yellowstone winter range (open circles); shading indicates the general period of increasing willow height on “high risk” sites. Long-term averages for each station are as follows: average annual snowpack depth is 21.1 cm (coefficient of variation [cv] \pm 24%, $n = 68$) for the Twenty-One Mile Snow Course in the upper Gallatin basin and 12.7 cm (cv \pm 24%, $n = 68$) for the Northeast Entrance Snow Course in the northern range; average annual peakflow is 149 m³/s (cv \pm 30%, $n = 74$) for the Gallatin River at Gateway and 261 m³/s (cv \pm 31%, $n = 65$) for the Lamar River near Tower Fall; average annual July flow is 36 m³/s (cv \pm 45%, $n = 71$) for the Gallatin River at Gateway and 39 m³/s (cv \pm 53%, $n = 64$) for the Lamar River near Tower Fall.

2000 to 2003, representing a progression of dry summers for these winter ranges, and then considerably above average in 2004 (Fig. 5C).

5. Discussion

Our analysis of chronosequence photographs showed widely suppressed willow heights (<2 m tall) before wolf re-introduction and increasing heights of various willow patches at 22 of the 42 photo retake sites since wolf re-introduction (Table 1). These results support earlier findings of recent height growth of willows on both ungulate winter ranges (Ripple and Beschta, 2003, 2004b). More recently, Beyer (2006) demonstrated an increase in growth of northern range willow coincided with the re-introduction of wolves, after accounting for hydrological and climatological factors. This occurrence of increased willow heights represents a major transition from the long-term suppression of willow and other woody browse species that occurred over much of the last century, as illustrated by chronologically sequenced photos and published

data on the condition of northern Yellowstone vegetation (Jonas, 1955; Houston, 1982; Romme et al., 1995; Kay, 1990; Meagher and Houston, 1998; Singer et al., 1998; White et al., 1998; Barmore, 2003).

Hypothesis 1 (*Willow height versus browsing intensity*).

The finding that willow height was inversely correlated to percentage of stems browsed supports Hypothesis 1 and corroborates recent studies in this region (Ripple and Beschta, 2003, 2004b; Beyer, 2006). This inverse relationship provides important evidence of a linkage between ungulate browsing and willow height. Additionally, long-term ungulate exclosures in our study areas show that high rates of herbivory are capable of maintaining willows of low stature over extended periods of time (Barmore, 2003).

Hypothesis 2 (*Higher ground hypothesis*).

Results indicated more browsing and shorter willows for riparian sites in upland areas relative to riparian sites along valley bottoms, supporting a “higher ground hypothesis” regarding risk avoidance by elk. Uplands and hillslopes may give elk advantages in terms of predator avoidance and escape terrain (Dekker, 1997). In our study area, upland steppe and shrub-steppe areas are typically closer to conifer forests than are riparian areas. Conifers may provide hiding cover for elk, which could increase their capability to avoid wolves (Creel et al., 2005; Fortin et al., 2005; Hernández and Laundré, 2005). Studies elsewhere have shown that uplands can provide ungulates with a significantly lower risk of predation, better escape terrain, and fewer escape barriers (Murie, 1944; Bibikov, 1982; Bergerud and Page, 1987; Festa-Bianchet, 1988; Kunkel and Pletscher, 2000, 2001; Lingle, 2002). Lingle (2002) found that mule deer (*Odocoileus hemionus*) standing high on slopes reduced both their risk of being encountered and attacked by coyotes (*Canis latrans*). In Idaho, Husseman et al. (2003) found wolf kills were more likely to occur in valley bottoms and riparian areas when compared to uplands. Other researchers have also found that ungulates located at elevations above wolves were safer (Murie, 1944; Kunkel and Pletscher, 2000, 2001). During elk-wolf encounters, Bibikov (1982) found that when ungulates were located higher on a slope and then fled upward, wolves usually did not follow them.

The results of this study indicate a lack of risk-sensitive foraging in the uplands. We found high levels of browsing and no release of willow regardless of view or impediment distances even though, on average, view distances were actually less for upland sites relative to lowland sites (Table 2). Thus, higher browsing levels in the uplands compared to the lowlands may be reflective of higher upland elk densities due to recent shifts in elk habitat use to reduce predation risk and/or avoid encounters with wolves along valley bottoms. When behaviorally mediated trophic cascades occur, the presence of carnivores will typically have net positive effects on some plants and net negative effects on other plants if they cause the herbivores to shift their habitat use to lower overall predation risk (Schmitz et al., 2000).

Surveys have shown a significant decrease in elk pellet densities in the Lamar valley-bottom between 1999 and 2001 (Ripple and Beschta, 2004b), during a period when the elk population remained relatively unchanged compared to the pre-wolf period, thus indicating that elk were beginning to spend less time foraging in the valley-bottom by 2001. This redistribution of elk densities has been corroborated by Boyce et al. (2003), who modeled and mapped elk habitat selection based on 93 radio-collared adult female elk from 2000 to 2002. In winter they showed lower levels of elk use in the Lamar valley-bottom compared to nearby uplands. Since valley-bottoms often provide wolf travel corridors as well as rendezvous and denning sites, elk may avoid browsing in these lower elevation areas to reduce the potential for wolf encounters even though willow biomass is increasing at these sites.

In the last few years, elk populations in the northern range have decreased. While reduced elk numbers may be contributing to the current low levels of herbivory for valley-bottom riparian systems, it is important to note the general upward trend in willow heights was initiated several years before the recent drop in the elk population (Ripple and Beschta, 2003, 2004b; Beyer, 2006).

Hypothesis 3 (*Willow heights associated with visibility and escape impediments*).

Hypothesis 3 was supported with data from our valley-bottom sites, but was not validated for our upland riparian sites (see Hypothesis 2 results above). Within valley-bottom riparian sites we found willow heights to be significantly related to visibility and escape impediment variables, individually (Table 3) and in combination (Fig. 4). Beyer (2006) using elk location data during daylight hours in northern Yellowstone and a viewshed model, documented how elk select sites that facilitate predator detection. Other terrain conditions that may be relatively unfavorable to ungulates include such features as deeply incised channels, multiple channels, oxbows, cut banks, terraces, and woody debris accumulations which may limit visibility and cause fleeing ungulates to lose speed and maneuverability during a chase (Bibikov, 1982; Bergman, 2003; Ripple and Beschta, 2003). Beyer (2006) also found that elk on the northern range tended to avoid sites near streams at all times of the day, presumably to lower predation risk. Likewise, Gula (2004), while studying wolves and ungulates in Poland, found that riparian terrain features appeared to be important for hunting strategies used by wolves. He discovered that wolves made most kills (74%) in ravines and creeks, where ungulates may be easier to intercept as they slow down and change their gait. In Glacier National Park, USA, wolves were most successful when they could closely approach ungulates without detection; the element of surprise appeared to be an important factor in their predation success (Kunkel and Pletscher, 2001).

Results of this study provide new insights regarding the potential importance of visibility and impediments to recent willow height increases in the upper Gallatin and northern Yellowstone winter ranges. For example, our multiple

regression analysis indicates that the taller willows in the valley bottoms of these winter ranges appear to be associated with the combined effects of impediments occurring in relatively close proximity (i.e., <30 m) and viewshed distances of 200–300 m or less. These results support those of Mao et al. (2005), which show that since wolf re-introduction elk have shifted to more open habitats on the northern winter range. Similarly, Bowyer et al. (1999) concluded that parturient female moose selected sites with both high visibility and high elevations to allow them to see approaching predators.

While regression analyses provided support to the hypothesis that viewshed and terrain factors, as quantified in this study, are related to risk-sensitive foraging, these results should only be considered as a first approximation of the relative importance of these two sets of variables. For example, while both elk and bison forage on deciduous woody species in the northern range (authors' observations), their individual contributions to willow herbivory as measured in this study are not known. Furthermore, bison are present in the northern range but entirely absent in the upper Gallatin valley. A more thorough understanding of the relative roles of viewshed and terrain variables associated with risk-sensitive foraging by both of these wild ungulates is obviously needed.

5.1. Moisture availability

We compared willow heights in 2004 to the heights of their respective root collars above the water surface of adjacent streams (an index of rooting access to shallow groundwater levels), to assess potential effects of moisture availability on plant growth. While willow root collars on upland riparian sites were generally closer to groundwater levels than those of valley-bottom riparian sites ($p < 0.01$), willows on upland sites were typically less than half as tall as those on valley-bottom sites ($p < 0.01$; Table 2). In addition, willow heights for valley-bottom sites were not significantly related ($p = 0.18$) to the corresponding height of their root collars above adjacent streams. Collectively, these results indicate a lack of association between willow height increases and moisture availability, as measured by the root collar elevations that were mostly less than 1.5 m above the local groundwater sources.

Willows associated with the upland and valley-bottom riparian areas were typically growing on alluvial soils within their respective floodplains. Thus, it is possible that the occurrence of taller willows along some valley-bottom sites following wolf re-introduction could be partially due to higher site productivity (e.g., soil type, moisture hold capacity, and organic matter content). However, the heights of both upland and valley-bottom willows were consistently short (<2 m in total height) prior to wolf re-introduction (Table 1), indicating that intense browsing was able to suppress any possible differences in site productivity. Similarly, while willows inside upland exclosures at both the Gallatin (Ripple and Beschta, 2004a,b) and Lamar areas (Fig. 1) exceeded 3–4 m in height, those immediately outside the exclosures were heavily browsed; the tallest averaged only 66 and 109 cm, respectively. This stark contrast in willow height along exclosure boundaries

tends to confirm that the short stature of willows currently existing at upland riparian sites is due to ungulate browsing rather than site productivity or moisture availability.

5.2. Roads

The distance to the nearest road was significantly greater ($p = 0.03$) for the upland riparian sites when compared to the valley-bottom riparian sites (Table 2), since roads follow the valley-bottoms in our study area. Within valley-bottom sites, willow height showed no relationship ($p = 0.86$) to distance from the nearest road (Table 3). Beyer (2006) found that northern range elk avoided close proximity to roads during the day, but selected for areas closer to roads at nights, a time when willow use is highest by elk. This nocturnal elk behavior may account for why we did not find a relationship between willow height and distance to roads. These results provide no evidence that a trophic cascade was mediated by human disturbance.

5.3. Forest cover

The mean distance to forest cover was lower for upland sites ($\bar{x} = 509$) compared to valley-bottom sites ($\bar{x} = 641$), but this difference was not significant ($p = 0.18$; Table 2). Similarly, within valley-bottom sites willow height was not significantly correlated with distance to forest cover ($p = 0.23$; Table 3).

5.4. Bison

An increasing bison population may be affecting the status of willow communities (i.e., spatial extent, density, and height) in Yellowstone's northern range. Although bison are generally not considered browsers, we have repeatedly witnessed them foraging on willows of short stature in and around the Lamar Valley. Bison are not only a relatively large herbivore, but in contrast to elk, which mainly use the northern range in winter, they forage across this winter range throughout the year. The effects of bison foraging on short willows appear to have been especially significant for several of our sampling sites located in the largely open valley-bottom of the Lamar River, an area bison frequent year-round.

The negative correlation between willow height and numbers of bison flops for valley-bottom sites (Table 3) indicates that bison may be using risk-sensitive foraging behavior. Laundré et al. (2001) noted that soon after wolf re-introduction, female bison increased their vigilance levels due to the presence of wolves, while more recently Hernández and Laundré (2005) found no evidence of predation risk effects on bison in the presence of wolves. A plausible hypothesis for bison is that they tend to forage in open areas regardless of any risk of predation. If this hypothesis is true, this may partially account for why we found visibility, a measure of openness, to be inversely correlated with willow height.

5.5. Hydrologic/climatic patterns

The three hydrologic/climatic variables available for analysis in the winter ranges (i.e., snowpack depth, peakflow, and July streamflow) show somewhat different trends from 1996 to 2004. Since the initiation of increased height growth by willows in the valley-bottom sites, which appears to have begun in about 1999, maximum snowpack depths have remained below average, perhaps contributing to reduced browsing pressure on valley-bottom riparian plant communities by allowing elk to increasingly forage in upland portions of the winter ranges. However, during periods of low snowpack depths during the decades prior to the re-introduction of wolves, increased heights of young willows did not occur, thus indicating that patterns of ungulate herbivory may have shifted in recent years. Peakflows since 1999 have ranged above and below the long-term average for rivers in both winter ranges, with no discernable upward or downward trend that might account for increased willow heights in recent years. The tendency for the Lamar River to generally have somewhat higher peakflows, relative to those for the Gallatin River (Fig. 5B), may reflect the effects of the 1988 fires, which burned large portions of the Lamar River watershed. Following the 1988 fires, annual peakflows for the Lamar River increased from 11 to 23% (Beschta, 2003).

With regard to summer flows, the four consecutive years of relatively low July streamflows would likely reduce the opportunity for widespread establishment of willow seedlings. However, for willows with well-established root systems that are able to access shallow groundwater sources associated with these stream systems, this period of annual low flows may have had little effect on limiting height growth. Indeed, the trend of increased height growth indicated in Fig. 3B appears to be occurring independently of temporal patterns of moisture availability as indexed by snowpack depth, peakflow, or July streamflow in these winter ranges. Instead, reduced browsing pressure, regardless of annual hydrologic/climatic conditions, seems to represent the overriding factor that is allowing willows to grow taller.

Because this study represents a preliminary attempt to quantify terrain factors associated with risk-sensitive foraging, we should note potential limitations of our efforts. For example, our willow survey sites were based on locations limited by available historical photos and thus were not randomly chosen. In addition, since we measured the tallest plants at a given site to follow those that were beginning to recover in recent years, the results cannot be used to characterize the height of the willow population on these winter ranges. Another limitation is that we did not analyze willow species separately, but it appears that treatment effect (i.e., substantial height growth with predation risk) was greater than any differences in responses due to species. As previously indicated, we were unable to differentiate browsing by ungulate species and thus are unsure about the relative effects of elk versus bison foraging on willows. Our measurements were taken in summer, but this study was

aimed at the winter behavior of elk in relation to predation risk. Escape impediments can be different in winter when compared to summer, depending upon snow and ice conditions. Finally, we anticipate that predator/prey dynamics and the resulting status of plants will likely change in the coming years.

Based on the results of this study, and consistent with a broader literature, perhaps the best measure of predation risk is the relative amount of herbivory occurring for various sites. Overall, willow height was inversely related to browsing intensity, thus supporting the concept that increasing plant heights may have been at least partially due to behaviorally mediated trophic cascades involving wolves and ungulates, via a mechanism of predation risk. It is important to note that in the late-1960s wolves were not present in Yellowstone's northern range, and as a result of Park Service culling operations (YNP, 1997) ungulate populations were relatively low (4000–5000 elk and <500 bison), yet a release of riparian plant species did not occur. In contrast, with wolves now present again on the northern range, increased willow height growth has been underway, even though the ungulate population is considerably larger (8300–13,400 elk and 500–1500 bison from 1999 to 2003).

Both spatial and temporal patterns of moisture availability (i.e., root collar elevations, peakflows, and July flows) had little relationship to increased willow heights. However, we are uncertain how future winters with deep snow conditions may affect the browsing of riparian vegetation. While deep snow around riparian willows can protect the base of these plants from extensive browsing, deep snow and ice on upland herbaceous vegetation may cause ungulates to concentrate at lower elevations and increase herbivory on woody species in valley-bottoms (NRC, 2002). We also are uncertain of how elk and bison numbers may change in the future and the potential impact of these population changes on the release of willows at the photographed study sites or other portions of the riparian systems that occur along valley-bottoms and across uplands, as well as any effects that may accrue to other woody browse species such as cottonwoods (riparian) and aspen (upland). Nevertheless, continued research involving the quantification of plant responses and the use of terrain by ungulates under the risk of predation by wolves will enhance our knowledge of how this apex predator may influence terrestrial food webs. Such information is crucial in helping to understand herbivore/vegetation relationships in areas where wolves were once extirpated and have now returned.

As prey move across a landscape, they are probably constantly assessing risk levels at varying spatial scales. Although we found no willow recruitment in upland riparian sites, we observed the initial stages of willow release for multiple willow species at various valley-bottom riparian sites where terrain features obscured viewsheds or provided potential impediments to flight. Overall, these results are supportive of the concept that in these recovering winter ranges, predation risk is a significant factor affecting patterns of ungulate herbivory.

6. Conclusions

With the return of wolves to northern Yellowstone ecosystems, our field studies over the last five years in the ungulate winter ranges (Ripple and Beschta, 2003, 2004b, 2005a), including this one, have consistently documented a spatially variable height release of deciduous woody browse species in riparian systems, beginning in the late-1990's. If these woody species continue to grow taller (some are now in excess of 3 m in height), expand in canopy cover, and increase their spatial distribution over time, benefits to ecosystem processes should similarly accrue. These benefits could include improved floodplain functioning, channel stabilization, increased shading on streams, improved food web support for both valley-bottom and upland faunal species, larger beaver populations (Baker et al., 2005), and an overall increase in biodiversity. Thus, the re-establishment of wolves in these ecosystems and their effects, via trophic cascades, point toward improved riparian plant communities as well as improved habitats and sustainability of numerous species of riparian-dependent wildlife.

Acknowledgements

We sincerely thank those that provided us with the photographs for the pre-wolf time period, including C. Gowl, E. Jensen, C. Kay, R. Keigley, J. Peco, and the Yellowstone National Park photo archives. R. Beschta also provided pre-wolf photographs, while both R. Beschta and W. Ripple re-photographed the sites in 2004. We thank Hawthorne Beyer, Cristina Eisenberg, Daniel Fortin, Josh Halofsky, and Julie Mao for reviewing an early draft of this paper. Comments and suggestions by anonymous reviewers were particularly helpful in manuscript revision.

References

- Allen, E.O., 1970. Migration Habits of the Gallatin Elk Herd. *Montana Outdoors* 9.
- Baker, B.W., Ducharme, H.C., Mitchell, D.C.S., Stanley, T.R., Peinetti, H.R., 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. *Ecol. Appl.* 15, 110–118.
- Barmore, W.J., 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Wyoming.
- Beckerman, A.P., Uriarte, M., Schmitz, O.J., 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl. Acad. Sci. U.S.A.* 94, 10735–10738.
- Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001a. A mammalian predator/prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* 11, 967–980.
- Berger, J., Swenson, J.E., Persson, I., 2001b. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291, 1036–1039.
- Bergerud, A.T., Page, R.E., 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Can. J. Zool.* 65, 1597–1606.
- Bergman, E., 2003. Assessment of prey vulnerability through analysis of wolf movements and kill sites. M.S. Thesis, Montana State University, Bozeman, MT.
- Beschta, R.L., 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. *Ecol. Appl.* 13, 1295–1309.
- Beschta, R.L., 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology* 86, 391–403.
- Beyer, H.L., 2006. Wolves, elk and willow on Yellowstone National Park's northern range. M.S. Thesis, University of Alberta, Edmonton, Alberta, 69 pp.
- Bibikov, D.I., 1982. Wolf ecology and management in the USSR. In: Harrington, F.J., Paquet, P.C. (Eds.), *Wolves of the World: Perspectives of Behavior, Ecology, and Conservation*. Noyes Publications, Park Ridge, NJ, pp. 120–133.
- Boyce, M.S., Turner, M.G., Fryxell, J., Turchin, P., 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10 (4), 421–431.
- Bowyer, R.T., Van Ballenberghe, V., Kie, J.G., Maier, J.K., 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. *J. Mammal.* 80, 1070–1083.
- Brown, J.S., Laundré, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399.
- Childress, M.J., Lung, M.A., 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behavior of conspecifics? *Anim. Behav.* 6, 389–398.
- Creel, S., Winnie Jr., J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397.
- Dekker, D.G., 1997. *Wolves of the Rocky Mountains from Jasper to Yellowstone*. Hancock House Publishers Ltd., Blaine, WA.
- Despain, D.G., 1990. *Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting*. Roberts Rinehart, Boulder, CO.
- Edwards, V.J., 1941. *Map of Average Winter Range of Gallatin Elk Herd*. Gallatin National Forest, Bozeman, MT.
- Festa-Bianchet, M., 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia* 75, 580–586.
- Fortin, D., Beyer, L.B., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330.
- Fortin, D., Boyce, M.S., Merrill, E.H., Fryxell, J.M., 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107, 172–180.
- Gula, R., 2004. Influence of snow cover on wolf *Canis lupus* predation patterns in Bieszczady Mountains, Poland. *Wildl. Biol.* 10, 17–23.
- Hernández, L., Laundré, J.W., 2005. Foraging in the landscape of fear and its implications for habitat use and diet quality of elk (*Cervus elaphus*) and bison (*Bison bison*). *Wildl. Ecol.* 11, 215–220.
- Houston, D.B., 1982. *The Northern Yellowstone Elk: Ecology and Management*. Macmillan Publishing Co., New York, NY.
- Huselman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., Quigley, H., 2003. Assessing differential prey selection patterns between two sympatric carnivores. *OIKOS* 101, 591–601.
- Jonas, R.J., 1955. A population and ecological study of beaver (*Castor canadensis*) of Yellowstone National Park. M.S. Thesis, University of Idaho, Moscow.
- Kay, C.E., 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Ph.D. Dissertation, Utah State University, Logan.
- Keigley, R.B., Frisina, M.R., Fager, C., 2003. A method for determining the onset year of intense browsing. *J. Range Manage.* 56, 33–38.
- Kunkel, K.E., Pletscher, D.J., 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Can. J. Zool.* 78, 150–157.
- Kunkel, K.E., Pletscher, D.J., 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *J. Wildl. Manage.* 65 (3), 520–530.
- Hebblewhite, M., Merrill, E.H., McDonald, T.L., 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111, 101–111.
- Larsen, E.J., Ripple, W.J., 2003. Aspen age structure in the northern Yellowstone ecosystem, USA. *Forest Ecol. Manage.* 179, 469–482.
- Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Can. J. Zool.* 79, 1401–1409.

- Lima, S.L., 1998. Nonlethal effects in the ecology and predator–prey interactions. *Bioscience* 48, 25–34.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Lingle, S., 2002. Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology* 83, 2037–2048.
- Lovaas, A.L., 1970. People and the Gallatin Elk Herd. Montana Fish and Game Department, Helena, MT.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100, 603–609.
- Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H., 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park, Wyoming. *J. Wildl. Manage.* 69, 1691–1707.
- McLaren, B.E., Peterson, R.O., 1994. Wolves, moose and tree rings on Isle Royale. *Science* 266, 1555–1558.
- Meagher, M.M., Houston, D.B., 1998. *Yellowstone and the Biology of Time: Photographs Across a Century*. University of Oklahoma Press, Norman, OK.
- Messier, F., 1994. Ungulate population models with predation: a case study with the American moose. *Ecology* 75, 478–488.
- Murie, A., 1944. *The Wolves of Mount McKinley*. U.S. National Park Service, Fauna Series no. 5. U.S. Government Printing Office, Washington, DC.
- National Research Council (NRC), 2002. *Ecological Dynamics on Yellowstone's Northern Range*. National Academy Press, Washington, DC.
- Patten, D.T., 1968. Dynamics of the shrub continuum along the Gallatin River in Yellowstone National Park. *Ecology* 49, 1107–1112.
- Paquet, P.C., Carbyn, L.N., 2003. Wolf, *Canis lupus*. In: Feldhamer, G.A., Thompson, B.C., Chapman, J.A. (Eds.), *Wild Mammals of North America: Biology, Management, and Conservation*. John Hopkins University Press, Baltimore, MD.
- Peek, J.M., Lovaas, A.L., Rouse, R.A., 1967. Population changes within the Gallatin elk herd, 1932–65. *J. Wildlife Manage.* 31, 304–316.
- Ray, R.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), 2005. *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, D.C., 521 p.
- Ripple, W.J., Beschta, R.L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecol. Manage.* 184, 299–313.
- Ripple, W.J., Beschta, R.L., 2004a. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* 54, 755–766.
- Ripple, W.J., Beschta, R.L., 2004b. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecol. Manage.* 200, 161–181.
- Ripple, W.J., Beschta, R.L., 2005a. Willow thickets protect young aspen from elk browsing after wolf reintroduction. *West. North Am. Nat.* 65, 118–122.
- Ripple, W.J., Beschta, R.L., 2005b. Linking wolves and plants: Aldo Leopold on trophic cascades. *Bioscience* 55, 613–621.
- Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biol. Conserv.* 95, 361–370.
- Ripple, W.J., Larsen, E.J., Renkin, R.A., Smith, D.W., 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. *Biol. Conserv.* 102, 227–234.
- Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in northern Yellowstone National Park. *Ecology* 76, 2097–2106.
- Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecol. Manage.* 181, 165–176.
- Russell, F.L., Zippin, D.B., Fowler, N.L., 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plant, plant populations and communities: a review. *Am. Midland Nat.* 146, 1–26.
- Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78, 1388–1399.
- Schmitz, O.J., Hambäck, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. *Am. Nat.* 155, 141–153.
- Singer, F.J., 1996. Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National park. In: Singer, F.J. (Ed.), *Effects of Grazing by Wild Ungulates in Yellowstone National Park*. USDA Department of Interior, National Park Service, Natural Resource Information Division, Tech. Rep. NPS/NRYELL/NRTR/96-01, Denver, Colorado, pp. 279–290.
- Singer, F.J., Zeigenfuss, L.C., Cates, R.G., Barnett, D.T., 1998. Elk, multiple factors, and persistence of willows in national parks. *Wildl. Soc. Bull.* 26, 419–428.
- Soulé, M.E., Estes, J.A., Miller, B., Honnold, D.L., 2005. Strongly interacting species: conservation policy, management, and ethics. *Bioscience* 55, 168–176.
- Smith, D.W., Peterson, R.O., Houston, D.B., 2003. Yellowstone after wolves. *Bioscience* 53, 330–340.
- Smith, D.W., Stahler, D.R., Guernsey, D.S., 2004. *Yellowstone Wolf Project*. National Park Service, Yellowstone Center for Resources, YCR-NR-2004-04. Yellowstone National Park, WY.
- Vucetich, J.A., Smith, D.W., Stahler, D.R., 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos* 111, 259–270.
- Waller, D.M., Alverson, W.S., 1997. The white-tailed deer: a keystone herbivore. *Wildl. Soc. Bull.* 25, 217–226.
- Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84, 1083–1100.
- White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildl. Soc. Bull.* 26, 449–462.
- White, C.A., Feller, M.C., Bayley, S., 2003. Predation risk and the functional response of elk–aspen herbivory. *Forest Ecol. Manage.* 181, 77–97.
- White, P.J., Garrott, R.A., 2005. Northern Yellowstone elk after wolf restoration. *Wildl. Soc. Bull.* 33, 942–955.
- Yellowstone National Park (YNP), 1997. *Yellowstone's Northern Range: Complexity and Change in a Wildland Ecosystem*. U.S. Department of Interior, Yellowstone National Park, Mammoth Hot Springs, WY.