

Recovering Riparian Plant Communities with Wolves in Northern Yellowstone, U.S.A.

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Abstract

Gray wolves (*Canis lupus*) were extirpated from Yellowstone National Park in the 1920s. The ensuing seven decades marked a period when wild ungulates, principally Elk (*Cervus elaphus*), extensively used woody browse species in the upper Gallatin and northern winter ranges, thus limiting the capability of establishing plants to grow more than 100 cm in height. Following the reintroduction of wolves in the mid-1990s, we evaluated patterns of woody browse species recovery within riparian areas of these winter ranges. Measurements indicated that cottonwood (*Populus* spp.) recruitment (growth of seedlings/sprouts into tall saplings and trees) was occurring for the first time in several decades. A spatially patchy increase in the heights of young willow (*Salix* sp.) and cottonwood in the upper Gallatin and northern winter ranges, respectively, was also found within riparian transects comprising nearly 20 km in total length. Within some

transects, heights of woody species have begun to exceed 200 cm (the approximate upper browse level of Elk). Results are consistent with the reestablishment of a tri-level trophic cascade involving wolves, ungulates, and riparian vegetation. We additionally present conceptual models of vegetation recovery, illustrating differences in plant height responses to behaviorally and density-mediated trophic cascades. Northern Yellowstone's "experiment in time," whereby wolves were removed and then reintroduced, provides new insights regarding how top predators can influence the structure and biodiversity of terrestrial ecosystems. Restoration ecologists and policy-makers should consider the potential benefits of large predators as an option for helping restore degraded ecosystems.

Key words: restoration, riparian ecosystems, trophic cascades, ungulates Yellowstone, wolves.

Introduction

Ecological restoration can include both active and passive approaches for reestablishing historical plant and animal communities, as well as the renewal of ecosystem functions necessary to sustain those communities (Kauffman et al. 1997). Active restoration, for example, might range from minimizing human interventions to the reintroduction of previously extirpated species, thereby allowing natural disturbances (passive restoration) to reorganize and restore an ecosystem over time. Inherent in any restoration effort is an adequate understanding of how ecosystems historically functioned (reference conditions) and how they have changed over time (Ripple & Beschta 2005). Such information is usually crucial for assessing the magnitude of historical and contemporary human effects, as well as establishing recovery goals.

Disturbances alter the function, species composition, and population structure of ecosystems. Wildfires and large floods represent "pulse" disturbances (Bender et al. 1984) because individual events can reset plant communities, often with extended time periods between occur-

ces. In contrast, annual herbivory by ungulates creates a "press" disturbance regime. Although the annual incremental cropping of vegetation may appear to be less significant than the effects of pulse disturbances, if such herbivory comprises a sufficiently large percentage of current annual growth and is persistent (occurs year after year), these disturbances can have major impacts on plant communities and ecosystems (Ohmart 1996; Belsky et al. 1999; Barmore 2003). Wolf predation throughout the year also represents a press disturbance and its effects on consumers (ungulates) may be transmitted to plant communities as a trophic cascade (Estes et al. 2001). Over time, and in conjunction with other predators, this wide-ranging carnivore may influence not only the size of prey populations (density mediation) but also their patterns of herbivory (behavioral mediation).

During the 1800s and early 1900s, Euro-Americans eradicated Gray wolves (*Canis lupus*) and Grizzly bears (*Ursus arctos*) from some 95 to 99% of their original range in the conterminous United States, thus allowing (1) the relaxation of predation as a selective force and (2) the irruption of herbivore populations (Berger 1999). Wolves, a large predator capable of affecting a variety of animal species (Soulé et al. 2005), were extirpated from northern Yellowstone's winter ranges in the early 1900s. During subsequent decades, the effects of wild ungulate herbivory, principally Elk (*Cervus elaphus*), upon riparian plant communities remained a controversial management and scientific issue

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(e.g., Chadde and Kay 1991; NRC 2002; Wagner et al. 2006). However, most of this debate occurred without considering the potential ecological role of wolves.

The general thrust of this article embraces a major premise—following the extirpation of Gray wolves (an apex predator), riparian plant communities within the winter ranges of northern Yellowstone were severely impacted by ungulate herbivory over a period of seven decades (mid-1920s to mid-1990s). This premise is briefly summarized in our description of study areas below. However, the primary goal of this study was to assess the extent that trophic cascades following the reintroduction of wolves in the mid-1990s may have initiated recovery of these plant communities. If removal, by humans, of a wolf-dominated disturbance regime allowed ungulate herbivory to significantly impact winter range riparian vegetation over multiple decades, then reinstatement of that disturbance regime may represent a prerequisite for initiating recovery of plant communities.

Study Areas

Roughly 80 km apart along the northern portion of Yellowstone National Park (YNP), the “upper Gallatin” and “northern” winter ranges comprise approximately 200 and 1,500 km², respectively, of lower mountain slopes and valley bottom terrain in the northern Rocky Mountains (Barmore 2003; Ripple & Beschta 2004b). Most of the upper Gallatin winter range occurs outside the park, whereas approximately two-thirds of the northern winter range occurs inside the park. Summers are short and cool, whereas winters are typically long and cold. Winter snowpacks are usually shallow along valley bottoms (elevation approximately 2,000 m) and south-facing slopes, with increasing snowpack depths at higher elevations.

Low-elevation portions of these winter ranges encompass shrub-steppe plant communities dominated by Big sagebrush (*Artemisia tridentata*), with patches of intermixed Douglas fir (*Pseudotsuga menziesii*), Lodgepole pine (*Pinus contorta*), and Aspen (*Populus tremuloides*). Riparian areas along the upper Gallatin River are dominated by willows (*Salix* spp.), whereas cottonwoods (*Populus* spp.), willows, and Aspen variously occur within riparian areas of Rose Creek, Soda Butte Creek, and the Lamar River in the northern range.

In addition to Gray wolves, Yellowstone’s large predators include Grizzly bear, Black bear (*Ursus americanus*), and Cougar (*Felis concolor*). Elk frequent both winter ranges along with smaller populations of Mule deer (*Odocoileus hemionus*), White-tailed deer (*Od. virginianus*), Moose (*Alces alces*), Pronghorn (*Antilocapra americana*), and Bighorn sheep (*Ovis canadensis*). Although Bison (*Bison bison*) have been historically absent from the upper Gallatin, a herd has been present in the northern range throughout the 1900s. In recent years, the size of this herd has been increasing.

Although YNP was established in 1872, market hunting of ungulates and predators continued until 1886 when the U.S. Army was assigned responsibility for protecting the park’s wildlife (YNP 1997). However, persecution of wolves continued inside and outside the park through the early 1900s. With the extirpation of wolves in the mid-1920s (Schullery & Whittlesey 1992), northern Yellowstone’s Elk had unimpeded access to winter range plant communities, and browsing impacts to vegetation were soon observed (Callahan 1923). In the upper Gallatin winter range, Elk numbers generally decreased in subsequent decades due to annual harvest (by hunting) of animals that migrated outside the park as well as periodic die-offs associated with a degraded winter range and the occurrence of severe winters (Peek et al. 1967). Annual hunting of Elk outside the park’s portion of the northern range also occurred. In addition, in the 1920s, the Park Service began capturing Elk within the northern range and shipping them to other locations, both to assist in the reestablishment of Elk herds in various parts of the western United States and Canada and to reduce browsing impacts. Eventually, the agency resorted to killing Elk within the park in an attempt to control their impacts upon vegetation and soils.

Even though reduced Elk numbers occurred during the decades following wolf extirpation in the upper Gallatin winter range, Lovaas (1970) indicated that upland plant communities were heavily grazed, Aspen ramets (root sprouts) were no longer able to grow above the browse level of Elk, and hillslope erosion became a concern. Riparian willow communities were also heavily browsed (Patten 1968; Ripple & Beschta 2004b), eventually leading to unstable channels and a hydrologically disconnected floodplain (Beschta & Ripple 2006).

Following the loss of wolves in the northern range, palatable woody species were increasingly unable to establish and grow above the browse level of Elk (NRC 2002; Barmore 2003). Similar to the upper Gallatin, once plant communities had been degraded, even reduced numbers of Elk were capable of continuing to suppress vegetative growth. The Park Service’s Elk culling program in the northern range was terminated in 1968, and within two decades, its Elk population of approximately 4,000 had irrupted to nearly 19,000 animals. This large Elk population only served to increase the severity of impacts to plant communities and to curtail the recruitment (i.e., growth of seedlings/sprouts into tall saplings or trees) of woody browse species (Chadde & Kay 1991; Ripple & Larsen 2000; Beschta 2005). Northern range vegetation studies that spanned over five decades (1935–1989) found that average heights of young willow, Aspen, and other woody browse species outside ungulate exclosures never exceeded 83 cm ($n = 81$ species-years), whereas the same species inside exclosures rapidly increased in height (Chadde & Kay 1991; Singer 1996; Barmore 2003). Fruit production of heavily browsed berry-producing shrubs outside exclosures was severely reduced or eliminated

(Kay 1995). With the deterioration of woody plant communities, Beaver (*Castor canadensis*) underwent decline, and by the early 1950s, only scattered colonies remained (Jonas 1955).

During March 1995, 14 wolves were released into the park with an additional 17 wolves the following winter. They were soon breeding and establishing packs across northern Yellowstone.

Methods

We summarized recent population estimates for wolves, Elk, and Bison in the upper Gallatin and northern winter ranges. In the northern range study area, we determined long-term patterns of cottonwood recruitment. A diameter at breast height (dbh) of 5 cm was chosen as a threshold diameter for measurement as it was assumed that cottonwoods of this diameter, and larger, would have attained a height well above the browse level of Elk. We thus searched for and measured the diameters of all cottonwood trees more than or equal to 5 cm in dbh during late summer of 2001 with reinventories in 2002, 2003, 2004, and 2006. The establishment date of each inventoried cottonwood was estimated from tree age versus dbh relationships to establish the age structure of cottonwoods in the northern range study area (Beschta 2005). From those results, we regressed tree frequency versus establishment date for the decades when wolves were present (pre-1920s). This exponential relationship provided a basis of comparison regarding cottonwood tree recruitment during recent decades.

We further characterized the general recovery status of riparian plant communities by measuring heights of young Booth willow (*Salix boothii*) in the upper Gallatin and young cottonwoods (*Populus angustifolia* and *Po. trichocarpa*) in northern range study areas. We selected these woody species because they commonly occurred in their respective riparian areas, are highly palatable, and appeared to reflect the general pattern of height growth for other woody browse species. Our sampling of plant heights in riparian areas was undertaken to provide a “leading edge” indication of ecosystem recovery in the decade following wolf reintroduction.

In the upper Gallatin study area, we initially measured Booth willow heights within a 3-km riparian transect along the Gallatin River in August 2003. This transect occurred along a predation risk gradient (low predation risk at the upstream end of the transect, with increasing risk in a downstream direction; Ripple & Beschta 2004b). Within each 100-m segment of the transect (30 segments in total), the three tallest Booth willow plants were selected. We undertook plant architecture measurements (Keigley 1998; Beschta & Ripple 2007) on the tallest stem (leader) of each selected plant to evaluate its browsing history and springtime height (after winter browsing) for the previous 2 years. In August 2006, we measured springtime and late-summer (after current annual growth had occurred) leader

heights of the three tallest Booth willows within each 100-m segment of the same 3-km transect. We used linear regression to illustrate trends in springtime willow heights, by year, along the 3-km transect. Using the linear relationship of 2001 as a reference, we used multiple regression to test for significant ($p \leq 0.05$) slope and intercept differences in subsequent years.

In the northern range study area, we measured late-summer heights of young cottonwoods along riparian transects paralleling major streams, including:

- (1) “Lower Lamar”—a 9.9-km transect (measured in August 2002 and 2006) along the Lamar River downstream from the Soda Butte Creek confluence.
- (2) “Rose Creek”—a 2.2-km transect (measured in August 2002 and 2006) encompassing three distributaries of Rose Creek that flow across the alluvial fan at the Lamar Ranger Station (Buffalo Ranch).
- (3) “Soda Butte Creek”—a 2.2-km transect (measured in August 2006) along Soda Butte Creek starting approximately 4-km upstream of its confluence with the Lamar River.
- (4) “Upper Lamar”—a 1.8-km transect (measured in August 2003 and 2006) along the Lamar River upstream of the Soda Butte Creek confluence.

Within each 50-m segment of a transect, we searched for the three tallest cottonwood seedlings or root sprouts more than or equal to 20 cm tall and averaged their heights. For evaluating height changes over time, we expressed segment heights of a transect as a percentile and compared any change in median height between sampling periods. Height measurements of woody browse species in both the upper Gallatin and the northern winter ranges, in conjunction with other Yellowstone studies and the broader literature, allowed us to develop conceptual models that demonstrate differences in plant community responses from behaviorally mediated (risk based) and density-mediated (mortality based) components of a trophic cascade.

Results

Wolves and Ungulates

Following the 1995–1996 reintroduction of wolves, their numbers began to increase. Over the past 5 years, northern YNP populations have ranged between 54 and 106 wolves (Smith et al. 2006). Only two Elk population estimates, ranging from 1,048 to 3,028 animals, were available in the upper Gallatin study area for the 10 years (1987–1996) leading up to wolf reintroduction. After wolf reintroduction, census estimates indicate that approximately 1,000 Elk have frequented this winter range (Fig. 1a). For the northern range, Elk populations peaked at approximately 19,000 animals in the decade prior to wolf reintroduction. Elk densities after wolf reintroduction have trended downward, whereas Bison densities have recently

begun to increase (Fig. 1b). Although Bison numbers remain lower than those of Elk, it should be noted that Bison are considerably larger than Elk and often forage throughout the year within this winter range, whereas Elk use is more seasonal (i.e., late fall to early spring). Thus, the foraging needs of the northern range Bison population are considerably greater than a simple comparison of population size between Bison and Elk would indicate.

Riparian Vegetation

In 2001, a total of 954 cottonwoods more than or equal to 5 cm in dbh were inventoried along the Lower Lamar, Upper Lamar, and Soda Butte Creek sites, of which 836 remained in 2006. This represented 12% mortality over the 5-year monitoring period (equivalent to an annual compound mortality rate of 2.6% per year). If this rate of overstory tree loss were to continue, the number of standing trees across these sites will be halved within approximately 26 years.

The 2001 cottonwood inventory also found that trees between 5 and 15 cm in dbh were entirely absent, thus indicating that cottonwood recruitment had ceased during

recent decades. During the 2002 and 2003 reinventories, we were unable to find any cottonwoods that had recently attained or exceeded the threshold dbh of 5 cm. However, in 2004, we found 19 cottonwoods more than or equal to 5 cm in dbh, and by 2006 (cottonwood stands were not inventoried in 2005), the count had increased to 76 cottonwoods (ranging between 5 and 11 cm in dbh). Cottonwood age structure over the past 200 years is presented in Figure 2 for the northern range study area, exclusive of data from the Rose Creek site where cottonwood recruitment was historically influenced by Park Service culling operations (Beschta 2005). The fitted exponential relationship, based on pre-1920 data when wolves were present, provides a general basis for identifying expected levels of recruitment after 1920.

For the 76 cottonwoods that had recently attained a dbh of more than or equal to 5 cm (with establishment dates in the mid- to late-1990s; Fig. 2), 29 occurred along the Lower Lamar site, of which 23 were found on a mid-channel island (Fig. 3a), 5 were associated with a gully, and 1 was physically protected from browsing by an accumulation of woody debris. However, large areas of bare alluvium (potential germination sites for cottonwood seedlings) along the Lower Lamar remain devoid of young cottonwood (Fig. 3b). Even where establishing cottonwoods (and willows) were present, they were typically heavily browsed and of short stature (<50 cm in height). Forty-seven cottonwoods more than or equal to 5 cm in dbh were found within the Upper Lamar site, typically near individual logs and accumulations of logs, at the base of an eroding tall terrace, or in association with the increasing heights of other woody plants (e.g., willows or alder [*Alnus* sp.]). Based on the exponential relationship of cottonwood frequency versus establishment date for when wolves were historically present (Fig. 2), the 76 cottonwoods more than or equal to 5 cm in dbh that established in the 1990s represented only one-fourth of the number needed for sustaining cottonwood populations at pre-1920 levels.

For the upper Gallatin study area, trends in willow heights in recent years along the 3-km riparian transect are illustrated in Figure 4. Linear regression of springtime plant height versus transect distance, by year, indicated that (1) willows were mostly less than 100 cm in height in 2001 and (2) height increases between 2001 and 2006 occurred mostly at the down-valley end of the transect. By late summer of 2006, 50% of the transect segments had average willow heights more than or equal to 200 cm (Fig. 5a). A willow height of approximately 200 cm appears to represent the normal upper browse level for Elk (Beschta & Ripple 2007).

For the northern range study area, riparian transects indicated major differences in temporal trends between sites based on the median (50th percentile) heights of young cottonwood. Here, the median cottonwood height for transect segments along the Lower Lamar remained 30 cm between 2002 and 2006, decreased from 70 to 52 cm along Rose Creek between 2002 and 2006, and increased

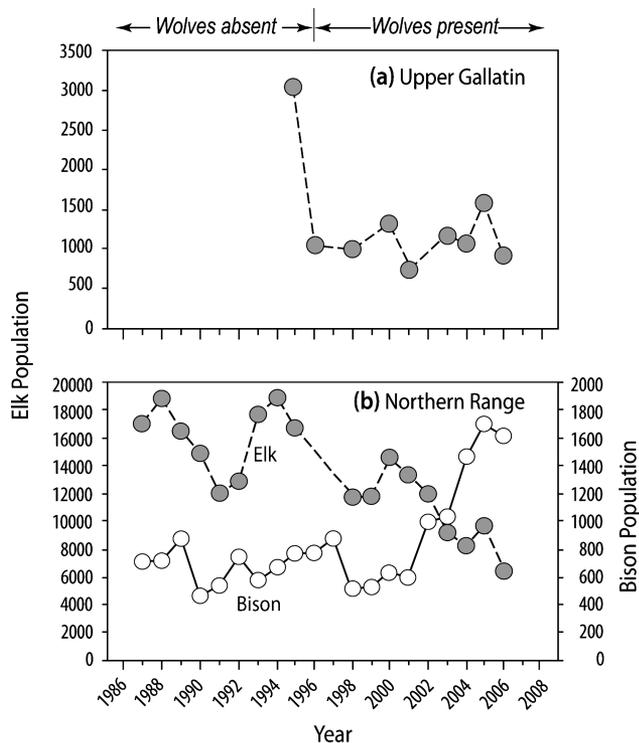


Figure 1. (a) Elk populations for the upper Gallatin winter range and (b) Elk and Bison populations for the northern winter range during the decade before and after wolf reintroduction, in YNP. Data sources: (a) 1995–2003 Elk counts from Ripple and Beschta (2004b); unpublished 2004–2006 Elk counts from Montana Department of Fish, Wildlife, and Parks and (b) 1987–2004 Elk and Bison counts from White and Garrott (2005b); unpublished 2005–2006 Elk and Bison counts from YNP. Elk counts for 1989, 1991, and 2006 likely underestimate populations due to poor survey conditions.

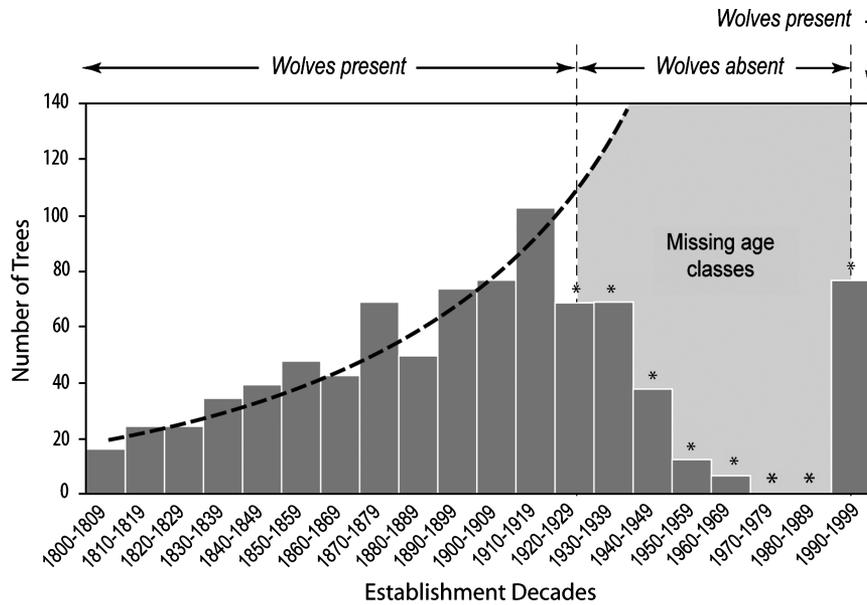


Figure 2. Frequency of cottonwood trees (Y) versus establishment date (X) within the northern range study area. The dashed line represents an exponential relationship ($Y = [1.22 \times 10^{-11}]e^{0.0154x}$, $r^2 = 0.92$, $p < 0.01$) based on decadal tree frequencies prior to 1920 (when wolves were present); the symbol “*” denotes that the number of trees for a given decade is less than the lower 95% confidence limit of the exponential regression line.

from 100 to 293 cm along the Upper Lamar between 2003 and 2006 (Fig. 5b). No change or a decrease in median height over time indicates that herbivory is continuing to suppress the height growth of these young cottonwoods.

In 2002, inspection of a 5-km reach of Soda Butte Creek (Ripple and Beschta 2003) above its confluence with the Lamar River found only one location with young cottonwoods more than or equal to 200 cm in height. Cottonwood measurements along the 2.2 km Soda Butte Creek transect in 2006 indicated a median height of 170 cm (Fig. 5b) and that 25% of the 50-m segments had heights (average of three tallest plants per 50-m segment) more than or equal to 200 cm, thus indicating increased height growth of young cottonwoods along this study reach in recent years.

Conceptual Models

Based on our field results and observations, as well as other published studies, we formulated conceptual models of vegetation response following the reintroduction of a top predator. These models illustrate how heights of establishing woody browse species may change over time (t) when behavioral or density mediation dominates a trophic cascade. To assess the relative importance of these two mechanisms, we considered three conceptual models using plant height as an index of recovering conditions. In each model, we assumed the following initial conditions:

- (1) Site productivity is constant across all foraging sites.
- (2) Foraging sites can be arrayed along a predation risk continuum (low to high).

- (3) The former extirpation of an apex predator has allowed large herbivores to maintain woody browse species in a suppressed condition (low stature) across all sites (e.g., woody browse species in the upper Gallatin and northern winter ranges after wolves had been eliminated).
- (4) The previously extirpated apex predator is reintroduced at $t = 0$, again completing the predator guild.

Our first conceptual model of plant height responses following reintroduction of an apex predator assumes behaviorally mediated foraging patterns. In this model (Fig. 6a), herbivores begin to avoid sites of high predation risk because of the presence of the reintroduced predator. Because predator avoidance represents learned behavior (based on predator–herbivore encounters), some time may be required before browsing levels decrease on high-risk sites and plants to increase in height. Height increases are initially greatest at high-risk sites, with moderate-risk sites demonstrating a slower rate of increase. Low-risk sites may actually experience a general loss of plant height due to increased herbivory (e.g., Rose Creek site in the northern range) as herbivores weigh foraging needs against predation concerns within a landscape of fear (Brown et al. 1999; Laundré et al. 2001; Ripple & Beschta 2004a; Hernández & Laundré 2005; Berger 2007). This model indicates that the occurrence of plants increasing in height (high-risk sites) and those which are unable to increase in height or are further suppressed by increased browsing (low-risk sites) can be attributed to behaviorally mediated foraging (Schmitz et al. 2000). Plant heights at $t = n$ reflect a balance between current annual growth and



Figure 3. (a) A high predation risk mid-channel island surrounded by significant escape impediments such as steep stream banks, woody debris, coarse gravel surfaces, and variable river depths where woody browse species have been increasing in height following wolf reintroduction and (b) a low predation risk riparian area with good visibility and few escape impediments where establishing woody browse species (e.g., cottonwood, willows) remain sparse, heavily browsed, and of low stature (mostly <50 cm in height) after wolf reintroduction; trees in center of the photo are mature cottonwoods and the ungulates are Bison. Photos (a) and (b) are for late summer of 2003 and 2006, respectively; both photos show portions of the Lower Lamar study site.

herbivory along a predation risk gradient. In this model formulation, only plants on high-risk sites can eventually grow above the upper foraging level of the prevalent herbivores.

Our second conceptual model of recovering vegetation involves only density-mediated foraging. In this model (Fig. 6b), we additionally assume that (1) herbivore densities have become sufficiently low at $t = 0$ that plant height increases begin to occur and (2) even though an apex predator was introduced at $t = 0$, herbivore use of foraging sites *occurs independently of predation risk*. Thus, palatable plants begin to increase in height on all sites ($t = 1, 2$) and continue to grow above the upper foraging level of the prevalent herbivores ($t \geq 3$). Eventually ($t = n$), full complements of height (and age) classes of riparian plants occur across all sites. Because site productivity was assumed constant, the time required for plant heights to exceed the normal upper foraging level of herbivores

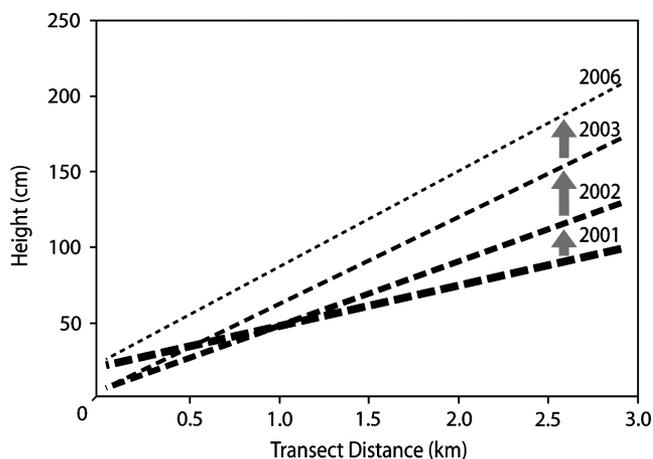


Figure 4. Linear regressions of springtime Booth willow heights versus transect distance, by year, for a 3-km transect along the Gallatin River in the upper Gallatin winter range ("0 distance" is the upstream end of the transect). Reintroduced wolves colonized the upper Gallatin in the mid-1990s. There was strong evidence ($F_{[3,94]} = 4.57, p < 0.01$) that the relationship between willow height (cm) and distance (km) differed among years. Although there was no significant difference in intercepts between 2001 and subsequent years ($p \geq 0.54$) or for slope between 2001 and 2002 ($p = 0.20$), slopes for the 2003 and 2006 relationships relative to 2001 were significantly different ($p < 0.01$).

would be inversely related to herbivore density. This conceptual model indicates that lower ungulate densities may be necessary before a more expansive recovery of riparian plant communities can occur in Yellowstone's northern ranges.

Our third conceptual model (Fig. 6c) combines the behavioral and density mediation effects of a trophic cascade by simply averaging, over time, plant height responses illustrated in the first two models. In this combined model, plants at high-risk sites experience the greatest increase in height for $t \geq 1$, although incremental height increases also occur at sites of moderate and low predation risk.

Discussion

Other than humans, who occupy an ecological niche as top predator in most ecosystems, Peterson et al. (2003) indicated that Gray wolves, by virtue of their widespread geographic distribution, group hunting, and year-round activity, represent the most significant ungulate predator in the Northern Hemisphere. If so, the loss or reintroduction of wolves may sufficiently alter trophic cascades within a predator–consumer–producer system such that major adjustments ultimately occur at the lower most trophic level.

The winter ranges of northern Yellowstone represent an experiment in time, whereby wolves were first extirpated and then reintroduced. Although these treatments were unplanned (i.e., the Park Service did not

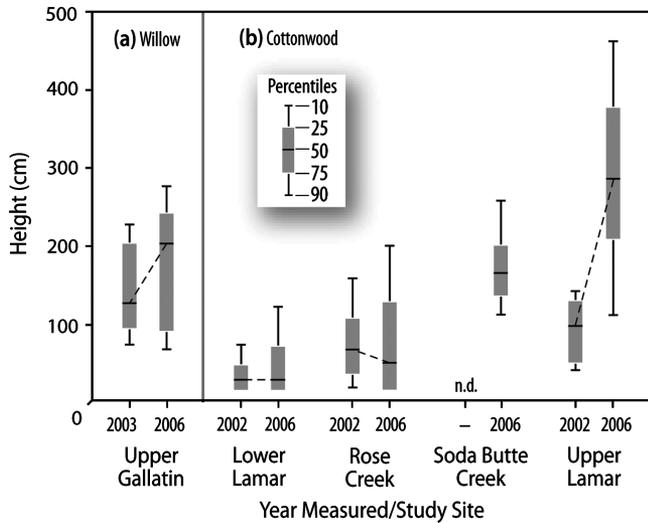


Figure 5. Box and whisker plots of late-summer plant heights (in percentiles) by year and site for (a) willows in the upper Gallatin winter range and (b) cottonwoods in the northern winter range; wolves were reintroduced in northern Yellowstone during the mid-1990s. “Percentiles” indicate the percentage of transect segments having a height (average height of the three tallest plants per 50-m segment) greater than the indicated height.

intentionally set out to manipulate wolf populations as an experiment), they nevertheless provide a unique opportunity to assess ungulate and plant community effects associated with the removal and return of a top predator. In terrestrial systems, examples of large carnivore trophic cascades have been uncommon (Borer et al. 2005).

After the extirpation of wolves in northern Yellowstone, Elk have generally been considered the principal herbivore of concern in both winter ranges. However, in the northern winter range, a decreasing Elk population and an increasing Bison population during recent years indicate that Bison may be having a more important role affecting plant communities. We observed noticeable levels of summertime foraging by Bison on young cottonwoods and willows (Ripple & Beschta 2006) along the Lower Lamar and Rose Creek sites. These observations of summertime herbivory, suppressed cottonwood heights, and the results of a radio-collared Elk study (Boyce et al. 2003), indicating a relatively low probability of Elk occurrence along the Lower Lamar and Rose Creek sites in recent years, suggest that Bison herbivory may be suppressing woody browse species at these sites. Although Bison represented less than 1% of wolf kills during 1995–2000 (Smith et al. 2004), this had increased to 9% by 2005 (Smith et al. 2006), indicating that prey switching from Elk to Bison may be underway.

Our results for the 3-km transect along the upper Gallatin River indicate that willow heights were increasing along a spatial gradient several years following wolf reintroduction. In an analysis of 1998–2002 willow heights along this transect, Ripple and Beschta (2004b) found (1) decreased browsing over time and (2) less browsing along

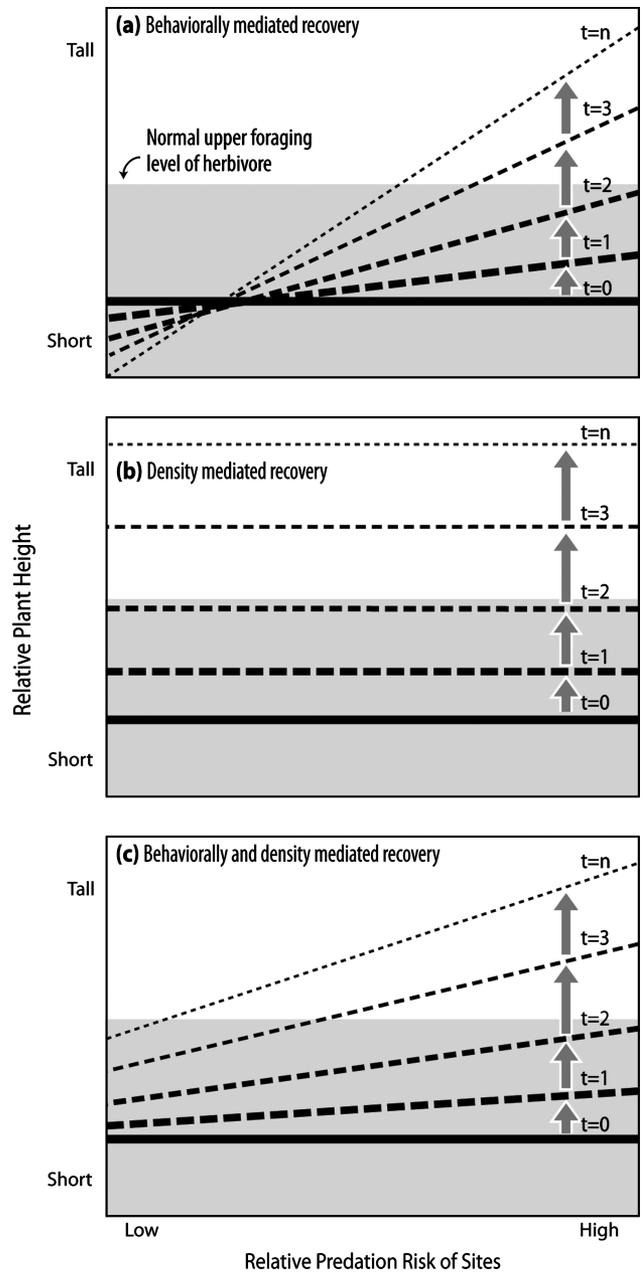


Figure 6. Conceptual models of woody plant height increases following the reintroduction of an apex predator (see text for details). Models represent (a) behaviorally mediated, (b) density-mediated, and (c) combined behaviorally and density-mediated trophic cascades over time ($0 \leq t \leq n$). For simplicity, we assume linear relationships.

the downstream end of the transect relative to the upstream end. At the downstream end of this transect, the width of the valley narrows, multiple channels occur in the floodplain, and a major highway comes relatively close to the river. Thus, increased willow heights appear to be associated with terrain and cultural features that can affect the capability of Elk to detect and escape from wolves, that is, predation risk (Ripple & Beschta 2004a).

For the northern range study area, increased median heights of young cottonwoods along the Upper Lamar site were often associated with scattered cottonwood and conifer logs that were relatively common along this reach in comparison to other riparian areas. In a few instances, these logs created local refugia by physically protecting woody browse species from ungulate herbivory. A tall terrace (10–15 m in height) occurred along the eastern edge of the floodplain, additionally limiting ungulate viewsheds and escape routes, thus increasing predation risk. Similarly, increases in the heights of young Aspen in recent years have been found to be greatest on high-risk sites (Ripple & Beschta 2007). In contrast, improvement in median heights was not found for the Lower Lamar site and an actual decrease in median heights occurred at the Rose Creek site. Both sites occur in the widest part of the Lamar Valley where there is good visibility over long distances, woody debris accumulations are generally absent, and other impediments to escape are relatively few and easily visible (low predation risk sites).

Winter climates in northern YNP can influence large herbivore populations and seasonal patterns of herbivory (e.g., deeper snowpacks tend to drive Elk to lower elevations) (Boyce et al. 2003; White & Garrott 2005a). However, during the seven decades when wolves were absent from northern Yellowstone's winter ranges and regardless of climate fluctuations, Elk had relatively unconstrained access to riparian plant communities and woody browse species were generally unable to grow above the browse level of these ungulates. Now that wolves are back, how variations in winter conditions (Vucetich et al. 2005) or long-term trends in climate might influence ungulate populations or patterns of herbivory in riparian areas remains to be seen.

Overall, our results, in concert with other recent studies in the upper Gallatin and northern winter ranges, indicate that willow, cottonwood, and Aspen recruitment is beginning to occur primarily within riparian areas where viewsheds, terrain, vegetation, or large wood features suggest locally high predation risk, even though streamside areas in general represent landscape conditions where Elk may be particularly vulnerable to wolf predation (Kunkel & Pletscher 2001; Gula 2004; Beyer 2006). The fact that cottonwood recruitment is again underway in some northern range riparian areas represents a fundamental departure from the downward trend in recruitment that occurred during the 1920–1960s and the total absence of recruitment in the 1970s and 1980s, when wolves were absent. Nevertheless, contemporary levels of ungulate herbivory are continuing to suppress the growth of young cottonwoods, willows, and Aspen within many areas of the northern range.

Our conceptual models indicate that spatially variable increases in plant heights would be an expected outcome of trophic cascades having a strong behavioral mediation component, whereas density mediation provides for recovery of plant communities across landscapes. However, where large predator and herbivore densities change

over time, particularly where multiple large predator and herbivore species are present, lower trophic-level responses of increased plant heights would likely assume a more complex pattern (e.g., the combined model, curvilinear relationships). Our results in the upper Gallatin indicate height increases along a spatial gradient until 2003 and more uniform height increases after 2003, perhaps illustrating a shift from primarily a behaviorally mediated trophic cascade to one where density mediation has become more important.

In the northern range, a downward trend in Elk populations and an upward trend in Bison populations during the most recent decade complicate attempts to decipher the relative importance of ungulate behavior versus ungulate density upon recovering woody browse species. Nevertheless, the occurrence of height increases (Soda Butte Creek and Upper Lamar sites) as well as no change or even a decrease in height (Lower Lamar and Rose Creek sites) for young cottonwoods during the first decade of wolf recovery indicates that behavior mediation has likely been a major mechanism influencing plant communities in this winter range.

We focused on palatable deciduous woody species in this study because of their fundamental importance to riparian plant communities as well as their capacity to index herbivore effects upon a broader range of plants and ecosystem processes over time. Prior to the extirpation of wolves, much evidence points to biologically diverse riparian plant communities in Yellowstone's northern winter ranges. Yet, during the seven decades of wolf absence, and regardless of ungulate densities or prevailing climatic conditions, various studies found widespread degradation of these plant communities. Following the reintroduction of wolves in the mid-1990s, increased heights of at least some willows, cottonwoods, and Aspen in Yellowstone's northern winter ranges suggest that linkages between large predators, herbivores, and plants are again being reestablished. The recent return of beaver colonies to the northern range (Smith et al. 2003) serves to reinforce this hypothesis. Nevertheless, numerous questions remain. Will increased heights of woody browse species continue to be associated primarily with high predation risk sites or will increases in heights become more widespread in the coming years? How will changing Elk and Bison densities in the northern range study area, in combination with shifting environmental variables (e.g., climate change), influence future outcomes for plants? Large predator reintroduction is a relatively new occurrence in the United States, and the scientific basis for predicting expected ecological outcomes is limited. The extent to which plant height increases during the first decade of wolf reintroduction will continue, or foreshadow a broader recovery of other native plant and animal species normally associated with biologically diverse riparian ecosystems, is yet to be determined.

Although these studies were conducted in the winter ranges of a national park, the occurrence of a trophic

cascade involving Gray wolves may have implications to other areas of the northern Rocky Mountains (e.g., parts of Idaho, Montana, and Wyoming) where reintroductions have occurred. For other parts of the American West, such as Oregon and Utah, dispersing wolves may eventually recolonize some of their former ranges (ODFW 2005; UDWR 2005). In the central Rocky Mountains, wolf reintroduction has been identified as a possible management alternative to help reduce the adverse ecological effects of a burgeoning Elk population (RMNP 2006). Previously, Ratti et al. (2004) evaluated factors affecting the feasibility of reintroducing wolves to the Olympic Peninsula of Washington State but did not consider potential ecological effects wolves might have on lower trophic levels (i.e., plant communities). Although long-term studies by McLaren and Peterson (1994) at Isle Royale (a 544-km² island in Lake Superior) indicate that trophic interactions have occurred between wolves, Moose (*Alces alces*), and Balsam fir (*Abies balsamea*), how these or other trophic cascades might relate to adjacent areas of Minnesota, Wisconsin, and Michigan where Gray wolves have recolonized in recent years has been little explored by the scientific community. In the Highlands of Scotland, where wolves have been absent since the mid-1700s and intensive foraging by Red deer (*Cervus elaphus*) is a serious environmental problem, a recent assessment indicated that ungulate densities could be significantly reduced through wolf reintroduction (Nilssen et al. 2007). If some of the trophic-level effects measured in this study occur where wolves have been reintroduced or expanded their ranges, improved sustainability and diversity of native flora and fauna may be one of the important outcomes of such endeavors.

Implications for Practice

- Annual herbivory by wild ungulates, in the absence of an apex predator, can have profound long-term effects on the composition, structure, and functioning of riparian plant communities. Reducing these effects represents a high priority for restoring altered ecosystems.
- The return of previously extirpated Gray wolves is allowing for passive restoration, via trophic cascades, of some riparian plant communities in Yellowstone's northern winter ranges.
- Managers and policymakers should consider the potential ecological benefits of large predators in efforts to recover/restore degraded ecosystems.

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