



Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA

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Abstract

We summarized the status of wolves (*Canis lupus*), elk (*Cervus elaphus*), and woody browse conditions during the 20th century for the upper Gallatin elk winter range in southwestern Montana, USA. During this period, wolves were present until about the mid-1920s, absent for seven decades, and then returned to the basin in 1996. A chronosequence of photographs, historical reports, and studies indicated willows (*Salix* spp.) along streams became heavily browsed and eventually suppressed following the removal of wolves, apparently due to unimpeded browsing by elk. However, after wolf establishment in 1996, browsing intensity on willows lessened in some areas and we hypothesized that, at both a landscape and fine scale, browsing pressure reflects terrain configurations influencing predation risk (nonlethal effects), in conjunction with lower elk densities (lethal effects). We measured browsing intensity and heights of Booth willow (*S. boothii*) along 3000 m reaches of the Gallatin River and a tributary to examine the potential influence of wolf/elk interactions upon willow growth. Where the Gallatin Valley is relatively narrow (high predation risk), willows began releasing in 1999 and by 2002 were relatively tall (150–250 cm). In contrast, willow heights along a wider portion of the Gallatin Valley, along the open landscape of the tributary, and an upland site (all low predation risk) generally remained low (<80 cm). We identified terrain and other features that may contribute to the perceived risk of wolf predation, by elk for a given site. Although alternative mechanisms are discussed, changes in willow communities over time following wolf removal and their subsequent reintroduction were consistent with a top-down trophic cascade model involving nonlethal and possibly lethal effects. If similar top-down effects upon vegetation hold true in other regions of North America and other parts of the world where wolves have been extirpated, wolf recovery may represent a management option for helping to restore riparian plant communities and conserve biodiversity.

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1. Introduction

When a top trophic level predator interacts with the next lower level herbivore and this interaction significantly alters or influences vegetation, a “trophic

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cascade” occurs. Recent studies are increasingly demonstrating the important role that large carnivores may have upon their ecosystems via cascading effects to lower trophic levels. For example, since herbivory by ungulates can affect plant community structure, succession, productivity, species composition, and overall habitat quality, vegetation communities and their ecological roles can be profoundly altered by ungulates when top predators are removed from ecosystems (White et al., 1998; Ripple and Larsen, 2000; Beschta, 2003). The effects of predator extirpation can range from altered predator-prey relationships to the loss of species interactions, resulting in simplified or degraded ecosystems (Soulé et al., 2003). There is increasing evidence that predation by top carnivores, via the process of trophic cascades, is crucial in the maintenance of biodiversity through both lethal effects (Terborgh et al., 1999; Estes et al., 2001) and nonlethal effects (Ripple and Beschta, 2004).

As an example of lethal effects that result in a trophic cascade, McLaren and Peterson (1994) found balsam fir on Isle Royale showed depressed growth rates, due to suppression by moose herbivory, when wolves (*Canis lupus*) were rare and moose (*Alces alces*) densities were high. In Venezuela, Terborgh et al. (2001) also discovered lethal effects in a study of recently created islands that were caused by a reservoir impoundment. When predators disappeared from the islands, herbivores increased, and the reproduction of canopy trees became suppressed in a manner consistent with a top-down theory.

A mechanism for understanding how nonlethal effects can effect a trophic cascade is that of “predation risk” whereby prey alter their foraging patterns, habitat use, and other behaviors depending upon the relative risk of predation (Lima and Dill, 1990; Childress and Lung, 2003; Ripple and Beschta, 2004). The idea that predators may influence the distribution of vertebrate prey goes back to the 1930s in research on small mammals (Errington, 1956). Leopold (1933) was perhaps the first to propose that wolves can affect the distribution of ungulates when he cited a case on Vancouver Island as an example of deer reaction (i.e., a change in spatial distribution) following the loss of predation by wolves. Much later, Hornocker (1970) and Peek (1980) also suggested that large carnivores influence the distributions of ungulates. More recently, following wolf reintroductions into Yellowstone

National Park (YNP) in 1995–1996, elk (*Cervus elaphus*) have increased their vigilance (Laundré et al., 2001) and changed their patterns of browsing (Ripple et al., 2001) both of which represent types of behaviorally mediated trophic cascades.

In central YNP, Bergman (2003) found that proximity to “hard edges” had a strong influence on the locations where elk were most vulnerable to predation and that wolves selected to travel along these edges. He defined a hard edge as any “structural change that could impede animal movements”, such as streams or sites with large amounts of downed timber, and indicated an inverse correlation between distance from these types of edges and successful wolf kills. He observed many chase sequences between wolves and elk that ended in successful capture of elk after crossing “hard edges”. He hypothesized that under such conditions any wrong or delayed decision by elk would allow wolves to narrow the gap during a chase. On the northern range of YNP, Mao (2003) similarly found that in the wintertime, elk selected for more open habitats after wolf reintroduction as compared to the period before wolf reintroduction. While studying wolves and ungulates (mostly elk) in Poland, Gula (2004), found that riparian terrain features appeared to be important for hunting strategies used by wolves. He found 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.

Riparian plant communities provide a variety of ecological functions such as stabilizing streambanks, imparting hydraulic resistance during overbank flows, enhancing deposition of organic matter and fine sediment onto streambanks and floodplains, moderating water temperatures and riparian microclimates via canopy shade, cycling nutrients, providing allochthonous inputs to aquatic systems, supporting the general food webs of riparian and aquatic organisms, and others (Wigington and Beschta, 2000; NRC, 2002b). The recent return of wolves in 1996 into the upper Gallatin Valley provided an opportunity to study initial trophic relations among wolves, elk, and riparian vegetation on the Gallatin National Forest, adjacent to the northwest corner of YNP. Furthermore, Ripple and Beschta (2003) hypothesized that following the reintroduction of wolves on the northern range of YNP, predation risk associated with various terrain conditions was playing a role in the selective

release of riparian cottonwoods and willows from browsing by elk in the Lamar Valley. In high-risk areas, where young cottonwood and willow plants had remained <100 cm in height for at least a decade before wolf reintroduction, they found these species had grown to heights of between 100 and 400 cm.

The willows of the Gallatin elk winter range, just as in the northern range of YNP, represent woody browse species that have declined dramatically over the course of the 20th century (NRC, 2002a). Various hypotheses have been suggested in an attempt to explain the decline of woody vegetation including climate change and/or fluctuation, lower water tables, ungulate browsing, wildfire suppression, chemical defenses of plants, beaver (*Castor canadensis*), Native American influences, changes to the northern range outside the park, and various combinations of these factors (Yellowstone National Park, 1997; NRC, 2002a). Since willows represent one of the most widespread and common genera of deciduous woody vegetation occurring along streams and rivers of the western USA and are common in the study area, our investigation focused on the potential cascading effects of wolves upon willow communities. The overall goal of this study was to develop an improved understanding regarding the potential effects of removing the gray wolf, and ultimately returning it, upon riparian plant communities within the winter range of the upper Gallatin elk herd. Specific objectives include:

- (1) Synthesize historical information regarding wolves, elk, willows, and associated climatic information during the 20th century to help assess the long-term effects of wolf extirpation and other factors upon willow communities.
- (2) Collect base-line data on existing willow communities to determine if they have begun to release (i.e., increase in total height) following wolf reintroduction. And, if so, assess whether increased height growth is associated with predation risk or environmental variables.

We hypothesized that browsing of willows on the winter range following wolf reintroduction will have decreased at high-risk sites (those where elk experience significant escape impediments during a potential wolf encounter), thus allowing for increased

height growth. Examples of escape impediments, occurring either individually or in combination, include rivers, gullies, cliffs, highways, terraces, cut-banks, downed woody debris, and others, particularly when partially or fully obscured under the cover of snow, that may increase the potential for a loss of footing, decrease in speed, or change in direction during flight (Table 1). We also expected that the initiation of release from herbivory in high-risk sites would follow soon after wolf reintroduction in YNP. Conversely, low-risk sites (areas without the escape impediments described above) will continue to be characterized by the suppressed stature of willow due to continued high levels of herbivory. Furthermore, we would expect greater contrasts for vegetation inside and outside of exclosures in areas of low predation risk.

Table 1
General types of factors that individually or in combination may contribute to an increase in predation risk

Terrain factors
Point bars
Wide channels
Multiple channels
Tributary junctions
Islands
Gravelly/rocky surfaces
Gullies
High, steep channel banks
High terraces, steep terrace sideslopes
Undulating terrain
Narrowing valley
Cliffs, steep slopes
Canyons
Rushing water (noise)
Biotic factors
Vegetation thickets
Woody debris
Jack-strawed trees
Beaver dams, ponds, and channels
Cultural factors
Roads/traffic
Fences
Snowpack factors
Aerial cover and drifts
Depth and density
Ice lenses and crusts
Frozen ground/ice

Note. While many of these factors may not be a concern to a fleeing ungulate during summertime conditions, when snow covers the ground they can represent an increased risk of injury.

2. Study area

Located in southwestern Montana, the Gallatin Mountains contain ridges, steep stream-cut and glacial valleys, and wide sloping hillsides. Within this range, the Gallatin River originates high in northwestern YNP and initially flows west to the edge of the park boundary. The river then flows northerly through a broad, open valley of the upper Gallatin Basin until encountering a relatively rugged canyon that discourages elk from moving farther down-valley in winter (Allen, 1970; Lovaas, 1970).

The upper basin has a continental climate whereby temperatures can vary greatly on a daily and seasonal basis. In winter, temperatures are cold and precipitation normally occurs as snow (NRCS, 1996). Annual precipitation ranges from 50 to 70 cm in the valley (elevation, ~2000 m) to more than 150 cm along adjacent mountain ridges. Annual snowfall amounts in the valley total approximately 250 cm with more than 750–1000 cm occurring at higher elevations (SCS, in press). Deep snow in the fall and winter force elk to move from high mountain terrain within YNP to winter range in the lower open valleys along the upper Gallatin River and its tributaries, from about Specimen Creek at the southern end down to Porcupine Creek at the northern end, as well as portions of the Madison River Basin (Lovaas, 1970).

Within the winter range, our study included a reach of the Gallatin River and that of a local tributary, Tepee Creek (Fig. 1). Both reaches have floodplains bordered by broad, open slopes of sagebrush (*Artemisia* spp.)-grasslands and open timber stands. The Gallatin River reach flows through floodplains up to 200 m in width before the valley narrows at its northern end due to steep hillslopes and rock outcrops. Floodplains along Tepee Creek are typically ≤ 20 m in width. Above its confluence with Tepee Creek, the Gallatin River drains 415 km² of mountainous terrain whereas Tepee Creek has a drainage area of only 15 km².

While several sagebrush species dominate the open hillslopes, rabbitbrushes (*Chrysothamnus* spp.), Idaho fescue grass (*Festuca idahoensis*), wheatgrasses (*Agropyron* spp.), and bluegrasses (*Poa* spp.) are also common. Lodgepole pine (*Pinus contorta*) is the dominant tree in this area although forest species of Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus*

tremuloides), Englemann spruce (*Picea engelmannii*), and lodgepole pine often occur in dense stands on north-facing slopes. Historically, willow thickets have been common along the Gallatin River and major tributaries. Elk on the Gallatin winter range primarily forage on graminoids and other herbaceous vegetation but also browse on woody species such as willow and aspen, especially as seasonal snow cover increases in depth. Conifers and sagebrush are browsed upon only in extreme conditions when little other forage is available (Lovaas, 1970).

3. Methods

Publications, government reports, and available databases were used to establish historical trends for wolf and elk populations, as well as the status of willow communities. We particularly searched for historical information and photographs indicating the condition of woody browse species in the study area. When we located historical photographs within our study area, we rephotographed the same scenes during late summer of 2003. From these we selected a subset of photographs, presented herein, that represented the general status of vegetation communities at various locations and over time in the upper Gallatin winter range.

A 3000 m willow transect along a continuum of from high to low predation risk was established in late August of 2003 along the streambank of the Gallatin River upstream of its confluence with Tepee Creek; a similar 3000 m transect was established along the lower portion of Tepee Creek (Fig. 1). The three tallest Booth willow (*Salix boothii*) plants (clumps) that were accessible to browsing were selected within each 100 m segment (30 segments in total) of each transect. Booth willow was used as our focal species since it was the most prevalent species of tall willow that occurred along each transect. For each selected plant we recorded (1) the maximum height above the ground of the previous year's growth (year 2002), and (2) whether the leader had been browsed. The previous year's leader height was measured because it had been exposed to browsing during the winter of 2002/2003, while the current year's growth had not yet been exposed to winter-time browsing (Keigley and Frisina, 1998). Only plants occurring along the tops of stream

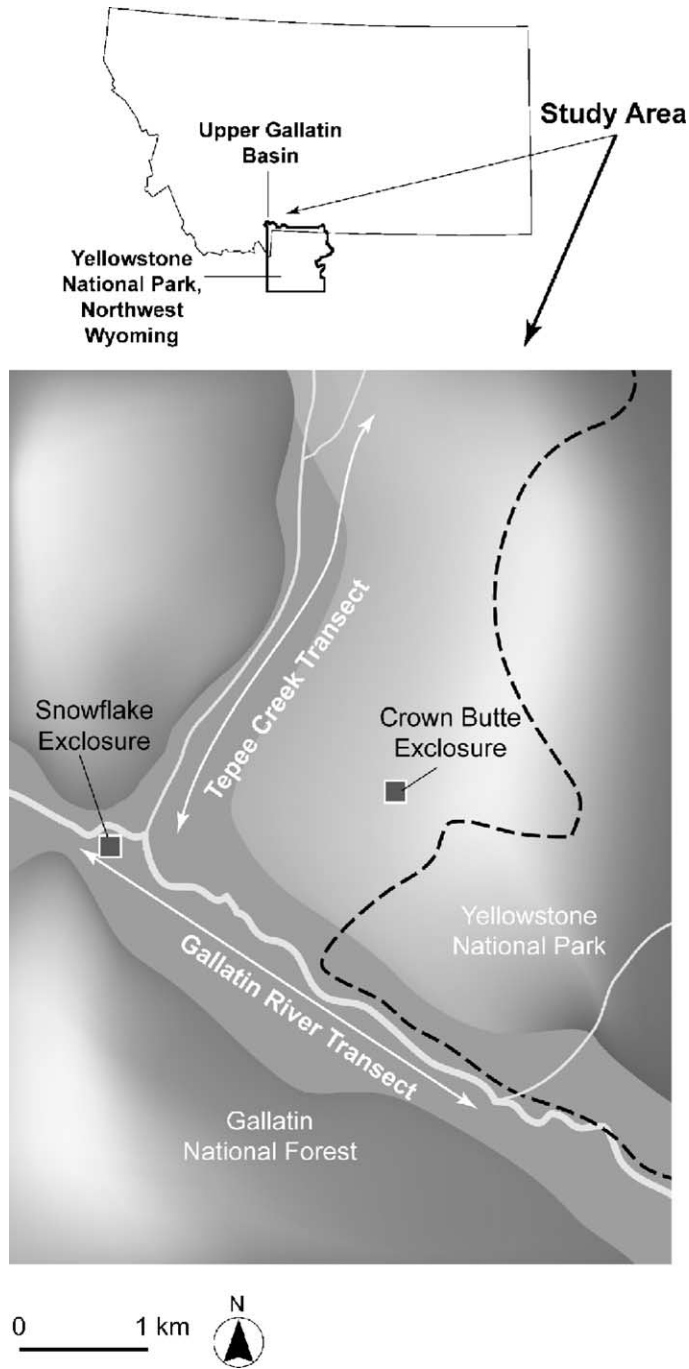


Fig. 1. Location map of study reaches along the Gallatin River and Tepee Creek, Gallatin National Forest, southwestern Montana. Dashed line represents the boundary of Yellowstone National Park.

banks were sampled since willow densities rapidly decrease with distance from the river (Patten, 1968). To assess spatial differences in moisture availability from subsurface water tables for sampled plants, the height of the streambank surface above the water surface was measured every 50 m along each transect.

Booth willow heights were also measured inside and outside of two exclosures that had been in place for over 50 years. One exclosure (high-risk location) was located in a riparian area (elevation 2000 m) near Snowflake Springs and adjacent to the downstream end of the 3000 m Gallatin River transect. Midway along each of the four sides of the Snowflake exclosure, 2 m × 10 m belt transects were established (each transect being parallel to and 1 m from the fence) for measuring willow heights. The second exclosure (low-risk location) occurred at an upland spring (elevation 2150 m) below Crown Butte. At the Crown Butte exclosure, heights were measured along a single 2 m × 40 m belt transect outside of the southeastern corner of the exclosure since willow only occurred inside the exclosure at that location. This 40 m long belt transect was adjacent to a small spring-fed stream which was flowing in September of 2003. At both sites, willow heights were measured inside the exclosure fence adjacent to the outside measurement locations, and using the same plot dimensions as those outside the exclosures. Along the length of each belt transect, the height of the tallest leader (current year's height) was measured within each 1 m segment of the transect length.

Outside each of the exclosures, we utilized "plant architecture" assessment techniques for determining past browsing history and height growth on the Booth willows (Keigley and Frisina, 1998; Keigley et al., 2003; Ripple and Beschta, 2003). Since elk usually consume segments of the stem from the current year's growth, browsing removes the terminal bud causing growth to emerge from a lateral bud. When this happens each year, the stem grows in a zigzag pattern leaving behind stubs representing annual segments that can be measured (Keigley et al., 2003). Thus, to assess elk browsing intensity, we determined whether each annual leader segment had been browsed for as far back in time as possible (typically two to five years). In addition, inspection for bud scars and stubs allowed us to determine annual leader heights for up to five of the previous years.

Annual flows were chosen to represent long-term climate trends in the upper Gallatin Basin since they integrate all meteorological conditions a particular watershed experiences and they also index the general availability of moisture that influences the establishment and growth of riparian plant communities. For streamflow data, we utilized the Gallatin River near Gateway, Montana streamgage (U.S. Geological Survey #060435; elevation 1585 m) which measures flow from a 2140 km² drainage area and is located 60 km downstream of the study reach. Linear regression of overlapping annual flows with (1) the Gallatin River at Logan (U.S. Geological Survey #060525) and (2) the Yellowstone River at Corwin Springs (U.S. Geological Survey #061915) were used to develop relationships for estimating missing annual flows at the Gateway gage. A moving average was used to represent the general pattern of annual flows during the 20th century.

Both snowpack and streamflow measurements were used to index climatic trends/fluctuations for the study area during the period of recent wolf reintroduction (i.e., 1996–2002). For snowpack depths we used the Twenty-One Mile Snow Course (NRCS Site 11E06; elevation 2180 m) located 13 km south of our study reaches and for streamflow (annual peakflow and July streamflow) we again used the Gateway gaging station. Snow is considered the "chief causative factor" causing elk migrations towards their winter range and snow conditions can vary greatly between years (Lovaas, 1970).

4. Results

4.1. Long-term conditions and trends

4.1.1. Wolves

Although wolves were thought to have a "dynamic balance" with the Gallatin elk herd prior to Euro-American arrival in southwestern Montana (Lovaas, 1970), limited quantitative information was available regarding the historical presence of wolves in the upper Gallatin Basin. Based upon Forest Service annual game reports, Lovaas (1967) indicated "up until 1922, according to the written record, the greatest factors in the annual loss of the elk were predatory animals, the legal hunter, and the poacher. Since that

date the greatest factors have been the legal hunter, old age, and ticks and starvation . . . Wolves were a serious problem in 1919 but have now [1933] entirely been eliminated.”

Weaver (1978) reported that several wolves were “killed on the Upper Gallatin River a few miles outside the park” in 1912. Large canids were occasionally sighted within YNP after 1914, but of the 56 recorded wolf kills during the period 1914–1923 and the 10 known wolf dens during the period 1916–1923, none occurred in the northwestern portion of the park. Although the last known wolf kills in YNP occurred in 1926, the exact timing of wolf disappearance from the upper Gallatin basin is not known. Based on informa-

tion presented by Lovaas (1967, 1970), and Weaver (1978), it is likely that this keystone predator was functionally extinct by the mid-1920s (Fig. 2a).

After approximately seven decades of absence, wolves returned to the upper Gallatin basin in the mid-1990s. The primary wolf pack in the upper Gallatin basin has been the Chief Joseph Pack starting with three individuals in 1996 and ranging from 8 to 13 members over the period 1997–2002. Although wide-ranging, the Chief Joseph Pack has spent much of its time denning and preying on elk within the Gallatin elk winter range. The pack’s traditional den site is located near our study site along a tributary of the Gallatin River (Smith et al., 2002).

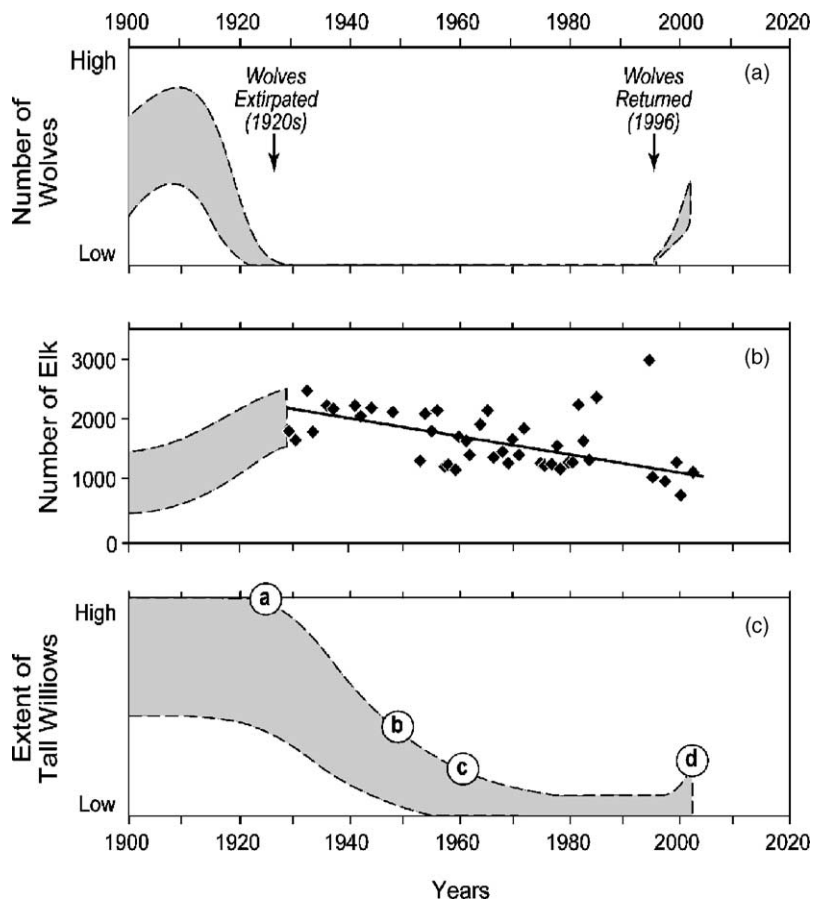


Fig. 2. Twentieth century time series of (a) wolf populations (Lovaas, 1967; Weaver, 1978), (b) elk population estimates (Graves and Nelson, 1919; Lovaas, 1970), elk counts and trend line (elk census data from Montana Fish and Game Department, Bozeman), and (c) status (i.e., height) of riparian willow communities (Lovaas, 1970; Patten, 1968, and photographs [Fig. 3, this study]). Shaded portions of a graph reflect variability (uncertainty); elk census data in (b) are represented by closed diamonds; closed letters in (c) refer to photo sequence shown in Fig. 3.

4.1.2. Elk

Using early reports (i.e., late 1800s and early 1900s) of elk sightings and valley conditions in the vicinity of the upper Gallatin elk winter range, Lovaas (1970) concluded that the “main Gallatin elk herd has

probably always dwelled year-long within the mountains” of the upper valley since “considerable winter range is available above the nearly impassible lower canyon”. While assessments of migration habits and winter range use by the upper Gallatin elk herd have

Table 2

Reported observations regarding elk herbivory, vegetation, soils and other ecological indicators in the upper Gallatin Elk Herd winter range for 1920–1963 (from Lovaas, 1970); primary references are included as ‘further reading’ at the end of this article

Year	Observations
1920–1921	Heavy elk grazing in several drainages; aspen there was overused (Callahan, 1921).
1923	Heavy grazing again observed in several drainages; elk took 100% of the willow browse (Callahan, 1923).
1924	Grazing in various drainages was heavy; browse in the game preserve was 100% utilized (White, 1924).
1925	Overgrazed conditions near the park boundary had occurred “as long as records of elk conditions had been kept”; on exposed areas elk fed on everything that could be reached leaving them as “bare as a floor” (White, 1925).
1933	Overgrazing and trampling by elk were damaging sites in the winter range; the more palatable forage plants were disappearing and soil erosion was evident (White et al., 1933).
1935	Elk fed heavily on browse plants during severe winter periods; willow, the most abundant and palatable browse, was overused by elk; willows were stunted and dying out along streams of the winter range (Wirch, 1935).
1936	Willows were 100% utilized on practically all winter range sites (Stock, 1936). Areas accessible to elk during critical periods showed serious advanced signs of overgrazing as demonstrated by “shoestring” and sheet erosion and in the killing of the more palatable species of forage plants; in many places elk have eaten the willow and aspen so closely that they have driven the beaver out and are “ruining the scenic values” of the canyon; the loss of willows and shrubs along the [Gallatin] river was expected to have a detrimental effect on fisheries (Stock et al., 1937).
1937	The Upper Gallatin Conservation Committee (UGCC) found mountain slopes were almost bare of forage and beginning to erode, willows and aspen killed from overbrowsing by elk, and conifer trees stripped of needles and twigs as high as elk could reach (BDC, 1937).
1938	UGCC observed soil from Lava Butte eroding down over the sagebrush to the edge of the highway (UGCC, 1939).
1944	Forest Service recommended “fencing off” barren areas of winter range that have been heavily utilized by game for rehabilitating the forage (BDC, 1944).
1945	The principal grass in several drainages is now western wheatgrass—a grass which ordinarily appears and persists after over-use has eliminated the more desirable native grasses; the “density” of grass is light and “pedestaled stools” show that sheet erosion is continuing (UGCC, 1945).
1946	UGCC members observed forage inside a meadow elk enclosure was “nearly normal” while that outside the enclosure was “extremely short”; inside the enclosure the healing of gullies had begun while outside unretarded erosion continued; members were “impressed” by the almost complete absence of aspen reproduction within several drainages and the extent to which willows had been consumed and partially killed; lodgepole, fir, and spruce reproduction likewise showed the effects of game use (UGCC, 1946).
1947	This was the first winter that an organized supplemental feeding program was undertaken. “Extreme overutilization of critical sites” occurred in February (Couey, 1947); “deteriorated range conditions” and soil erosion were observed (UGCC, 1947).
1949	Poor range conditions noted due to “drought” (Bozeman Courier, 1949).
1952	Elk ate browse extensively, including sagebrush, evergreen needles, aspen shoots and bark, and three year’s growth of willows in some areas (BDC, 1952).
1953	Elk range within Yellowstone National Park (in the upper Gallatin) shows deterioration in the loss and size of vegetation; forage was “licked clean” in some areas during the past two falls and winters (BDC, 1953).
1962	Several acres of sagebrush plants were killed by elk; of 150 willow plants examined in the spring, all but one were “decadent”, 144 were severely hedged from browsing, and four years of growth were removed from many plants (Lovaas, 1962).
1963	Range survey in Yellowstone National Park found areas usually unavailable to elk in generally good condition but that steep grassland sites had been severely grazed for many years and were in low to fair condition, the grasses were all very low in vigor, the rabbitbrush was browsed extremely heavily, and there was much bare ground, erosion, and soil displacement (Ross, 1963).

generally confirmed these conclusions, during some winters elk will also migrate into the upper Madison Valley (Allen, 1970).

Elk herd size on the upper Gallatin winter range was estimated at 1600 in 1919 (Graves and Nelson, 1919) and increased to an estimated 2000 by 1924 (Lovaas, 1970; Fig. 2b). Early winter herd counts of the upper Gallatin elk by the state of Montana date back to 1929 and have continued, with several gaps in data collection, until the present (Fig. 2b). Considerable variability exists in herd number estimates from year-to-year, perhaps reflecting the fact that censusing techniques are susceptible to large errors (Lovaas

et al., 1966). Nevertheless, the number of elk counted averaged 2100 (11 elk/km²) animals [S.D., ±240] for 1929–1948, 1600 (9 elk/km²) animals (S.D., ±360) for 1953–1985, and 1025 (5 elk/km²) animals (S.D., ±235) after 1995. These estimates reflect an increase in the elk population during the time wolves were being extirpated followed by a general long-term trend of decreasing herd size for the upper Gallatin Basin since the 1930s. In addition to deteriorating range conditions (Lovaas, 1970), hunting has likely been a significant contributor to the long-term downward trend in elk numbers. For example, from 1946 to 1965 hunters in the upper Gallatin Basin annually

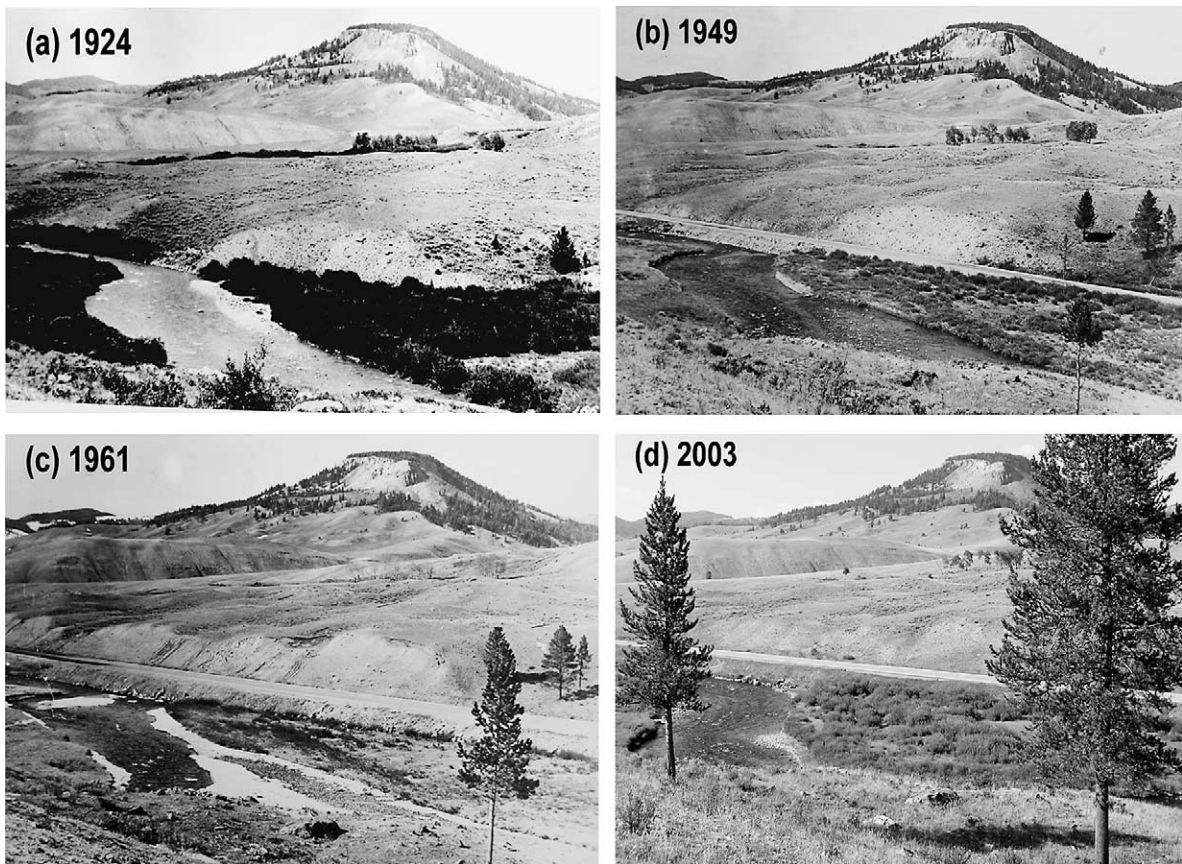


Fig. 3. Time series photographs of the Gallatin River floodplain (foreground) and an unnamed tributary (center) showing the status of riparian willow communities in (a) summer of 1924, (b) summer of 1949, (c) late spring of 1961, and (d) summer of 2003; Crown Butte occurs in the upper-right. Riparian vegetation associated with the floodplain and the unnamed tributary in 1929 shows progressive decline in subsequent photos. Also, “high-lining” of conifers in the foreground has become evident in the 1949 and subsequent photos. The willow along the Gallatin River were taller in 2003, but the willow along the unnamed tributary in the upland have not grown taller in 2003. The floodplain between the Gallatin River and road may not only represent an area of high risk for elk due to poor escape terrain if attacked by wolves, but also from increasing levels of traffic on the highway since 1961.

harvested an average of 476 elk (S.D., ± 286) (Peek, 1967).

4.1.3. Vegetation

Based on various government reports and other published records, Lovaas (1970) chronicled the general utilization and conditions of woody browse species from the early 1920s to the early 1960s (Table 2). Those records indicate that a period of long-term suppression of woody browse species by wild ungulates was initiated in the 1920s and was followed by increased soil erosion that continued at least through the mid-1960s. The impacts to riparian plant communities summarized by Lovaas (1970) are also supported by a chronosequence of photographs for the years 1924, 1949, and 1961 that show conditions along the Gallatin River and Crown Butte (Fig. 3). Healthy willows occupy the entire river floodplain in the 1924 photograph and along an unnamed tributary in the background. However, by 1949 considerable mortality has occurred in the willow community and accelerated stream bank erosion is evident along the river. Degradation of the riparian communities continued, both along the river floodplains and in the background, as evidenced in the 1961 photograph. In contrast, the photograph for 2003 shows willows growing taller along the Gallatin River, but not taller in the unnamed tributary in the background.

Patten (1968) studied a riparian area along the Gallatin River upstream of this study and found, in

1963, that willows dominated the riparian shrub community. While all shrubs showed “signs of browsing”, he found that the effects were especially evident with willows and sagebrush (*A. tridentata*). Using a chronosequence of photographs for his study reach, he concluded that “between 1924 and 1964 most of the willows died out”.

Based on reported observations of willow communities and other woody browse species (Lovaas, 1970), chronosequences of historical photographs (Fig. 3), and Patten’s (1968) study, general changes in willow communities during the 20th century are presented in Fig. 2c. Robust and healthy willow communities are indicated early in the century until approximately the mid-1920s, followed by a precipitous decline in the stature and spatial distribution of willows until the early 1960s. While willow communities largely consisted of scattered plants of low stature during the following decades, increased height growth of willows in recent years has been noted for some riparian areas (Fig. 3d).

4.1.4. Climate

During the period 1931–2002, 65 years of measured annual flows were available for the Gallatin River near Gateway. Regression analysis between annual flows at the Gateway gage and annual flows of the (1) Gallatin River at Logan ($r^2 = 0.94$) and (2) Yellowstone River at Corwin Springs ($r^2 = 0.67$) were used to estimate an additional 33 years of annual flow

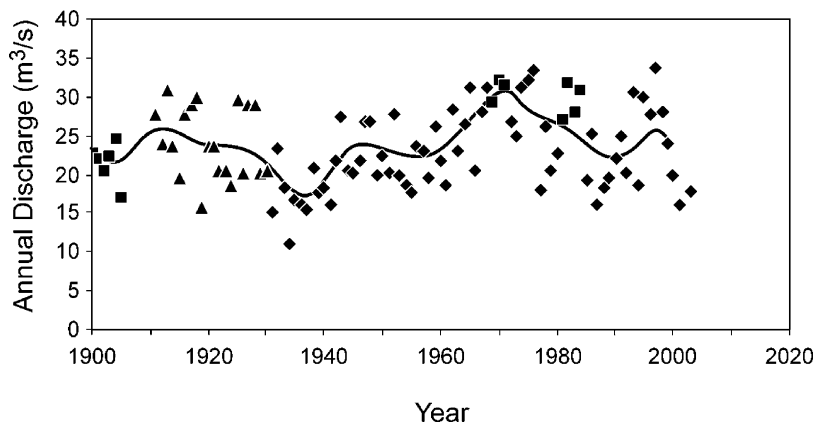


Fig. 4. Annual flows of the Gallatin River near Gateway, Montana. The solid line represents a moving average of annual flows, diamonds represent measured flows for the Gallatin River near Gateway, rectangles represent estimated flows from regression analysis with the Gallatin River at Logan, and triangles represent estimated flows from regression analysis with the Yellowstone River at Corwin Springs.

for the Gateway gage; 13 years estimated from the Logan gage and 20 years from the Corwin Springs gage. Based on these extended flow records (including both measured and estimated values), the annual flow for the Gallatin River near Gateway averaged $23.4 \text{ m}^3/\text{s}$ (S.D., ± 5.1) over the period 1911–2002 (Fig. 4). In the early part of the 20th century, annual flows generally fluctuated around the long-term average until the late 1920s when a decrease occurred. Annual flows during the 1930s were relatively low and indicative of droughty conditions. This period of low annual runoff was followed by several decades, from the late 1930s to the early 1980s, of generally increasing flow magnitudes. In the 1980s and 1990s, flows tended to again fluctuate around the long-term average. Since most streamflow in the upper Gallatin basin is derived from snowmelt runoff, the general pattern of annual flows illustrated in Fig. 4 also index annual patterns of snowpack accumulation in the upper Gallatin winter range.

4.2. Conditions since wolf reintroduction

4.2.1. Field measurements

In 2002, Booth willow heights averaged 97 cm (S.D., ± 66 , $n = 77$) along the Gallatin River and 86 cm (S.D., ± 53 , $n = 37$) along Tepee creek. The proportion of sampled stems browsed in 2002 averaged 44% along the Gallatin River and 75% along Tepee Creek with taller willows generally associated with low browsing pressure. For example, browsing intensity was lowest and willows were tallest along the downstream portion of each transect, near Snowflake Springs, where the streams and their floodplains became increasingly constrained by steep slopes, rock outcrops, cliffs, and a highway (Fig. 5). We found greater amounts of browsing and shorter willow along portions of the Gallatin River and Tepee Creek transects located farther upvalley from the Snowflake area (i.e., channel distances >1000 m). Streambank heights above the water surface averaged 75 cm (S.D., ± 14 , $n = 57$) and 85 cm (S.D., ± 16 , $n = 58$) for the Gallatin River and Tepee Creek transects, respectively.

Comparison of photographs of the Snowflake enclosure in the Gallatin River floodplain indicate suppressed willow communities in 1969 (Fig. 6a), the early stages of release in 1999 (Fig. 6b) for some

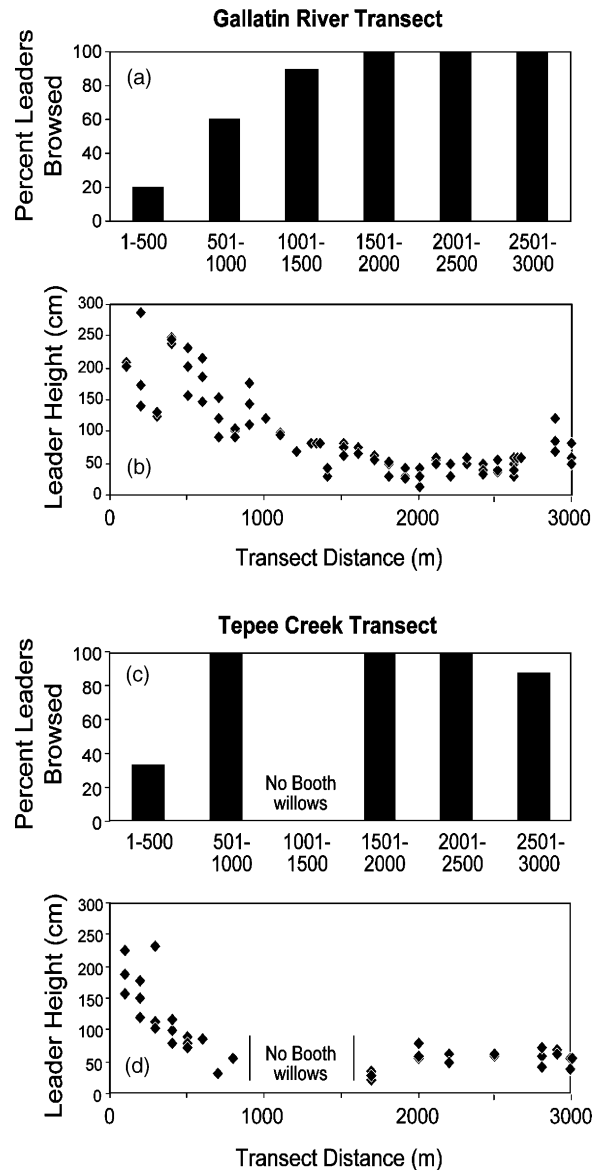


Fig. 5. (a) Percent of leaders browsed, (b) leader heights of Booth willow for a 3000 m transect along the Gallatin River, (c) percent of leaders browsed, and (d) leader heights of Booth willow for a 3000 m transect along Tepee Creek. Leader heights were recorded for the previous year, which was 2002 (see text for details). Both transects start near Snowflake Springs and proceed upstream.

portions of the floodplain, and their continued release into tall willows in 2003 (Fig. 6c). In 2003, Booth willow heights outside the Snowflake enclosure averaged 227 cm (S.D., ± 35 , $n = 35$) compared to an

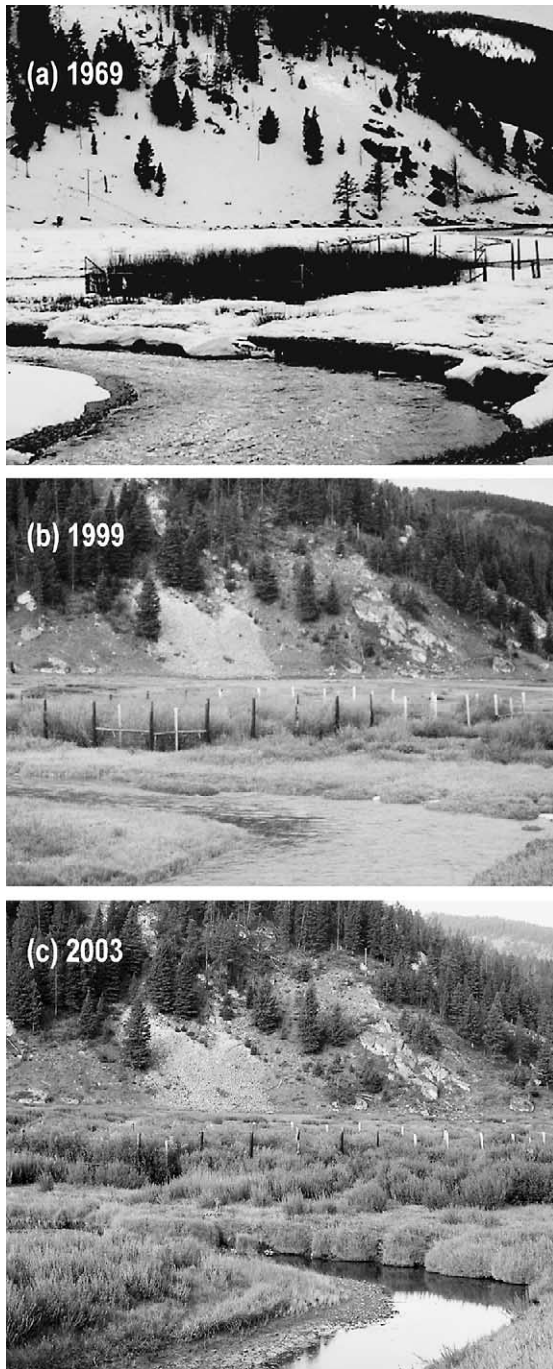


Fig. 6. Comparison photographs of the Snowflake enclosure in the Gallatin River Floodplain illustrating the status of willow communities: (a) winter of 1969, during suppression from long-term browsing, (b) spring of 1999, during the very early stages of release following wolf recolonization in 1996, and (c) summer of 2003,

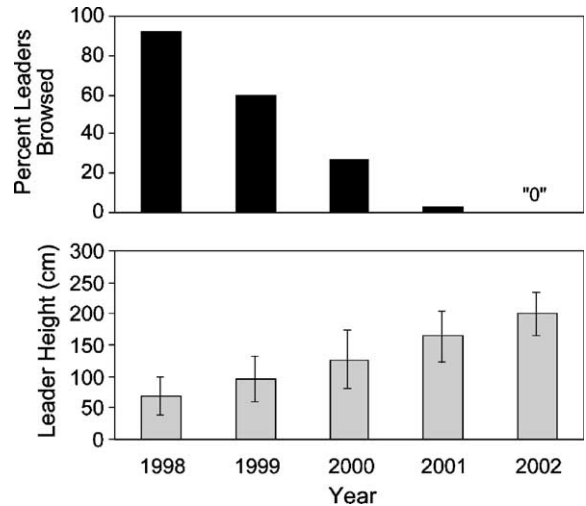


Fig. 7. (a) Percent of leaders browsed, and (b) leader heights of Booth willow outside the Snowflake enclosure.

average of 307 cm (S.D., ± 52 , $n = 37$) for willows inside the enclosure (Fig. 6c). Based on plant architecture measurements, the percentage of willow stems browsed outside the Snowflake enclosure decreased from a high of 92% in 1998 to 0% in 2002 and willow height increased in each of those years (Fig. 7). In contrast, there has been little change in willow height outside the Crown Butte enclosure in recent years (Fig. 8). In 2003, willow heights averaged 20 cm (S.D., ± 6 , $n = 23$) and 264 cm (S.D., ± 69 , $n = 24$) outside and inside, respectively, of the enclosure (Fig. 8b). Examination of plant architecture for willows outside the Crown Butte enclosure indicated very short plants (<20 cm in height) and a high percentage of stems browsed in both 2001 (83%) and 2002 (95%) (Fig. 9).

4.2.2. Climate

Annual values of the selected climatic variables (i.e., maximum snowpack depth, peakflow, and July streamflow) are presented in Fig. 10 for the period 1996–2002. Of particular importance are potential patterns or trends for the years 1999–2002 since this

during continued release into tall willows. These willows are growing taller apparently because of impediments to escape (i.e., the presence of nearby steep canyon walls and rock outcrops [see background in photos], a wide river, vertical streambanks, beaver pond, and highway). Note the eroding banks in the 1969 photo that have become increasingly revegetated in the 1999 and 2003 photos.

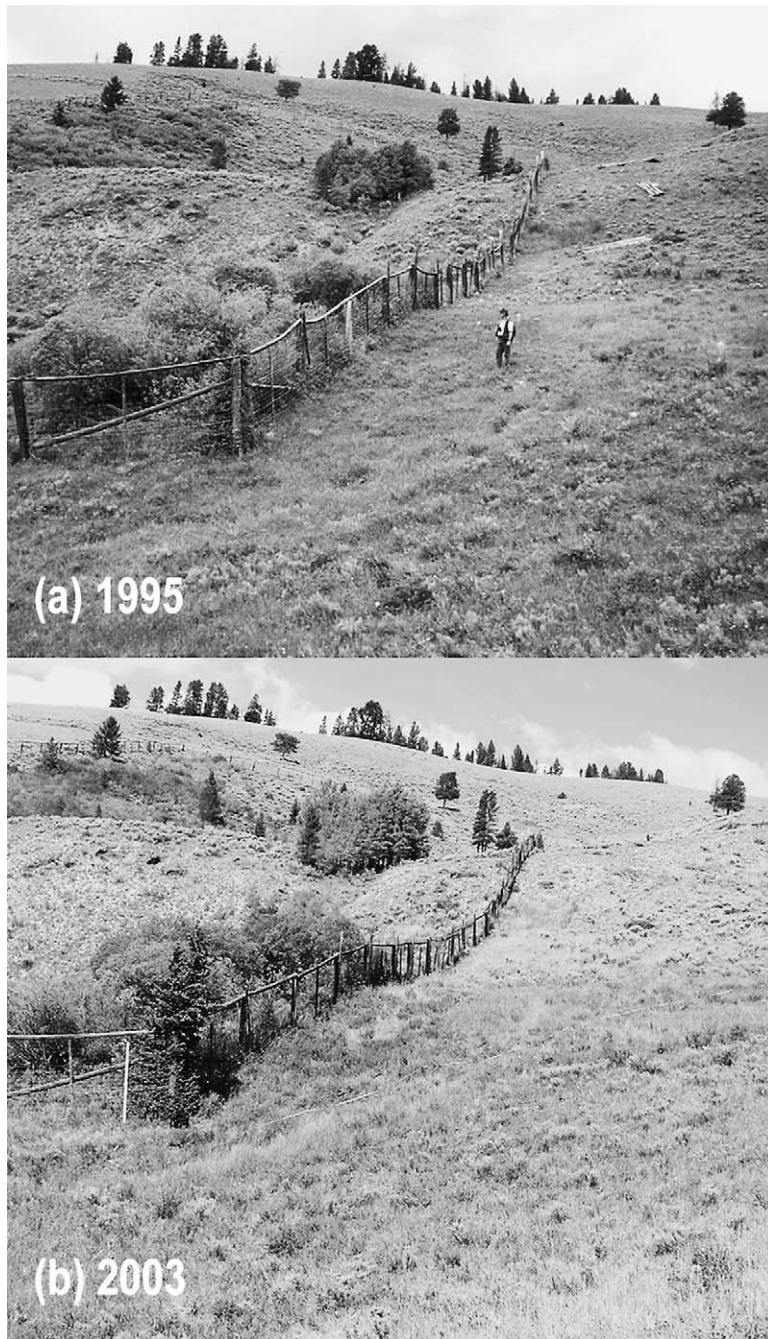


Fig. 8. Comparison photographs of the Crown Butte enclosure illustrating: (a) summer of 1995, suppression of willows by elk browsing outside the enclosure, and (b) summer of 2003, continued suppression following wolf reintroductions due to the relatively low level of predation risk at this upland enclosure. The vertical white pole adjacent to the “high-lined” conifer at the near corner of the enclosure in 2003 is 2 m in height.

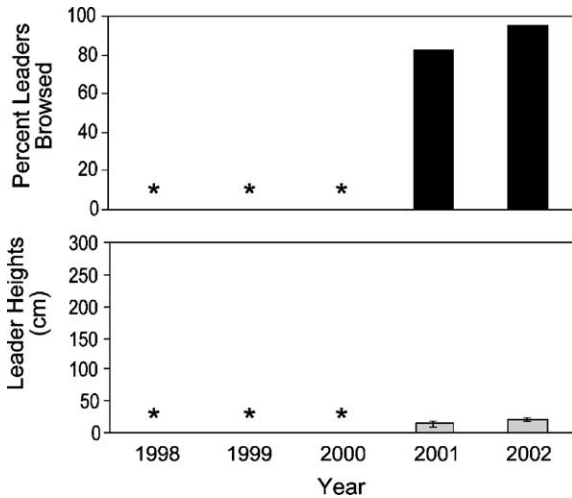


Fig. 9. (a) Percent of leaders browsed and (b) leader heights of Booth willow outside the upper Crown Butte exclosure. Asterisk indicates we were unable to record browsing history and plant height data for 1998–2000 because the plants were heavily browsed, thus making it difficult to obtain plant architecture measurements that far back in time.

is a time of increasing willow heights. Relatively deep snowpack depths (exceeded only seven times over the period of record) were recorded at the Twenty-One Mile Snow Course in both 1997 and 1999 with years after 1999 having depths less than the long-term average (Fig. 10a). A record high peakflow occurred in 1997 followed by peakflows that were generally at or below the long-term average (Fig. 10b). Summer-time flows for the Gallatin River, as indexed by July conditions, indicate a slightly different temporal pattern. During 1996 through 1998, July flows were greater than the long-term average (Fig. 10c). Although the July flow in 1998 was considerably greater the long-term average, it is much less than the record high that occurred in 1975. In 1999, the July flow was the same as the long-term average and then dropped to below average for the three subsequent years.

5. Discussion

5.1. Pre-1925, wolves present

The effects of pre-EuroAmerican hunting upon the upper Gallatin elk herd are largely unknown since

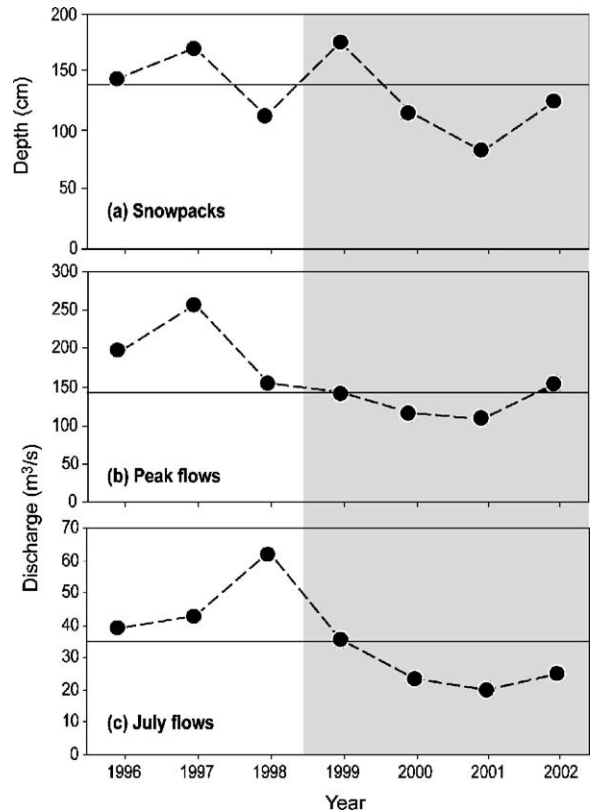


Fig. 10. (a) Annual maximum snowpack depth, (b) annual peakflow, and (c) July streamflow over the period 1996–2002 in the upper Gallatin Basin, southwestern Montana. Annual maximum snowpack depth averaged 137 cm (S.D., ± 33) over the period 1937–2002 at the Twenty-One Mile Snow Course; annual peakflow averaged 147 m³/s (S.D., ± 45) over the period 1931–2002, and July streamflow averaged 35 m³/s (S.D., ± 17) over the period 1930–2002 for the Gallatin River near Gateway streamgauge. Shaded area represents a period of increasing willow height.

Indians were “gathered up” from the Yellowstone region and moved to reservations before 1880 (Lovaas, 1970). However, a scarcity of game around Bozeman and the lower Gallatin Valley in the late 1800s caused settlers to travel up-valley through the canyon to reach more “abundant” game in the upper drainage.

The 1890s mark the beginning of livestock grazing in the upper Gallatin Basin and “very heavy” grazing was reported by 1896 (Lovaas, 1970). A lack of fences in the upper basin continued to attract livestock grazing into the early 1900s. Although the Gallatin Forest Reserve was created in 1899, it was not until 1905 that

the U.S. Forest Service was established. Because of a need “to protect the elk which come out of the park to graze in winter”, areas south of the Tepee Creek–Buffalo Horn Creek divide and south of the Taylor Fork–Sage Creek divide were closed to grazing by the Forest Service in 1908 with additional land closed to grazing in 1911 (Lovaas, 1970). Since this study was undertaken in the area where cattle and sheep had been removed during the first decade of the 1900s and photographs for the mid-1920s indicate the occurrence of robust willow communities (e.g., Fig. 3a), historical grazing was not likely a factor regarding vegetation changes in the study area that appear to have began after the mid-1920s.

5.2. 1925–1995, wolves extirpated

Throughout much of the 20th century, the management of the Gallatin elk herd and its winter range has involved a variety of conflicts and controversies (Penggelly, 1963; Lovaas, 1970; Singer et al., 1998). Initially, the effects of predators and livestock grazing were of major concern. Livestock grazing was the first to be eliminated from major portions of the winter range. The capability of wolves to affect herbivory patterns and total numbers of elk was subsequently eliminated by the mid-1920s. From then on, management issues tended to involve elk carrying capacity and herd size, the effects of elk upon forage species, browse species, soils, and erosion, the desirability and effects of supplemental feeding, the number of annual hunting permits, and others. Over the years, these issues generated considerable discussion and concern by the general public, a wide range of interest groups, and various state and federal agencies.

Lovaas (1970) reported that the drought of the 1930s was sometimes identified as a potential cause of willow loss and degradation of plant communities in the upper Gallatin Basin. While the relatively dry years of the 1930s, as indicated by streamflow patterns in Fig. 10, may have been particularly stressful to upland plants, established woody plants growing in riparian areas are generally able to access relatively shallow groundwater tables associated with a stream or river (NRC, 2002b) and thus obtain sufficient moisture to survive even in otherwise dry years. Furthermore, if periods of drought are considered to be an important factor limiting the growth and survival

of riparian willows and the cause of degradation for these plant communities, then increased levels of annual streamflow beginning in the early 1940s and continuing through the mid-1970s should have contributed to a resurgence in willow communities. Such resurgence was neither observed (Fig. 2c) nor documented (Patten, 1968).

Following the extirpation of wolves, annual elk census information generally indicates a long-term decline in population size (Fig. 2b), some of which is likely attributable to hunting kills and winter mortality. Regarding these factors, Peek et al. (1967) evaluated Gallatin elk herd data from 1932 to 1965 and concluded that the general long-term decline of the elk population was primarily due to deterioration of the winter forage availability caused by excessive elk grazing for at least 40 years.

Based on various sources of information, we have charted the general status of wolves, elk, and willow during the 20th century in Fig. 2. Overall, the widespread loss of willows (and other woody species) followed soon after the elimination of wolves. These impacts to riparian browse species occurred even though total numbers of elk slowly declined (due to a combination of annual hunting pressures, a reduced forage base, and periodic occurrences of high winter mortality) following the extirpation of wolves. While willows in the upper Gallatin winter range have continued to exist along riparian systems over a period of 70 years in the absence of wolves, the unimpeded browsing from elk during this period has greatly diminished the stature, densities, and spatial distribution of these important streamside plant communities.

5.3. Post-1995, wolves reintroduced

Following the return of wolves to the upper Gallatin winter range, the increased height growth in recent years of some willow communities represents a major departure from previous decades of widespread willow suppression. In general, riparian vegetation in the upper Gallatin winter range that has experienced reduced browsing pressure in recent years has been growing taller.

We attribute the varying levels of height “release” along transects and between enclosure sites to behaviorally mediated trophic cascades involving wolves and elk and which cause elk to engage in risk-sensitive

foraging behavior. The predation risk signal observed in the vegetation was generally easy to identify since the willow growth we found was in stark contrast to the deteriorated conditions that existed prior to the return of wolves. It should be noted that the predation risk signature represented in the willow communities of this study represents a “perceived” risk of predation by elk. While the “actual” predation risk might be represented by the relative frequency of elk kills associated with specific sites or categories of sites, even kill data contain a certain degree of ambiguity since the initiation of a chase and the end point of a chase are typically not the same.

We considered whether the observed willow height increases associated with high predation risk sites may have been assisted by the combined effects of relatively low snowpacks and low elk populations (relative to historical levels). For example, maximum snowpack depth for the last three years averaged 23% below the long-term average. These relatively shallow snowpacks may have resulted in lower “effective” elk densities in riparian systems since more forage on the uplands would have been available for elk grazing. Similarly, the relatively lower numbers of elk (based on an annual census data) in the most recent decade may have contributed to decreased browsing pressure. However, neither of these conditions, by themselves or in concert, explain the patchy nature of release that is indicated by the results of this study.

Overall, riparian sites with increased willow height growth were found on those portions of the landscape that appeared to represent relatively high-risk locations (e.g., Snowflake Springs area) and may be primarily due to increased difficulty of escape because of terrain features. Terrain features that increase the risk of predation include any obstacle, or combination of obstacles, that could cause an elk to slow or stop fleeing, require directional changes, delay decision-making, or cause confusion during a chase by wolves (Table 1).

We also found lower browsing intensities along the Gallatin River compared to Tepee Creek. We believe this is due to the Gallatin River having more escape impediments than Tepee Creek, such as closer proximity to the highway, a wider stream, more gullies and multiple channels, islands, and a relatively wide and complex floodplain. We also observed that willows growing on islands in the Gallatin River (high-risk

sites) were typically taller than the willows growing on the corresponding banks (W.J. Ripple and R.L. Beschta, unpublished data). Ripple and Beschta (2003) similarly documented taller woody vegetation on an island in northern YNP and noted the island was an early release site following the reintroduction of wolves.

A lack of increased willow stature on sites with good escape terrain was recorded along stream (Fig. 5b and d at transect distances >1000 m) and upland sites (Fig. 3d and Fig. 8b) within our study area. We also observed a consistent lack of recruitment in upland aspen stands in the study area. These patterns of herbivory indicate that elk may be avoiding certain riparian areas (i.e., those with multiple terrain features contributing to an increased level of difficulty during an escape situation) along the study reaches and selecting for higher ground as a risk-sensitive foraging strategy. In support of such a “higher ground” hypothesis, following wolf reintroductions in 1995, elk pellet groups in low elevation areas (<65 m above the Lamer River floodplain in YNP) decreased ($P = 0.008$, $n = 17$) between August 1999 and August 2001. Conversely, no change in the number of elk pellet groups ($P = 0.923$, $n = 21$) was found at higher elevations (>65 m above the Lamar River) for this same area (W.J. Ripple, unpublished data). In comparison to many riparian areas, uplands may provide ungulates with a significantly lower risk of predation, better escape terrain, and fewer escape barriers (Bibikov, 1982; Bergerud and Page, 1987; Kunkel and Pletscher, 2000, 2001; Ripple and Beschta, 2003), and more conifer forests as hiding cover for avoiding wolves.

The results we report here on predation risk effects are consistent with three recently published works involving wolves and elk (Bergman, 2003; Mao, 2003; Gula, 2004) as well as two reporting trophic cascades among wolves, elk, and woody vegetation (Ripple and Beschta, 2003, 2004). It is important to note that even though wolf introductions occurred in the northern range of YNP in 1995 and 1996 and wolves started spreading into the upper Gallatin area in 1996, it was not until 1999 that some of the earliest vegetation responses began to occur, indicating that wolf establishment on the Gallatin winter range was gradual and/or a lag time was needed before elk began to understand the significance of this “new” predator

and began to alter their patterns of herbivory (Laundré et al., 2001).

Herbivory and growth information from specific plants occurring along discrete spatial gradients allowed us to assess relative degrees of predation risk within our study area. We were able to determine temporal (year-to-year) and fine-scale spatial patterns (within several meters or tens of meters) of elk foraging and to identify a close correspondence with escape impediments. Such plant-based measurements are ideal for sampling risk sensitive foraging since browsing/growth signatures in the vegetation are clearly defined and each plant is always present and available for browsing. Conversely, elk telemetry data are not capable of confirming foraging patterns at fine spatial scales and, instead, are likely to be more appropriate for analyzing generalized elk movements and occurrences at larger scales.

In our attempt to consider the general moisture regime of willow communities, we measured streambank heights along each transect and compiled annual data for selected climatic variables that directly or indirectly can affect the moisture available to riparian plant communities. Streambank heights, on those portions of each 3000 m transect where we documented accelerated height growth, were similar to the remainder of their respective transects (where increased height growth did not occur).

With regard to variation in climatic variables, relatively deep snowpacks occurred in both 1997 and 1999, the peakflow of record occurred in 1997, and a relatively high July streamflow occurred in 1998. However, the release of willows did not generally begin until 1999 and continued through subsequent years when all three measures of moisture availability were consistently indicating generally below average conditions for streams and rivers of the upper Gallatin Basin. While the abnormally wet years could contribute to increased establishment of seedlings/suckers as well as accelerated height growth during those years, they do not explain the differential height response along transects or the fact that most height growth has occurred during periods of below-average moisture conditions. Thus, if moisture is playing a role in the differential release of willows documented in this study and which has been occurring only since 1999, it must involve some factor other than those considered in this study.

Alternatives to our predation risk hypotheses for the recent willow growth in the Gallatin include: (1) changes in elk distributions as a result of changing winter severity; (2) the long-term decrease in the Gallatin elk population; and (3) decreases in moose browsing. Since winter weather can affect both elk distributions and foraging patterns, the occurrence of shallow snowpacks since 1999 (Fig. 10) may have allowed elk to forage on upland grasses causing less browsing pressure on willows growing in valley bottoms. Even so, elk remaining in the uplands would not account for the spatial variability in browsing intensities that we found in riparian areas. Additionally, we could find no supporting evidence (photographs, published reports, or other information) indicating there has been a historical release of willows during any of the mild winters that occurred when wolves were absent from this area. Since deep snow can cause additional browsing on woody vegetation when herbaceous plants are buried and woody plants are the only forage exposed (NRC, 2002a), severe winter weather in the future could increase browsing pressure on valley-bottom willows.

Declining elk populations, by reducing overall herbivory and interacting with predation risk effects, may have contributed to the patterns of willow release currently underway in this study area. However, the lower elk population alone probably did not cause the willow release since the elk numbers in the Gallatin have been decreasing for decades yet there was no evidence of willow release until wolves came back into the system. Similarly, in the northern range of YNP, elk densities were reduced to 3–5 elk/km² by the 1960s during a period without wolves and a general release of woody vegetation in riparian systems did not take place (Barmore, 2003; Beschta, 2003; Ripple and Beschta, 2004). Also, Leopold et al. (1963), in their assessment of wildlife management in national parks, apparently recognized the importance of using wolves rather than shooting to help control ungulate populations by concluding “In so far as possible, control [of ungulates] through natural predation should be encouraged.”

In the long run, a smaller elk population in the upper Gallatin winter range may ultimately develop through the combined effects of periodic and severe winter weather events (e.g., Smith et al., 2003), incremental and persistent wolf predation, sport hunting,

and other causes of elk mortality. For example, if high levels of elk mortality were to occur during a period of severe winter weather, subsequent wolf predation in conjunction with reductions caused by other predators (e.g., grizzly bears [*Ursus arctos*] and mountain lions [*Felis concolor*]) and hunting by humans may keep elk populations from rebounding (NRC, 2002a; Smith et al., 2003). Researchers in Alaska have found that the coexistence of wolves and bears usually maintains ungulate prey at low populations (NRC, 1997). A lower elk population than currently exists in the upper Gallatin Basin would likely result in less intense browsing of both riparian areas and uplands. Decreased elk numbers may actually be a prerequisite situation before woody browse species in the uplands of the historical 1924 photo in Fig. 2a again began to recover and ultimately provide an improved winter forage base for future elk populations.

Although moose are browse specialists, we believe potential changes in moose browsing did not result in the willow release in our Gallatin study area since we documented a similar release of willow in the Lamar Valley of YNP northern winter range where moose were at extremely low densities both before and after wolf reintroduction (Ripple and Beschta, 2003). On the other hand, we are uncertain if moose in the Gallatin study area have changed their distribution or browsing behavior since wolf reintroduction.

If willow communities continue to grow taller and expand spatially as a result of re-establishment of trophic cascades associated with wolf reintroduction, numerous long-term ecological benefits will accrue to riparian and aquatic habitats. Such ecological “spin-offs” might include increased above- and below-ground plant biomass, improved streambank stability and floodplain functioning, better food web support for a wide number of terrestrial and aquatic organisms such as beaver, river otter (*Lutra canadensis*), fish, birds, amphibians, insects, as well as increases in overall riparian biodiversity. For example, beaver populations may increase due to the new willow growth. Beaver, in turn, have important roles in riparian ecosystems by altering hydrogeomorphic processes and thereby increasing sediment retention, maintaining wetlands, modifying nutrient cycling, and ultimately influencing plant, vertebrate, and invertebrate diversity and biomass (Naiman et al., 1988). In a study of Wyoming streams, McKinstry et al. (2001)

found approximately 75 times more waterfowl in streams with beaver ponds relative to similar areas without beaver. Increased willow growth may also interact with processes in the soil such as litter quantity, soil carbon and nitrogen pools, and microbial respiration (Paster et al., 1988) and may ultimately improve site productivity.

The results we report here are significant since studies of long-term processes of terrestrial food chains are rare, especially terrestrial cascades involving large carnivores (Pace et al., 1999; Estes et al., 2001). Our results corroborate three other tree ring studies of wolves, ungulates, and vegetation. McLaren and Peterson (1994), using a trophic system reconstruction with tree rings from 1958 to 1994, found that gray wolf predation on moose increased balsam fir (*Abies balsamea*) productivity on Isle Royale in Lake Superior. Later, the description of these same cascades on Isle Royale were lengthened by Post et al. (1999) to include winter weather, wolf behavior, moose, and balsam fir. In the northern range of YNP, long-term linkages of wolves, elk, and aspen were also discovered by Ripple and Larsen (2000) from tree rings of the current aspen overstory and aspen diameters measured by researchers in the 1920s. They found aspen recruitment only during the period with wolves present (pre-1920s) and a lack of recruitment during the period without wolves (1930s–1990s). This aspen research was recently confirmed by Beschta (2003) when he found a similar lack of riparian cottonwood recruitment in northern YNP during the same 60 plus year period when wolves were absent. In addition, our results are also consistent with other studies in the Rocky Mountains involving wolves, moose, and willow (Berger et al., 2001), wolves, elk, and cottonwood (Ripple and Beschta, 2003), and wolves, elk, and aspen (White et al., 2003). Taken collectively, the evidence provided by these recent studies for a three-level trophic cascade caused by wolves is becoming increasingly persuasive.

6. Conclusions

The salient finding of this study is that the willows of the upper Gallatin Range declined soon after wolves were extirpated (Table 2), exhibited a diminished stature and density during the 70-year wolf-free

period (Figs. 3 and 6), and are growing taller in some high-risk areas since wolf reintroduction (Figs. 3, 5–7). It is important to note that our study took place on national forest service lands outside of YNP, but the timing of willow release (late 1990s) matches with that observed following the mid-1990s wolf reintroduction in northern YNP. These results support our earlier work where predation risk, associated with wolves and terrain, was identified as the primary forcing mechanism for trophic cascades at early stages of willow and cottonwood recovery in valley bottoms in northeastern YNP (Ripple and Beschta, 2003). In addition, the current study illustrates trophic cascades at a larger spatial scale than discussed by Ripple and Beschta (2003).

Our results preclude variations in climate as a main factor causing the long-term willow decline during the wolf-free period as well as the recent willow release since wolf reintroduction. While willow declines in the 1930s may have been exacerbated by low annual runoff in the 1930s, the improving moisture regime in the 1940s and subsequent decades apparently had no effect on height growth or relative abundance of willows and they remained in a diminished state into the late 1990s. Therefore, lower than average flow is unlikely to be a major cause of the long-term decline in willow communities and their lack of recovery. After wolf reintroduction, the release of willows did not generally begin until 1999 and later even though moisture conditions were below average for streams of the upper Gallatin Basin. The increased willow heights we documented are only occurring in certain areas and appear to be doing so independently of spatial (bank height) or temporal (annual maximum snowpack accumulations, annual peakflows, July flows) indices of soil moisture availability for these riparian plant communities.

We found that browsing levels decreased and willow height increased with increasing levels of predation risk for sites in the upper Gallatin Basin. While the increases in plant height reported herein may signal the initial phase of a broader ecosystem recovery, it is too early to predict long-term trends for an array of woody browse species and other plants in the upper Gallatin winter range or the extent to which such recovery might occur spatially. For example, we are uncertain how the future winters with deep snow conditions may affect such relationships and resulting

browsing on riparian vegetation. While deep snow around riparian woody plants can protect them from extensive browsing, deep snow and ice on upland herbaceous vegetation may cause ungulates to move lower and increase herbivory on riparian woody species (NRC, 2002a). It may well be that a lower elk population, as a result of severe winter weather, predation (other than wolves), wildfire, continued hunting pressure, or other influences in conjunction with wolf predation and much more time are required before a generalized release and recovery of woody plants is observed across the winter range.

Increasingly, it would appear that the loss of a keystone predator, the gray wolf, across vast areas of the American West may have set the stage for previously unrecognized and unappreciated ecological changes in riparian and upland plant communities and the functions they provide. Furthermore, the results reported herein add to the scientific knowledge base by providing empirical evidence for strong top-down effects of a large terrestrial carnivore. If similar top-down effects hold true in other areas of North America and parts of the world where wolves have been previously removed, wolf recovery may represent a management tool for helping to restore riparian plant communities and conserve biodiversity.

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