

River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA

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Abstract

Historical records indicate that gray wolves (*Canis lupus*) were extirpated from the upper Gallatin River Basin in the early 1900s. Following the removal of these large carnivores, elk (*Cervus elaphus*) began to increasingly browse streamside vegetation in the winter range, causing widespread loss of formerly extensive willow (*Salix* spp.) communities. Historical aerial photographs and chronosequences of ground photographs were used to characterize general changes in vegetation and channel morphology over time. In August of 2004, riparian vegetation and channel cross-sections were surveyed along three reaches of the upper Gallatin River. Reach A was located upstream of the elk winter range (control reach) whereas reaches B and C (treatment reaches) were located within the elk winter range. Willow cover on floodplains averaged 85 per cent for reach A, but only 26 per cent and 5 per cent for reaches B and C, respectively. The average return period of calculated bankfull discharges was 3.1 yrs for reach A but increased to 32.4 yrs and 10.6 yrs for reaches B and C, respectively. The long-term loss of streamside vegetation allowed channels to generally increase in hydraulic capacity (*via* increases in width, incision or both) and decrease their hydrologic connectivity with adjacent floodplains. This study documents, perhaps for the first time, the resultant impacts to riparian vegetation functions and stream channel characteristics following the extirpation of a large mammalian carnivore. Copyright © 2006 John Wiley & Sons, Ltd.

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Introduction

The physical, biological, and chemical role of streamside vegetation has become increasingly recognized in recent years (Lovett and Price, 1999; Wigington and Beschta, 2000; National Research Council, 2002b). Riparian plant communities can influence bank stability, moderate microclimates and water temperatures, cycle nutrients, produce organic carbon that is an essential component of food-webs for many terrestrial and aquatic organisms and others (Cummins, 1974; Gregory *et al.*, 1991; Naiman and Decamps, 1997). Furthermore, it is widely recognized that high levels of herbivory along streams and rivers can, over time, have potentially large impacts on terrestrial and aquatic habitats (Platts, 1991; Ohmart, 1996; Kauffman *et al.*, 1997; Dobkin *et al.*, 2002).

During overbank flow, the hydraulic roughness of above-ground stems and branches of floodplain plant communities reduces water velocities and enhances the deposition of fine sediment and organic matter (Sedell and Beschta, 1991; Darby, 1999; Gyssels and Poesen, 2003; Smith, 2004). Additionally, the root systems of riparian plants help to stabilize streambanks by slowing or preventing streambank erosion (e.g. particle entrainment, mass wasting) (Simon and Collison, 2002; Murray and Paola, 2003), thereby reducing rates of channel migration for floodplain systems (Hickin, 1984; Micheli and Kirchner, 2002a). Recent studies have begun to report specific relationships relating the role of roots to streambank stability (Micheli and Kirchner, 2002b; Murray and Paola, 2003; Gray and Barker, 2004) as well as how these root systems are affected by environmental gradients (Dwire *et al.*, 2004) and herbivores (Kauffman and Krueger, 1984; Belsky *et al.*, 1999; Brookshire *et al.*, 2002). However, little is known regarding how the presence, or absence, of top predators can influence patterns of herbivory by native ungulates, which, in turn, may affect streamside plant communities and their channels.

By the early 1900s, the formerly wide-ranging North American gray wolf (*Canus lupus*) had been extirpated from nearly all of the contiguous 48 United States (US) due to an extensive and systematic program of hunting, trapping and poisoning (Musiani and Paquet, 2004). With the elimination of wolves from Yellowstone National Park and surrounding areas (Weaver, 1978; National Research Council, 2002a), elk (*Cervis elaphus*) were able to browse winter-range plant communities unimpeded by wolf predation. This increased browsing pressure had severe consequences to aspen (*Populus tremuloides*) across uplands as well as willows (*Salix* spp.) and cottonwoods (*Populus* spp.) along riparian areas (Chadde and Kay, 1996; Kay, 2001; Keigley, 1997; Barmore, 2003). High levels of browsing were so pervasive throughout the winter range in northeastern Yellowstone National Park following the removal of wolves that recruitment (i.e. the growth of seedlings and root sprouts into tall saplings or trees) of deciduous woody species was essentially terminated over a period of many decades (Ripple and Larsen, 2000; Larsen and Ripple, 2003; Beschta, 2003, 2005; Ripple and Beschta, 2004a).

With the extirpation of wolves in the mid-1920s from the upper Gallatin Basin in the Park's northwestern corner, elk populations were similarly able to increase browsing pressure on riparian plant communities. As a result, formerly extensive willow communities on the Gallatin River floodplain began to disappear. The chronosequence of photographs presented in Figure 1 suggests that changes in the character of the river channel within the elk winter range were initiated as willow communities began to die (additional photographs can be found in the work of Ripple and

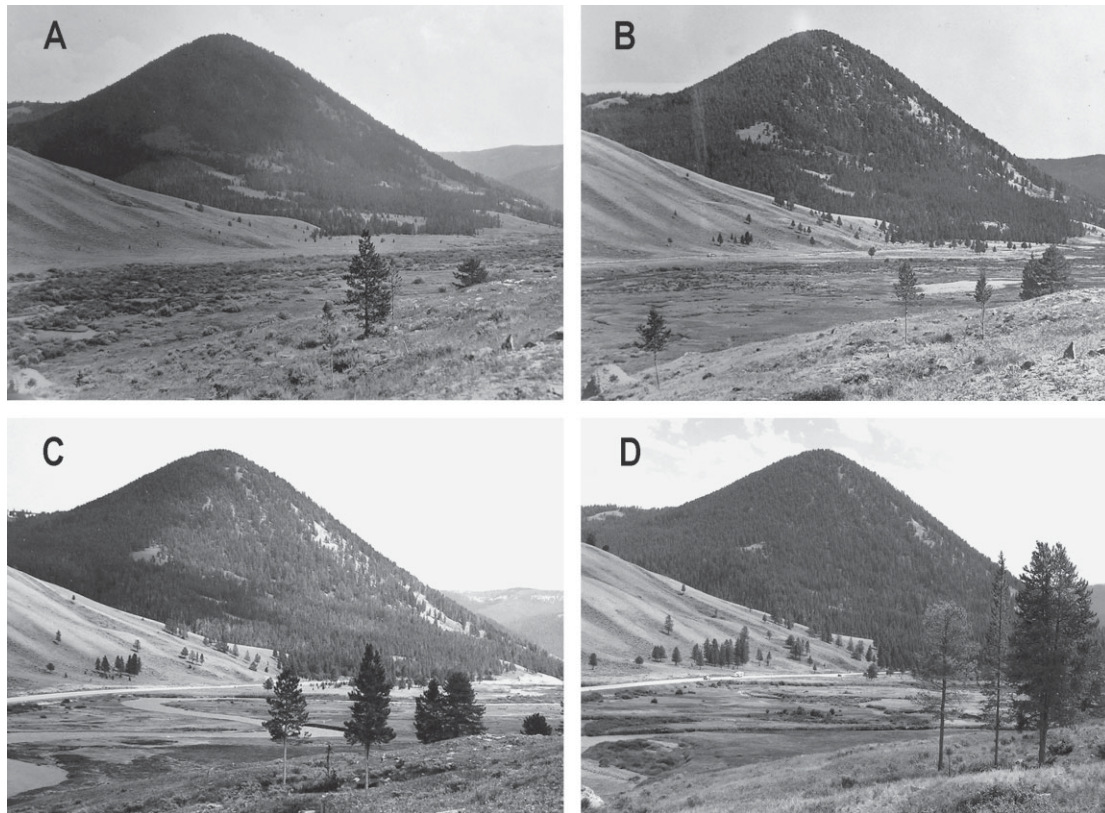


Figure 1. Photo chronosequence of the Gallatin River and floodplain showing the status of riparian willow communities along reach B in (A) summer of 1924, (B) summer of 1949, (C) late spring of 1961, and (D) summer of 2003. 'Highlining' (i.e. loss of lower branches from browsing) of relatively unpalatable conifers in the foreground is common in the 1949 photo, indicating heavy browsing pressure from elk. Extensive riparian willow communities associated with the floodplain in 1924 show progressive decline in the 1949 photo and are largely absent by 1961. Major channel changes occur between the 1949, 1961 and 2003 photos. Reach B cross-section measurements (see methods) were obtained along the floodplain shown in the right-center portion of the photos (but are largely obscured by conifer vegetation in the 2003 photo). Since wolves returned to this basin in the mid-1990s, clumps of willows have begun to grow taller and become more common as shown on the lower left portion of (D) (see also Ripple and Beschta, 2004b). Black Butte is the prominent peak in the center of each photo. [Photos: (A), (B), (C), Montana Fish, Wildlife and Parks; (D), W. J. Ripple.]

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Beschta (2004b)). However, the effects of willow loss upon channel morphology have not been previously reported. Thus, this study was undertaken (1) to assess potential differences in willow cover and channels for floodplain systems in the upper Gallatin Basin winter range and (2) to evaluate whether any differences in channels are attributable to the loss of streamside vegetation (following extirpation of wolves) or whether they represent responses to flow regimes, land use or other factors.

Study Area

The upper Gallatin Basin in Yellowstone National Park consists of prominent mountain peaks and ridges along catchment boundaries, shrub-steppe and forested hillsides, and open valley bottoms with willow communities. The basin has a continental climate with characteristically cold winters. Annual precipitation ranges from 50–70 cm in the valley (elevation ~2000 m) to more than 150 cm along mountain ridges. Annual winter snowfall averages approximately 250 cm along the valley bottom to upwards of 750 cm at higher elevations (Soil Conservation Service, 1972). Because of seasonal snow accumulations, each autumn elk migrate from high elevations (summer range) in the Gallatin Mountains towards 180–250 km² of lower-elevation terrain (winter range) along the upper Gallatin River and its major tributaries (Figure 2).

As Euro-American settlers spread across the western US and into southwestern Montana, grazing by cattle, horses and sheep in portions of the upper Gallatin Basin occurred during the late 1800s and into the early 1900s. Yellowstone National Park was established in 1872, thus closing park lands to domestic livestock grazing. In 1908, US Forest Service lands bordering the park along the upper Gallatin River were also closed to livestock grazing to help maintain satisfactory forage conditions for the elk winter range (Lovaas, 1970). Gray wolves, a strongly interacting species (Soule *et al.*, 2005), maintained a presence in the basin through the early 1900s and, in conjunction with widespread hunting by humans, affected elk populations up until the 1920s (Lovaas, 1970; Weaver, 1978).

In 1919 the size of the elk herd using the upper Gallatin winter range was estimated at 1600 (7 elk km⁻²) animals (Graves and Nelson, 1919). Following the eradication of wolves, herd size began to increase. From a high of 1700–2500 elk (8–12 elk km⁻²) in the 1930s, elk populations declined to a low of 800–1300 elk (4–6 elk km⁻²) by the late 1990s because of (1) a deterioration of foraging conditions in the winter range (due to high rates of herbivory) in combination with the periodic occurrence of severe winters, during which significant numbers of elk starved, and (2) annual harvest by hunters (Peek *et al.*, 1967; Patten, 1968; Lovaas, 1970; Ripple and Beschta, 2004b). Elk that utilize portions of the upper Gallatin winter range outside of Yellowstone National Park are annually hunted, while those that winter inside of park boundaries are not.

Methods

We obtained historical photographs (both ground and aerial) for documenting the status of riparian plant communities and river channels along the upper Gallatin River and for qualitatively assessing general changes over time. These photos were also inspected for land use or other factors that might affect channel characteristics.

Since riparian plant communities are often dependent upon hydrologic disturbance regimes (Patten, 2000; National Research Council, 2002b), we utilized the historical record of annual peak discharges as an indicator of climatic influences in the upper Gallatin Basin. Discharge records were obtained for the Gallatin River near Gateway, located ~60 km downstream of the study area (including USGS No. 060435, catchment area = 2140 km², and USGS No. 060440, catchment area = 2160 km²). To estimate peak discharge for years of missing record at the Gateway gage, regression analysis was undertaken with (1) the Gallatin River at Logan (USGS No. 060525), which is located ~40 km downriver from the Gateway gage, and (2) the Yellowstone River at Corwin Springs (USGS No. 061915), which drains mountainous terrain immediately east of the upper Gallatin Basin.

We selected three floodplain reaches, designated A, B and C (Figure 2), along the Gallatin River, for detailed assessment of channel cross-sections. At each of the selected reaches, overall floodplain widths were several multiples of contemporary channel widths, thus lateral channel migration and other channel adjustments could occur in response to changing conditions of flow, sediment availability or riparian vegetation.

We used an 'above' and 'below' experimental design. An untreated control reach (reach A) was selected upstream of the upper Gallatin elk herd winter range, where heavy browsing of deciduous woody plants does not occur. Treatment reaches B and C were located within the elk winter range between the confluences of Specimen Creek to the south and Tepee Creek to the north; willows along these reaches have experienced significant browsing pressure from the mid-1920s until recent years (Patten, 1968; Lovaas, 1970; Ripple and Beschta, 2004b). Since reach A

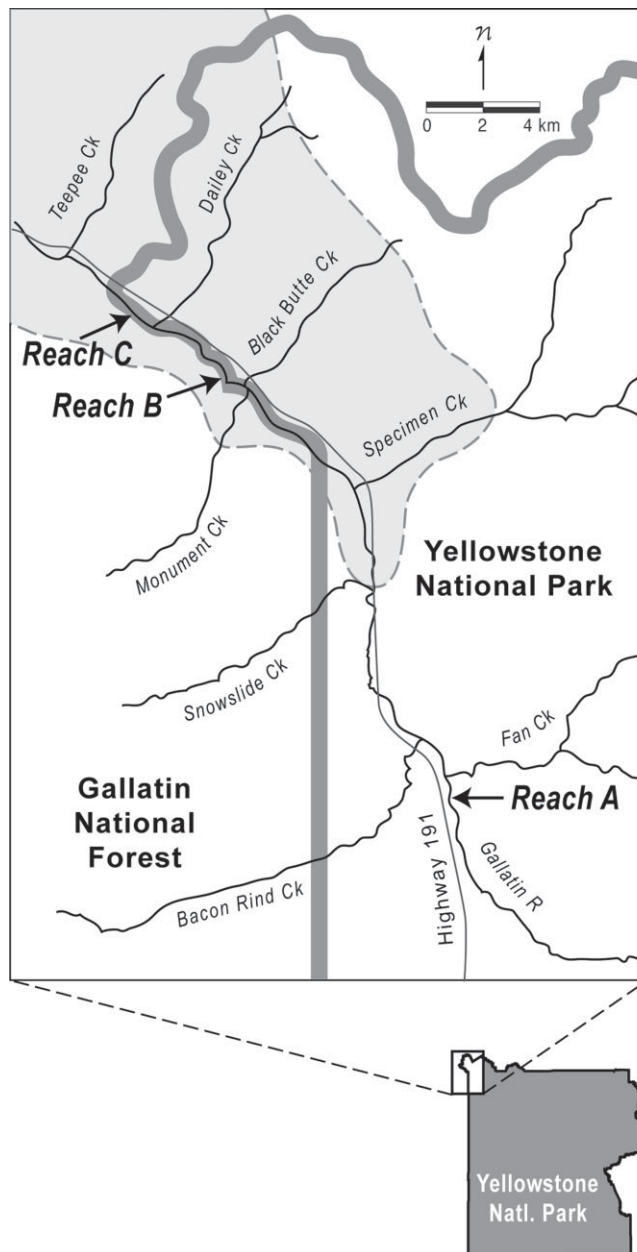


Figure 2. Location map of study reaches and delineation of winter range (shaded area) for the northern Gallatin elk herd (adapted from Edwards, 1941, and Allen, 1970).

(control) lies upstream of the elk winter range, the drainage area above this reach was only 92 km², in comparison to 412 and 450 km² for reaches B and C, respectively. The elevations of reaches A, B and C were 2200, 2070 and 2050 m, respectively. Along reaches B and C, the Gallatin River represents a common administrative boundary for Yellowstone National Park and the Gallatin National Forest (Figure 2).

In August of 2004, we surveyed (level, stadia rod) channel and floodplain elevations along linear transects established perpendicular to the channel. Four transects were set up within each study reach and each transect traversed the entire floodplain and its channel. Willow cover (expressed as a percentage of transect length) was recorded along each transect. Detailed measurements of wetted width and depth were obtained for the channel at each cross-section as well as bankfull channel dimensions (i.e. width, depth). 'Bankfull' herein is defined as the situation at which water

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within the contemporary channel begins to flow onto the floodplain. Water surface slope was measured where transects crossed the river; stream discharge was measured for each reach.

The spacing between cross-sections was typically 200 m, although this distance was sometimes varied by up to 50 m so that measurements could occur in relatively straight and uniform portions of the channel to aid in slope–area calculations of discharge (Hicks and Mason, 1991). Field observations of soils, vegetation, topography and ground-surface elevations along each reach were used to identify floodplain surfaces. *t*-tests were used to investigate for significant differences ($p \leq 0.05$) in width/depth ratios of treatment reaches (B and C) versus the control reach (A). Average bankfull widths for each study reach were also compared to those of streams in the Upper Yellowstone–Central Mountain Region of Montana (Parrett and Johnson, 2004).

Hicks and Mason (1991) provide measured hydraulic parameters over a range of stream discharges for a large number ($N = 78$) of channels across New Zealand. Based on the average annual discharge, water slope and type of vegetation within the study reaches, a comparable reach was identified in Hicks and Mason (1991, p. 13). Regression analysis of hydraulic radius (h , $\text{m}^2 \text{m}^{-1}$) and Manning's n measurements for the selected reach (No. 71129) were used to establish a power function between these two variables ($n = 0.034 h^{-0.290}$, $r^2 = 0.88$). This relationship, in turn, was used to estimate Manning's n for calculating bankfull discharge from the measured channel dimensions of each cross-section.

Parrett and Johnson (2004) provide a relationship between peak discharge and return period, assuming a log-Pearson type III probability distribution, for the Gallatin River near Gateway. From this relationship and in conjunction with an estimation procedure for ungaged basins in the Upper Yellowstone–Central Mountain Region (Parrett and Johnson, 2004, p. 34), we established a discharge–frequency relationship for each study reach. Thus, a return period could be estimated for the calculated bankfull discharge of each cross-section. Return periods for cross-sections within reaches B and C (treatment reaches) were compared graphically with those of reach A (control reach).

Results

Aerial photographs

The variable quality, scale and availability of the aerial photography precluded systematic quantification, over time, of channel dimensions within the three study reaches. Reach A, the control reach, was particularly problematic, since aerial coverage was only available for 1979 and 2001 and the photography was of a relatively small scale (1:30 000–1:45 000). Nevertheless, visual inspection of the aerial photographs for reach A indicated the channel experienced little change in location or planform morphology over the 22 yr period.

Aerial photography for reaches B and C was available approximately every decade since 1947 (i.e. 1947, 1962, 1971, 1981, 1990 and 1999) with scales ranging from 1:17 000 to 1:52 000. In 1947, the Gallatin River had mostly a single-thread meandering channel with little unvegetated alluvium (e.g. exposed point bar deposits) evident along its channel. However, post-1947 photographs indicated increasing divergence in planform morphology and the amount of area comprising unvegetated alluvial deposits. Over time, such deposits became increasingly frequent along reach B as the channel underwent changes in location, pattern and active width. The planform morphology of the river channel along reach C was relatively straight in 1947 and remained similar in subsequent aerial photographs, although some localized widening and increases in unvegetated alluvial deposits was noted. Post-1947 photos indicated that channel avulsions, braiding and/or widening of the active channel, such as observed for reach B, were also occurring upstream and downstream of reaches B and C.

The potential effects of state highway 191 were also considered during inspection of the aerial photographs. At reach A, the highway occurs along the west side of the valley and is well outside the floodplain. For reaches B and C, the highway generally occupies lower portions of hillslopes along the east side of the valley although it locally impinges onto the valley-bottom alluvium at a few locations upstream/downstream of these study reaches. Reconstruction of this highway in the 1950s appeared to have had little effect on the channel morphology of reaches B and C.

Historical peak discharges

In southwestern Montana, maximum discharge during the annual snowmelt hydrograph typically occurs between mid-May and mid-June. A 110 yr chronology of annual peak discharges (Figure 3) was constructed from (1) 91 yr of recorded peaks for the Gallatin River near Gateway, (2) 6 yr of estimated peaks from regression analysis with the Gallatin River at Logan ($r^2 = 0.84$) and (3) 13 yr of estimated peaks from regression analysis with the Yellowstone River near Corwin Springs ($r^2 = 0.67$). For this extended period of record (Figure 3), annual peak discharges averaged

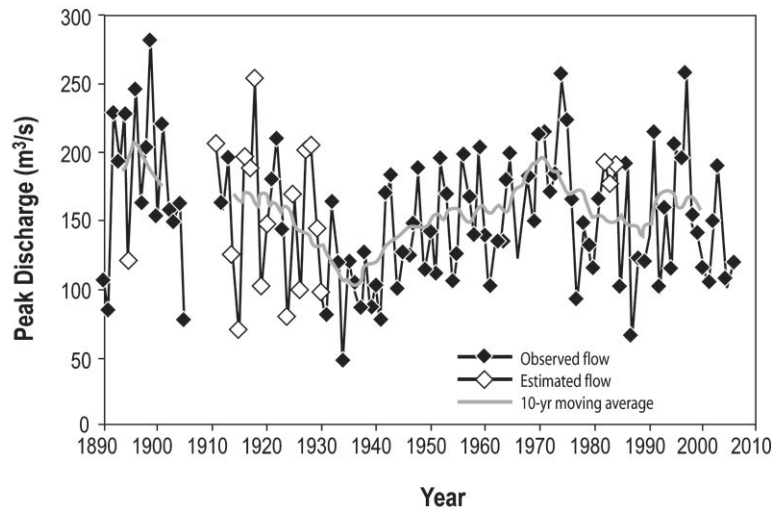


Figure 3. Annual peak discharge from 1890 to 2003 for the Gallatin River at Gateway based on gauged data (91 yr) and estimates derived from regression analysis of the Gallatin River near Gateway with the Gallatin River at Logan (6 yr) and the Yellowstone River near Corwin Springs (13 yr).

$155 \text{ m}^3 \text{ s}^{-1}$ (coefficient of variation ± 31 per cent). While autoregression analysis of this time series resulted in a lag₁ autocorrelation coefficient of only $+0.21$ ($r^2 = 0.04$), indicating little year-to-year correlation, below-average peak flows were relatively common from the 1920s through the mid-1960s. During that period, annual peak discharges never exceeded $213 \text{ m}^3 \text{ s}^{-1}$ (i.e. < 6 yr return period). The occurrence of drought conditions in the 1930s across much of the western US is reflected in the relatively low annual peak flows for the Gallatin River during that decade (Figure 3).

Floodplains and vegetation

The floodplain surface along reach A had considerable microtopography due to sediment deposition at the base of well established willows that were prevalent across this surface. In addition, several small distributary channels (typically < 1 m in width and depth) and/or beaver channels occasionally dissected the floodplain surface.

Surveying measurements across the valley bottom and field observations (soil texture, vegetation, drift deposits) at reaches B and C indicated the occurrence of two floodplain surfaces, varying in elevation relative to each other by approximately 0.15–0.5 m. Both geomorphic surfaces were absent the microtopography that was such a prevalent feature of the floodplain at reach A; small distributary channels were similarly absent. Reaches B and C had predominantly sand-textured soils of variable thickness (often ≥ 1 m) overlying a cobble substrate. On the uppermost of these two surfaces, drift deposits of flood debris were entirely lacking, indicating that in recent decades it had not been hydrologically connected (i.e. not experiencing overbank flows) with the Gallatin River. On the elevationally lower surface, widely scattered and infrequent deposits of flood debris were found but the frequency and magnitude of flows that contributed to these deposits is not known. Within reaches B and C, the lower-most of these two geomorphic surfaces was used as the floodplain elevation for bankfull discharge calculations.

Vegetation measurements in 2004 indicated significantly less ($p < 0.01$) average willow cover associated with the floodplains of reach B (26 per cent) and reach C (5 per cent) in comparison to reach A (85 per cent). Scattered plants of shrubby cinquefoil (*Potentilla fruticosa*), a shrub of low stature and low palatability, and indicative of sites with heavy browsing (Shaw *et al.*, 2004), were observed on floodplain surfaces associated with reaches B and C, but were not present at reach A. Similarly, tall saplings of lodgepole pine (*Pinus contorta*), a tree that typically occupies dry sites, have become established at several locations on the floodplain immediately downstream of reach C, indicating this surface has become drier in recent decades. At reach A, not only was the floodplain well vegetated with willow communities, but both shrubby cinquefoil and lodgepole pine were absent (Figure 4). Sedges provided nearly continuous cover along each streambank at Reach A and often extended for several meters away from channel margins. Sedge cover along the streambanks of reaches B and C was generally absent. Instead, raw vertical banks indicative of channel widening and/or lateral channel migration were common along both of these reaches. In addition, active beaver dams were present on the floodplain associated with reach A, but absent from reaches B and C.

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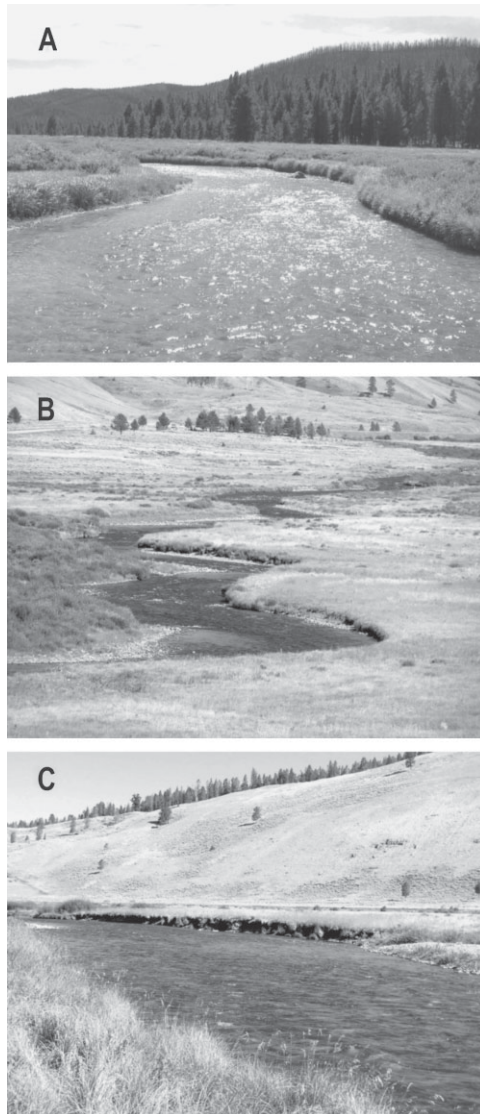


Figure 4. Photographs of (A) reach A, (B) reach B and (C) reach C along the Gallatin River in August of 2004. Note extensive cover of sedges and willows along streambanks and across the floodplain at reach A. While the willows shown along the left side of the reach B photograph represent some that have begun to recover since wolves returned to this basin in the mid-1990s, willows remain largely absent and eroding banks are common for most of reaches B and C. (Photos: R. L. Beschta.)

Channel measurements

Channel gradients measured in August of 2004 (Table I) ranged from 0.0032 to 0.0121 m m^{-1} for individual cross-sections and averaged 0.0074, 0.0056 and 0.0078 for reaches A, B and C, respectively. For the discharges encountered in late August of 2004, Manning's n ranged from 0.033 to 0.072 for individual cross-sections and averaged 0.052, 0.057 and 0.067 for reaches A, B and C, respectively. Wetted width/depth ratios for reach B (55 m m^{-1}) and reach C (49 m m^{-1}) were not significantly different ($p > 0.05$) from reach A (38 m m^{-1}).

Although a single main channel occurred through reaches A and C, for which cross-section estimates of bankfull discharge were calculated, the cross-sections at reach B represented a more complex hydraulic condition. Inspection of the historical aerial photographs indicated that reach B had experienced considerable lateral erosion, channel avulsion and/or channel widening over the last half-century. In some locations, the channel appeared to have widened and aggraded: aggradation presumably a result of increased sediment derived from channel widening, incision or avulsion

Table I. Channel dimensions and hydraulic characteristics for cross-sections in reaches A, B and C, at the indicated discharges (Q) in August 2004 [CV (%) = coefficient of variation.]

Cross section No.	Water slope (m m^{-1})	Wetted width (m)	Average depth (m)	Width/depth (m m^{-1})	Cross-section area (m^2)	Hydraulic radius ($\text{m}^2 \text{m}^{-1}$)	Manning's n
Reach A							
($Q = 1.2 \text{ m}^3 \text{ s}^{-1}$)							
1	0.0071	8.7	0.27	33	2.3	0.26	0.065
2	0.0097	9.1	0.23	40	2.1	0.23	0.062
3	0.0032	7.3	0.25	29	1.9	0.24	0.033
4	0.0094	9.4	0.20	53	1.8	0.19	0.048
Average	0.0074	8.6	0.24	38	2.0	0.23	0.052
CV (%)	40	10	13	28	10	13	27
Reach B							
($Q = 3.9 \text{ m}^3 \text{ s}^{-1}$)							
1	0.0025	14.9	0.49	30	7.3	0.48	0.058
2	0.0121	22.9	0.20	115	4.6	0.20	0.044
3	0.0047	15.5	0.38	41	5.9	0.38	0.055
4	0.0029	16.5	0.48	34	7.9	0.48	0.068
Average	0.0056	17.5	0.39	55	6.4	0.38	0.057
CV (%)	80	21	36	73	23	34	18
Reach C							
($Q = 3.9 \text{ m}^3 \text{ s}^{-1}$)							
1	0.0098	20.1	0.31	65	6.2	0.30	0.072
2	0.0063	17.7	0.34	52	6.0	0.34	0.060
3	0.0068	14.0	0.40	35	5.6	0.39	0.065
4	0.0081	15.8	0.37	43	5.9	0.37	0.071
Average	0.0078	16.9	0.37	49	5.9	0.35	0.067
CV (%)	21	15	11	27	11	11	7

at upstream locations. This situation resulted in a wide gravel/cobble surface or secondary channel adjacent to the main channel, both of which carried water during periods of high discharge. The average width/depth ratio at bankfull discharge (Table II) for reach B (118 m m^{-1}) was significantly greater ($p = 0.02$) than the control reach A (42 m m^{-1}), whereas reach C (39 m m^{-1}) was not significantly different ($p = 0.83$) from the control. Although average bankfull widths for reaches A and C were within the 99 per cent confidence limits for mountain streams in western Montana, the average bankfull width for B was well outside these limits (Figure 5).

The coefficient of variation for calculated bankfull discharges was similar for cross-sections within reaches A (21 per cent) and C (22 per cent) but was much larger for reach B (78 per cent). The average return period for bankfull discharge at reach A was 3.1 yr, much less than the 32.4 and 10.6 yr at reaches B and C, respectively (Table II). The estimated return periods associated with bankfull discharge for two cross-sections at reach B and for three cross-sections at reach C occurred well outside of the range of return-period estimates found within reach A (Figure 6).

Discussion

When wolves were present in the upper Gallatin Basin, their effects upon elk were primarily twofold: (1) they could affect elk populations through direct predation and (2) they could behaviorally mediate patterns of herbivory (Brown *et al.*, 1999; Ripple and Beschta, 2004a). Thus, after wolves had been removed elk were able to graze/browse riparian plant communities unimpeded by the presence of this apex predator. Even with a decreasing elk population during the seven decades following the loss of wolves, willow and other plant communities in the winter range continued to deteriorate (Figure 1(b) and (c); Lovaas, 1970). However, following the return of wolves to this basin in the mid-1990s, some willows have begun to recover (Ripple and Beschta, 2004b). An initiation of riparian willow and cottonwood recovery has similarly been documented for winter range in the northeastern portion of Yellowstone National Park (Ripple and Beschta, 2003). Thus, it appears that the presence or absence of this apex predator can

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Table II. Bankfull channel dimensions, hydraulic characteristics, discharges and return periods for cross-sections in reaches A, B and C. Return periods determined from regional relationships (see text for methods) [CV (%) = coefficient of variation.]

Cross section No.	Width (m)	Average depth (m)	Width/depth (m m ⁻¹)	Hydraulic radius (m ² m ⁻¹)	Manning's <i>n</i>	Discharge (m ³ s ⁻¹)	Return period (yr)
Reach A (average water surface slope = 0.0074)							
1	11.0	0.53	21	0.50	0.043	7.4	3.5
2	14.8	0.36	41	0.35	0.048	4.7	1.8
3	25.0	0.36	70	0.34	0.048	7.8	4.0
4	49.0	0.44	34	0.42	0.046	6.9	3.2
Average	14.9	0.42	42	0.41	0.046	6.7	3.1
CV (%)	37	20	50	19	5	21	29
Reach B (average water surface slope = 0.0056)							
1	71.0	0.45	160	0.74	0.038	50.0	23
2	44.2	0.48	92	0.51	0.043	23.6	3.3
3	65.8	0.82	81	0.97	0.035	109.9	>100
4	58.5	0.42	140	0.45	0.044	23.9	3.4
Average	59.8	0.54	118	0.67	0.040	51.9	32.4
CV (%)	19	34	32	36	11	78	142
Reach C (average water surface slope = 0.0078)							
1	31.1	0.73	42	0.67	0.040	38.9	9.5
2	21.9	0.95	23	0.88	0.037	46.4	22
3	27.1	0.64	42	0.62	0.041	27.5	4.0
4	31.7	0.66	48	0.65	0.040	34.6	7.0
Average	28.0	0.75	39	0.71	0.039	36.9	10.6
CV (%)	16	19	28	17	5	22	75

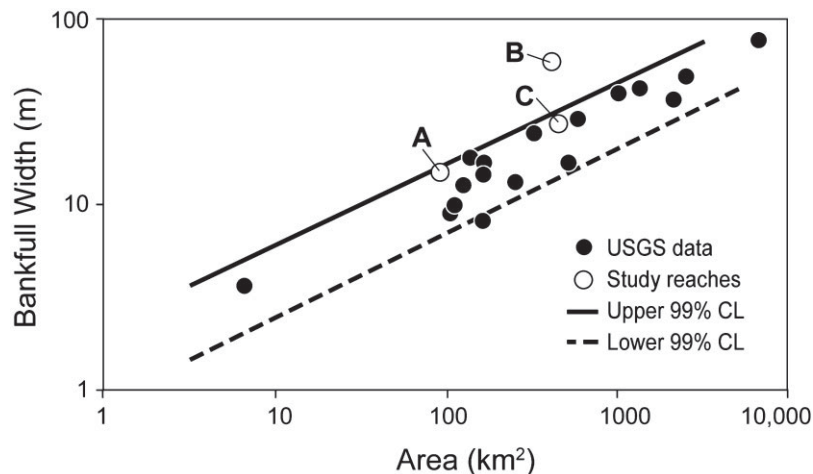


Figure 5. Average bankfull width for each study reach relative to those of mountain streams in the Upper Yellowstone–Central Mountain region of Montana, where annual basin precipitation exceeds 75 cm (US Geological Survey data from Parrett and Johnson, 2004). Each data point represents an average of three or four measurements.

impart important effects upon lower trophic levels: first to elk, then to willows and finally to hydrogeomorphic processes associated with floodplain systems (Figure 7).

Several factors indicated that the channel associated with reach A has been stable for many decades: (1) the reach is located outside the normal winter range of the upper Gallatin elk herd and there is no historical record (Lovaas, 1967,

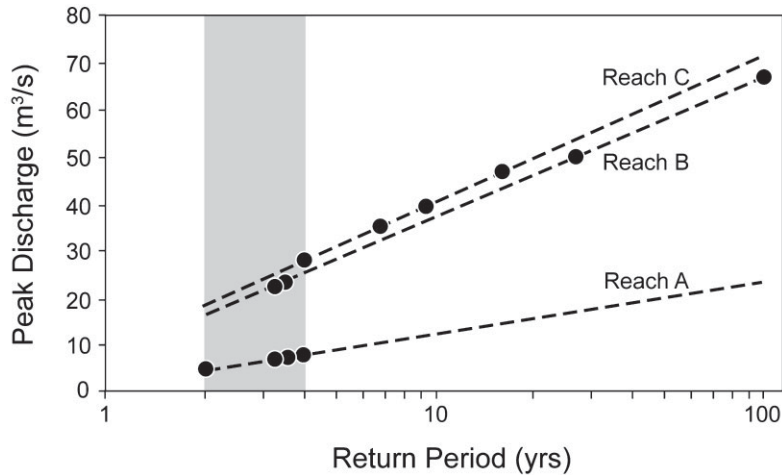


Figure 6. Discharge–frequency relationships (dashed lines) for reaches A, B and C (from regional equations in Parrett and Johnson, 2004). Plotted points represent calculated bankfull flows and associated recurrence intervals for individual cross-sections at each study reach; the shaded area encompasses the range of return periods for reach A (control).

Conceptual Model	Wolves Present	Wolves Absent
Predators	Wolves cause mortality and increase predation risk to elk populations	---
↓	↓	⊘
Prey	Elk numbers and patterns of habitat use result in low–moderate browsing of riparian vegetation	Increased elk numbers and/or unimpeded habitat use result in heavy browsing of riparian vegetation
↓	↓	↓
Plants	Woody browse species in riparian areas able to establish, grow, and reproduce; high levels of above- and below-ground biomass contribute to hydraulic roughness and bank stability	Reduced above- and below-ground biomass of woody browse species causes loss of hydraulic roughness and root strength
⋮	⋮	⋮
Channel Morphology	Gallatin River has a relatively stable, meandering, single-thread channel in long-term balance with its flow regime	Accelerated bank erosion results in widespread channel adjustments including widening, incision, and avulsion; some over-widened reaches aggrade
⋮	⋮	⋮
Hydrologic Connectivity	Occurrence of bankfull flows approximately every 2–4 years (on average) in conjunction with high water tables provide soil moisture conditions that sustain riparian plant communities	Occurrence of bankfull flows generally exceed 2–4 years in conjunction with lowering of groundwater levels cause soil moisture conditions that no longer sustain riparian plant communities

Figure 7. Summary of ‘top-down’ trophic cascades (solid arrows) and hydrogeomorphic processes (dashed arrows) conceptual model with and without wolves for floodplain riparian systems in the upper Gallatin elk winter range. Potential effects of bottom-up influences and interactions (see, e.g., Bower *et al.*, 2005) involving such factors as environmental carrying capacity (*k*), climate, plant succession and others are not included.

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1970) indicating that willows along this reach had been heavily browsed, either before or after the removal of wolves, (2) field observations in 2004 indicated streambanks were well vegetated by both sedges and willows and that a dense community of mature willows occurred across the floodplain and (3) inspection of available aerial photographs (1979 and 2001) indicated the channel had remained stable during that period. Collectively, these factors indicate that reach A represents a reasonable choice of a control reach for comparing treatment effects associated with reaches B and C. Inspection of aerial photographs spanning approximately half a century (i.e. 1947–99), when wolves were absent, indicated differential channel responses for reaches B and C during the period when sedge-willow communities were undergoing degradation. Channel geometry measurements in 2004 of bankfull cross-sections at these two reaches tended to confirm these interpretations (see, e.g., Figure 5).

Periods of flooding provide a high-energy environment for the detachment, transport and deposition of sediment, thus high flows can be a factor affecting channel adjustments such as widening, incision and avulsion (Rinaldi, 2003). Streamflow records for the Gallatin River (Figure 3) indicate peak discharges greater than or equal to the magnitude of a 6 yr event occurred seven times from 1890 to 1919, yet the 1924 photograph (Figure 1(A)) provides little evidence that these flows adversely affected willow communities within the winter range or resulted in a destabilized channel. In contrast, photographs for 1949 and 1961 (Figure 1(B) and 1(C)) indicate streambank erosion was becoming increasingly common even though annual peak discharges from the 1920s through the 1960s never exceeded the magnitude of a 6 yr event.

Since the period of low-to-moderate peak discharges, in conjunction with the general drought conditions of the 1930s, corresponds to the general timing of deteriorating sedge-willow communities within the elk winter range, it could be hypothesized that these hydrologic patterns are an important contributor to the degradation of these plants. If so, then the increasing magnitude of runoff in the 1970s through the 1990s (Figure 3) should have initiated a resurgence of these plant communities, but such was not the case, and willows continued to decrease in stature and canopy cover while channels became increasingly unstable. Furthermore, we are unaware of any evidence indicating a deterioration of sedge-willow communities in riparian areas immediately outside of the winter range (e.g. reach A). Collectively, these factors indicate that variations in peak-flow magnitudes were not the primary cause of sedge-willow decline in the upper Gallatin winter range or of initiating the channel changes that ensued. However, once streamside plant communities were degraded by heavy grazing/browsing, peak flows of low-to-moderate magnitude were able to erode streambanks and contribute to widespread channel changes.

Data of Gray and Barker (2004) indicate that the tensile strength of willow roots ($\bar{x} = 26$ MPa, std dev. = 12 MPa, $n = 4$) is comparable to that of trees ($\bar{x} = 28$ MPa, std dev. = 13 MPa, $n = 20$), which are known to stabilize hillsides (Sidle *et al.*, 1985; Abe and Ziemer, 1991). Thus, willows can provide significant mechanical reinforcement of floodplain soils, without the concomitant liability of trees, resulting from their greater above-ground weight, rigidity and tendency for windthrow. The smaller diameter and flexibility of individual willow stems may also make these plants less likely to accumulate drift or cause hydraulic scouring around their bases during periods of overbank flow. Sedges and other graminoid species can also contribute considerable root strength to streambank soils (Micheli and Kirchner, 2002b).

Willows, sedges and related hydrophytic plants found in many riparian systems typically require moist-site conditions for their establishment and growth and thus are well adapted to the annual patterns of snowmelt runoff in the Rocky Mountains (Braatne *et al.*, 1996; Patten, 2000). This annual disturbance regime of seasonally high runoff and periodic over-bank flows is not only an important source of moisture and nutrients for hydrophytic plants (Goodwin *et al.*, 1997) but also prevents mesic or xeric plant communities from becoming established on streambanks and floodplains. For example, Chapin *et al.* (2002) found that hydrophytic plant communities in southwestern Oregon were sustained on those portions of a floodplain where overbank flows occurred more frequently than once every five years.

For the calculated bankfull flows, an average return period of 3.1 yr was obtained at reach A, whereas average return periods at reaches B and C were approximately 10 and three times larger, respectively. This indicates that floodplains within the elk winter range have become hydrologically disconnected (i.e. reduced frequency of overbank flooding) from the natural flow regime of the Gallatin River. Whether due to channel widening or incision, or both, the net result is that the seasonal availability of moisture to floodplain plant communities has decreased.

When channel incision occurs, not only is the frequency of overbank flows on adjacent floodplains reduced, but local ground water tables are also likely to be lowered. Both of these factors contribute to the loss of moist-site riparian plants and a conversion of floodplain plant communities to species that can tolerate drier conditions (Rost and Rasmussen, 2004). In snowmelt systems of the Sierra Nevada range, Micheli and Kirchner (2002a) found that when streambank heights were >1 m above the low-flow water surface, riparian habitats became dominated by dry-site vegetation. In eastern Oregon's snowmelt systems, Otting (1998) concluded that channel incision of ~0.5 m in a floodplain was sufficient to shift riparian plant communities from hydrophytic to mesophytic species.

For reach A, the difference in elevation between the low-water surface in August of 2004 and the bankfull floodplain averaged 0.37 m. However, for reaches B and C, where return periods of bankfull discharges were generally greater than those of the control reach, water surface elevations at bankfull discharge averaged 0.71 and 0.65 m, respectively, above the water surface in late summer. This greater height of floodplain above the low-flow water surface for reaches B and C may be partially due to the fact that these channel cross-sections receive flows from a larger drainage area than that of reach A and hence have larger channel dimensions. Nevertheless, the increased capacity of these cross-sections (i.e. larger recurrence interval flows required, on average, to attain bankfull conditions) compared with reach A indicate a condition of decreased water availability for streamside vegetation.

A reduced frequency of flooding, whether due to channel widening, channel incision or both, effectively reduces the capability of floodplains to support extensive willow communities and other hydrophytic vegetation. The effects on riparian plant communities of a deterioration in hydrologic connectivity are in addition to the direct impacts of heavy grazing/browsing over time. Others (e.g. Naiman *et al.*, 2000) have similarly noted that foraging by native herbivores can cause important biophysical effects to riverine systems.

Dwire *et al.* (2004) found the below-ground biomass of dry-meadow vegetation to be only one-fifth to one-third that of wet-meadow plant communities. Micheli and Kirchner (2002a) indicate a tenfold increase in bank erosion rates where hydrophytic vegetation has been replaced with plants characteristic of drier sites. Thus, the hydrologic decoupling of floodplains from their flow regimes is likely to accelerate rates of streambank erosion.

Along the Little Bighorn River in south-central Montana, Beschta (1998) found that the loss of streamside vegetation by grazing and mechanical methods initiated a period of accelerated channel adjustments, including increased channel widths, channel incision, and decreased sinuosity. More recently, Smith (2004) evaluated the role of reduced riparian shrub densities on the stability of floodplains along the Clark Fork of the Columbia River in west-central Montana using a process-based model for overbank flow. Modeling results indicated that a dense shrub community, which historically existed along the Clark Fork, was able to maintain a single-thread, meandering channel during large floods. However, with a decrease in the density woody vegetation, model results indicated that the flow velocity over the floodplain and the boundary shear stress on the floodplain surface increased sufficiently to allow for the destabilization of the former single-thread channel.

The catastrophic geomorphic transformation of floodplain channels (i.e. unraveling of streambanks *via* accelerated bank erosion and/or incision, sometimes in conjunction with channel aggradation in downstream reaches) can have serious ecological consequences (Smith, 2004). Channel incision can be of particular importance because it subsequently allows a river's hydraulic forces to increasingly occur below the root zone of any remaining vegetation. The mixing of coarse streambed sediments with an influx of finer sediment during floodplain erosion decreases the median size and sorting of sedimentary material on the bed, making them relatively mobile. This increased mobility during lower flows makes benthic habitats more inhabitable for many insect larvae that normally live within the interstices of the coarse bed sediments. Even where streambeds remain stable, the intrusion of fines can effectively fill gravel interstices (Beschta and Jackson, 1979). Rapidly eroding streambanks and wider channels allow for increased stream temperatures (due to shallower depths and lack of shading vegetation along the banks) and a loss of overhanging banks typically used as cover and refugia for fish (Platts, 1991). A loss of vegetative cover along streambanks and floodplains also decreases their habitat values for avian communities, beaver, and other fisheries/wildlife species, and effectively truncates allochthonous inputs to a stream that can be a major source of organic carbon for many aquatic organisms (Ohmart, 1996; Dobkin *et al.*, 2002).

Conclusions

Overall, the extirpation of wolves from the Yellowstone area has had a cascading effect on lower trophic levels (first elk and then willows) along the Gallatin River, where it flows through the elk winter range. Even though the long-term trend in elk numbers following wolf extirpation was one of decline due to the annual harvest of elk *via* hunting, predation by other large carnivores and the periodic occurrence of mortality during severe winters, this situation was unable to prevent the continued decimation of streamside vegetation. The heavy annual browsing of willow communities after the loss of wolves ultimately generated major changes in floodplain functions and channel morphology. To the best of our knowledge, we are the first to connect a large, highly interacting carnivore to the characteristics of a river floodplain and its channel.

In the western US, many millions of hectares of public land exist where direct human impacts have been limited but where grazing/browsing by livestock and wild ungulates commonly occurs. For the vast majority of these lands, wolves are no longer present, although there have been efforts in recent decades at restoring them in some locations. While this study focused specifically on the effects of heavy browsing by native ungulates upon riparian plant

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communities dominated by willows, within the broader context of other studies that have evaluated grazing/browsing effects of domestic livestock the message is clear. Persistent, heavy grazing/browsing of streamside vegetation by either wild or domestic ungulates can lead to impoverished plant communities, channel instability and loss of hydro-logic connectivity, all of which adversely affect the quality and extent of habitats for a wide range of aquatic/terrestrial biota.

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