Wolves, Elk, and Woody Plants of Yellowstone National Park: A Photographic History of a Trophic Cascade

Part 3 - Bison Limit a Trophic Cascade

American Bison

(Photo – RL Beschta)

A Look Back in Time at Wolves and Elk

Following the extirpation of gray wolves, and cougar, from Yellowstone National Park in the 1920s, elk browsing increased in the park's northern range and, over time, suppressed many woody plant communities, including those of aspen, willow, and cottonwood. By the 1990s, woody plants across the northern range were being suppressed by elk browsing and unable to grow above the reach of elk.

With the reintroduction of wolves in 1995-1996, thus re-establishing the park's large carnivore guild, elk behavior and numbers started to change. Elk browsing began to decrease in various portions of the northern range and woody species began to grow taller.

Over time, the botanical resurgence became increasingly widespread--with one major exception: That exception now occurs where large numbers of bison forage.

American Bison

As ecosystem engineers, large numbers of bison have the capability to influence plant species composition and distribution across northern Yellowstone's shrub-steppe and grasslands, as well as contributing to more localized effects *via* forage selection, hoof action, wallows, nitrogen availability, and others.

The distribution of bison in the United States originally extended from east of the Appalachians to west of the Rocky Mountains, with most herds residing on the Great Plains. While bison may have historically totaled 30 million animals and comprising vast herds on the Great Plains, their numbers declined rapidly in the 1800s due to market hunting. By the 1880s, bison had been driven to the brink of extinction.

(Photo – RL Beschta)

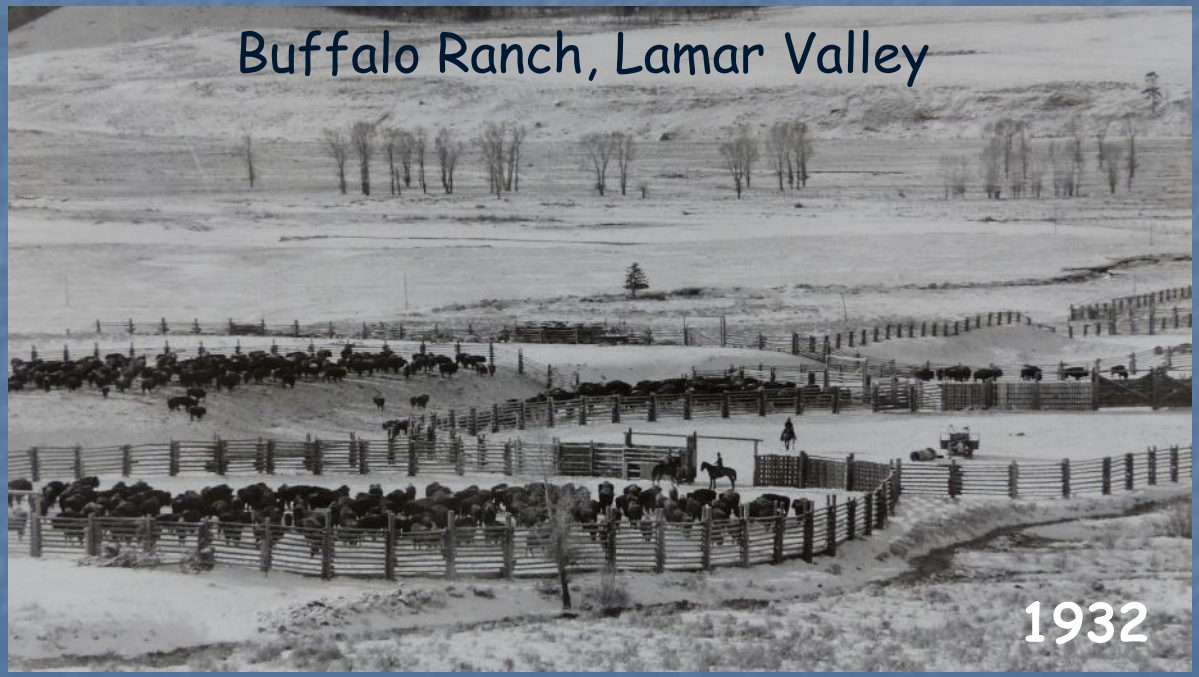
Bison Occurrence Prior to Park Establishment

Although bison were a common occurrence in areas adjacent to the Rocky Mountains, there is little evidence of a consistent bison presence during prehistorical times within the area now encompassed by Yellowstone National Park. Based on various indicators and lines of evidence, such as archeological information, a severe climate during the Little Ice Age (ca. 1450-1850), topographic barriers to migration, and first-person journals by Euro-Americans, it appears unlikely that large herds of bison resided in the park. Additionally, continuous cottonwood recruitment throughout the 1800s in the northern range indicates that ungulate populations appear to have had a minimal affect on woody plant establishment during that century.

In a recent assessment of the prehistoric bison in the Yellowstone area prior to park establishment, Keigley (2019, p. 11) concluded: "it appears that bison had an insignificant role in shaping Yellowstone's prehistoric landscape."

Northern Range Bison in the 1900s

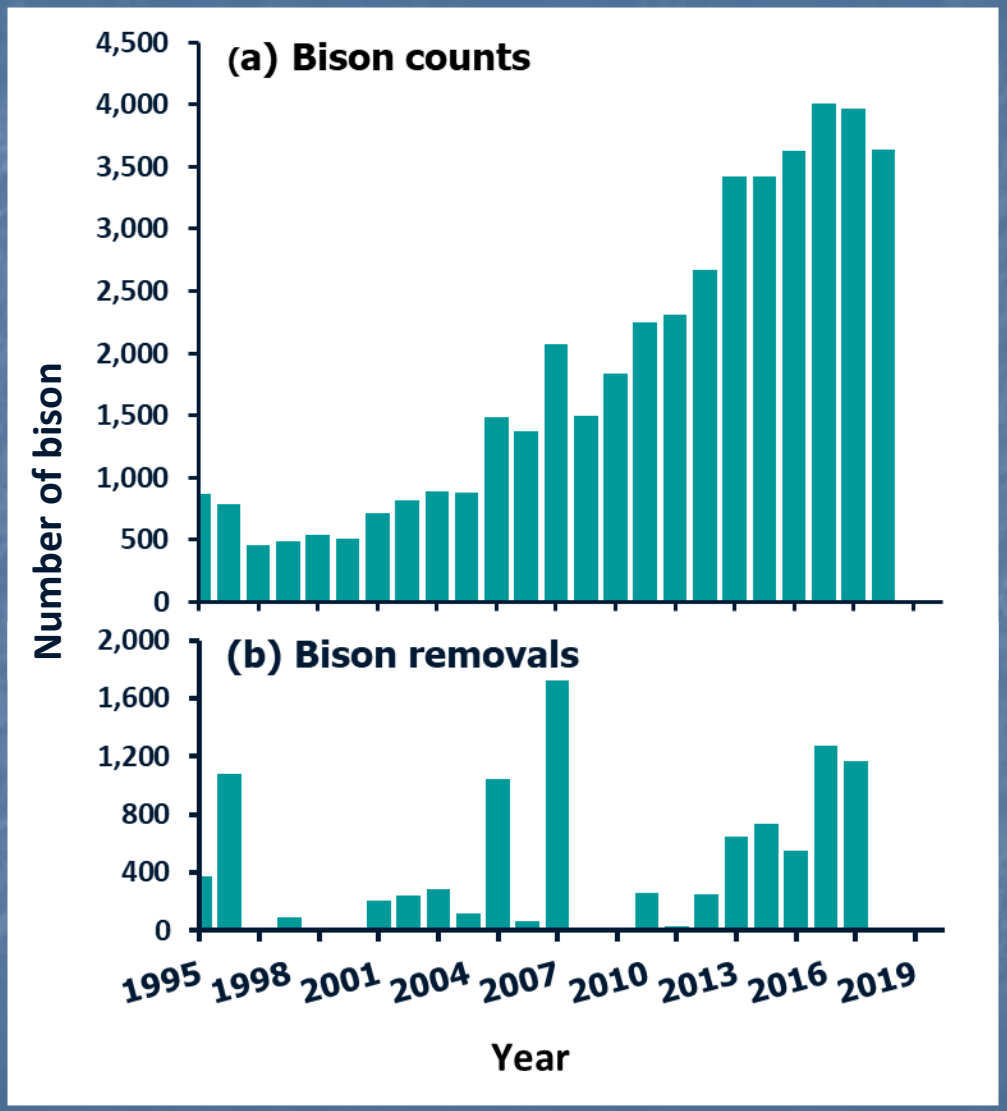
When the park was established in 1872 several small herds of bison occurred within its boundaries and within a couple of decades only a few animals remained because of poaching within the park. Bison became fully protected after 1901 and ranching operations in the Lamar Valley helped support their population. For example, haying was conducted at Buffalo Ranch from 1908-1952 to provide winter feed for Bison.



(Photo – GM Wright)

To reduce the adverse effects ungulate herbivory was having on northern range plant communities, both bison and elk were culled by the Park Service after 1925. Culling ceased in 1968 at which time there were ~100 bison in the northern range. By the mid-1990s their population had grown to almost 1,000 bison.

An Increasing Northern Range Bison Population



(a) In the last 10-15 years, the number of bison in northern Yellowstone has significantly increased. Bison numbers currently are at record highs in the northern range, with their total biomass greatly exceeding that of elk. Whereas elk primarily use the northern range for wintering, bison are present year-round.

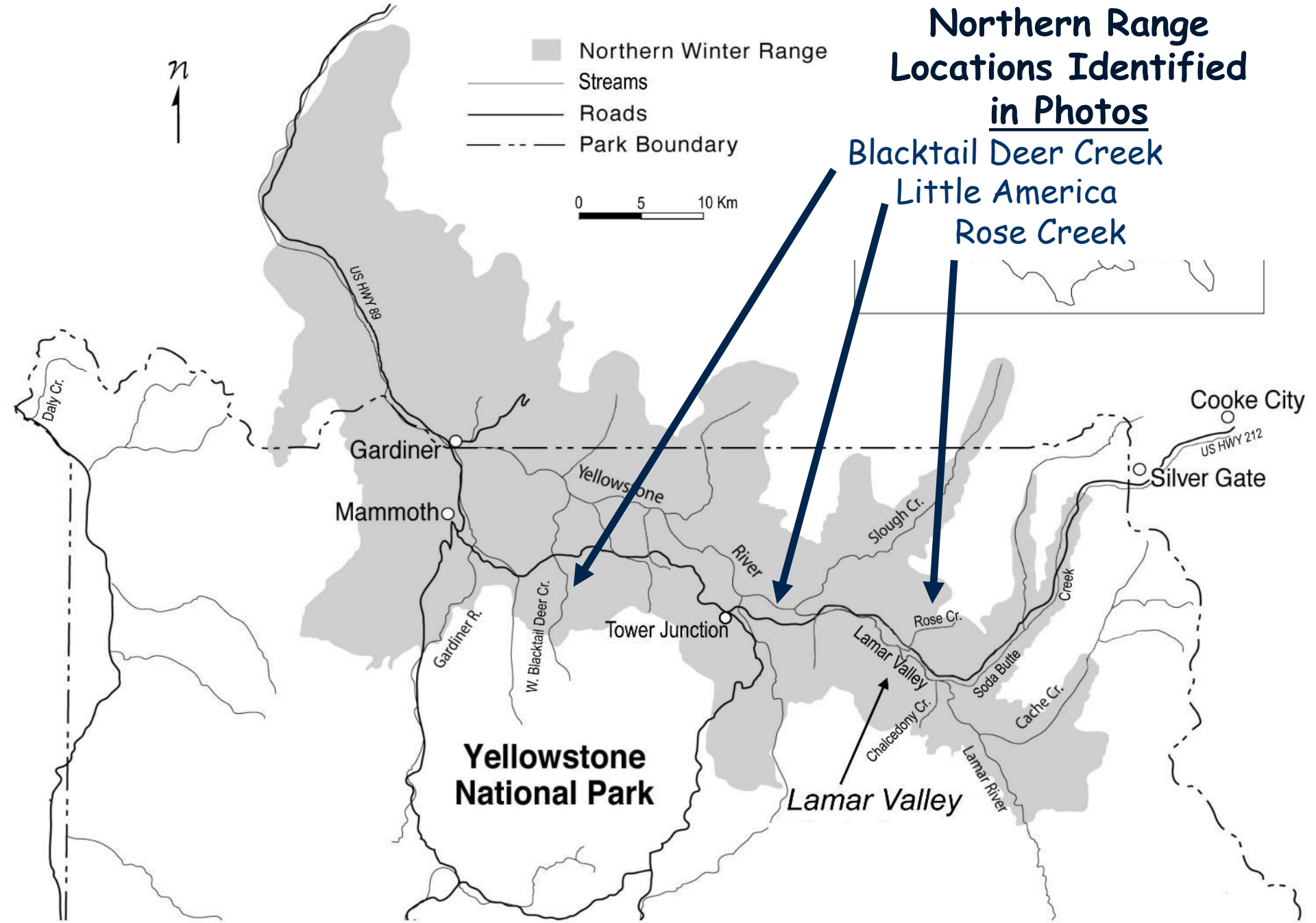
(b) Bison culling (removals) during the last 25 years has not prevented a major increase in their population. However, without culling bison numbers would likely be even greater.

(Bison data – National Park Service)

Photographic Record

Bison are large ungulate herbivores that normally consume herbaceous vegetation, such as grasses, sedges, and forbs to meet their foraging needs and thus are typically characterized as grazers. However, bison also browse woody plants during certain seasons of the year or when other sources of forage may be in limited supply.

The photographs that follow illustrate some of the ecosystem effects of bison in Yellowstone's northern range, particularly during the last two decades. Importantly, these effects continue, and in some cases accentuate, those previously attributed to elk during the period when wolves were absent (1920s to 1990s).


Northern Range Locations Identified in Photos
Blacktail Deer Creek
Little America
Rose Creek
Northern Winter Range
Streams
Roads
Park Boundary
0 5 10 Km
n
US HWY 89
Daly Cr.
Gardiner
Mammoth
Yellowstone River
Tower Junction
Gardiner R.
W. Blacktail Deer Cr.
Slough Cr.
Rose Cr.
Lamar Valley
Soda Butte Creek
Cache Cr.
Chalcedony Cr.
Lamar River
Cooke City
US HWY 212
Silver Gate
Yellowstone National Park
Lamar Valley

Bison Central: The Lamar Valley

Located in the eastern portion of the northern range, the Lamar Valley experiences heavy bison use throughout much of the year, and it is here that many of the ecosystem effects of high bison numbers are readily apparent.

(Photo – RL Beschta)

Willows again on the Wane

Willows had been growing taller in many portions of the northern range, but with greater numbers of bison in recent years, many have been altered by bison. Bison often break branches with their teeth and browse the lower portion of a plant, up to ~1 m (3.3 ft) above the ground. The result, as shown here, is a mushroom-shaped willow.

With continued stem breakage, an entire plant or willow stand can be removed by bison. This willow grew tall in the early 2000s but has since been broken down by bison.

(Photos – LE Painter)

Quaking Aspen in Trouble

Stands of quaking aspen have existed for many thousands of years across northern Yellowstone and they normally support a diverse understory community of shrubs, grasses, and forbs.

(Photo – RL Beschta)

Aspen stands on valley bottoms and adjacent hillsides are often used by bison. These stands generally consist of mature trees and an understory of plants eaten by bison.

The heights of young aspen sprouts here are being suppressed by browsing from bison, continuing the effects of elk that occurred before the return of wolves.

If aspen sprouts are unable to grow taller, overstory aspen trees will eventually die and aspen stands in areas of high bison use will continue to vanish from the northern range.

Disappearing Aspen Saplings

Aspen saplings have become established in many areas over the last two decades due to reduced elk herbivory, thus beginning a recovery of aspen stands following wolf reintroduction. However, for many aspen stands found along valley bottoms, heavy use by bison is now killing many of these previously established saplings.

(Photo – RL Beschta)

This recovering aspen stand is losing its saplings because of bison.

Berry-Producing Shrubs Taking a Beating

Normally, a wide range of wildlife species, including birds, bears, coyotes, and others, use the fruit from berry-producing shrubs. When heavily browsed, their ability to produce berries is limited.

(Photo – WJ Ripple)

During the period when wolves were absent in the northern range, elk herbivory suppressed berry-producing shrubs. However, following the return of wolves, many berry-producing shrubs have begun to grow taller in various portions of the northern range.

An important berry-producing shrub in the northern range is serviceberry, shown in this photo. However, in front of this kneeling person serviceberry plants are only 0.6 m (2 ft) tall and bison browsing continues to suppress their heights.

Stunted Cottonwood Seedlings

High snowmelt flows each spring often establish bands of cottonwood seedlings along the Lamar River alluvium, such as those shown below. These young cottonwoods are several years old, but average only 50 cm (20 in) in height. Their heights remain suppressed due to frequent browsing by bison.

(Photo – RL Beschta)

A survey of young cottonwoods along the Lamar River found their heights seldom exceeded 20 cm (8 in) due to heavy levels of browsing by bison (Beschta & Ripple 2015).

Doomed Seedlings and Cottonwood Groves

In 2001, this Lamar River side channel contained many hundreds of cottonwood seedlings (inside the dashed line). Within a few years, all seedlings were dead, primarily due to bison browsing and trampling. This pattern of seedling establishment, followed by bison-caused mortality, is repeated year-after-year for seedlings of cottonwood, willow, and other woody plants along the Lamar River and its side channels. In the background are mature cottonwoods that are experiencing increased bark damage over time from bison horning and rubbing.

(Photo – RL Beschta)

Cottonwood groves across much of the Lamar Valley consist mainly of old trees, with few young or middle-aged trees. Unless seedlings can again grow tall, mature cottonwoods will continue to diminish over time and not be replaced.

Summer Foraging by Bison

In summer, bison intensively utilize grasslands on floodplains and terraces in the Lamar Valley. By the end of summer herbaceous plants will have been grazed multiple times with stubble heights of 5 cm (2 in), or less, thus leaving little forage for elk when they arrive each winter.

The horizontal rod is ~7.5 cm (3 in) tall and completely visible, since nearly all above-ground plant biomass in this area has been removed by bison. Such high levels of grazing are particularly detrimental to native grass and forb communities.

(Photo – RL Beschta)

Increasing Exotic Plants

Exotic pasture grasses and forbs were grown at Buffalo Ranch during the early 1900s to provide supplemental bison feed in winter. Some of these species have persisted on the valley floor as well as spread across the landscape. For example, Kentucky bluegrass is now the dominant grass species in dry meadows of the Lamar Valley. Another pasture grass, meadow timothy, commonly occurs across many hillslopes, such as the one in the photo below.

(Photo – RL Beschta)

Increased foraging pressure by bison in recent years is likely contributing to the continued spread of exotic grasses and forbs in the northern range. These species have greatly altered the presence and density of native plants in many areas.

Rivers, Streams, Springs, Seeps, and Wetlands in a Land of Bison

With the loss of riparian vegetation due to intensive browsing by bison goes the binding roots and bank protection such vegetation normally provides during high flows. In addition, the wet soils found along rivers, streams, springs, seeps, and wetlands are particularly vulnerable to the trampling effects of bison herds.

Repeated Trampling of Riverbanks

(Photos – RL Beschta)

Normally, dense riparian vegetation would help to protect banks from fluvial erosion as well as provide important habitat for various aquatic, amphibian, and terrestrial wildlife species. Here, repeated foraging and trampling by bison has essentially obliterated riparian vegetation and created exposed banks.

The loss of shrub-sedge communities along the edge of this channel allows for accelerated erosion and bank collapse to occur. Ancient floodplain soils, irreplicable at human time scales, are now being lost as the channel migrates laterally.

Eroding River Channels

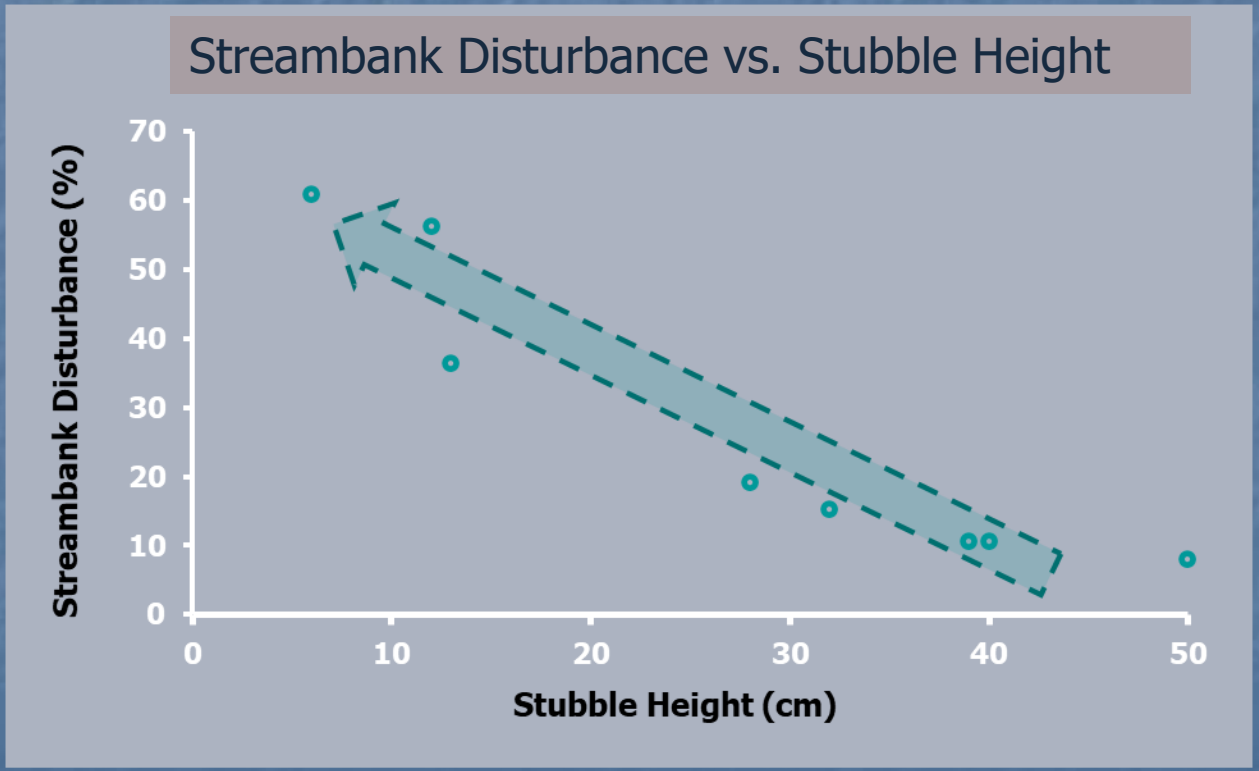
(Photos – top, JB Kauffman; bottom, RL Beschta)

Without willow-shrub communities, riverbanks are more susceptible to accelerated erosion from high flows during springtime snowmelt.

Accelerated bank erosion has led to a widening of the Lamar River channel, resulting in extensive areas of gravel/cobble deposits that are exposed at low flow. Bison herbivory prevents plants from growing on these alluvial deposits and they have become barren areas in what would normally be one of the most biologically productive portions of the Lamar Valley.

Connecting Foraging Intensity to Streambank Disturbance

Stubble height represents the general height of grasses after the summer grazing season. Here, low stubble heights that result from intensive grazing indicate nearby streambanks have more disturbance from bison.



(Unpublished data for eight northern range streams in late July of 2020, from JB Kauffman)

Desolate Streams

Repeated bison use along this portion of Rose Creek, a tributary to the Lamar River, has denuded it of nearly all riparian vegetation.

In the absence of riparian vegetation, this channel will continue to widen over time. It will also have little capability of providing productive habitat for aquatic and terrestrial wildlife.

(Photo – RL Beschta)

Disrupting Springs and Seeps

The trampling effects of bison are readily apparent in springs and seeps where they degrades water quality, plant communities, and wildlife habitat in general.

The physical churning of soils by the hooves of bison, a process referred to as "post-holing", is particularly destructive to the ecological integrity of spring and seep habitats.

(Photos – top, WJ Ripple; bottom, RL Beschta)

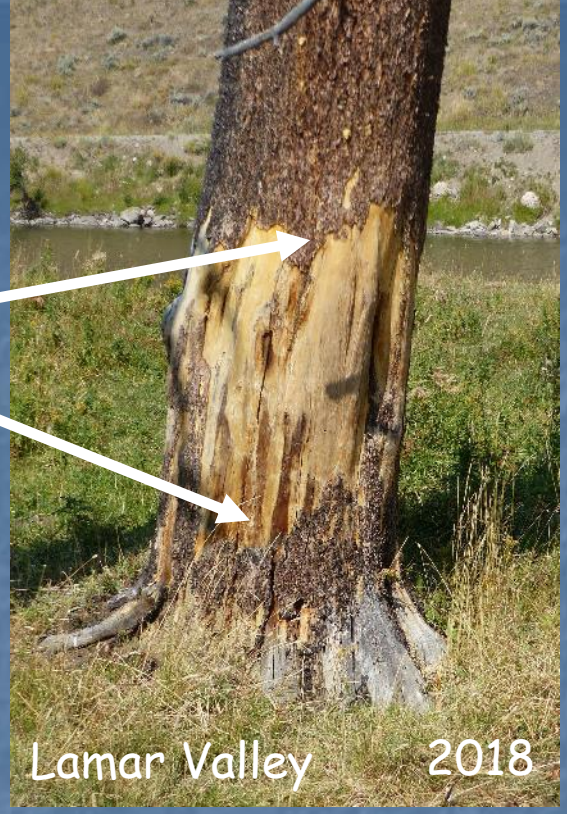
Transforming Wetlands

Trampling and foraging by bison herds among wetlands can significantly impact the habitats used by amphibians, nesting birds, and other wildlife.

(Photos – RL Beschta)

Rupturing Cambium

Bison often scrape their horns and rub their bodies against trees. Horning and rubbing typically occur at a height of approximately 0.4-1.2 m (1.3-4.0 ft) above the ground. For example, lodgepole pine trees are found at several locations along the Lamar River and it has relatively thin bark that allows the underlying cambium to be easily destroyed by bison horning and rubbing.



(Photo – RL Beschta)

Over time, the loss of cambium effectively kills the tree.

Dying Conifers

In the late 1970s, a group of conifer trees had been growing along this reach of the Lamar River for many years.

In 2020, the conifers were dead. All had severe bark loss due to bison horning and rubbing.

(Photos – top, J Schmidt; bottom, RL Beschta)

The Threats of Bison to the Recovery of Yellowstone's Northern Range Ecosystems

Population size - The current bison population is at an historical high. Multiple lines of evidence indicate bison use in the area that eventually became Yellowstone National Park was relatively limited. Even if bison herds entered the park area in summer, it is unlikely they would have overwintered.

Forage Consumption - Bison are larger and heavier than elk, thus the foraging needs of individual bison are appreciably greater than that of elk.

Foraging Patterns - Whereas elk normally use the northern range for winter habitat, bison remain throughout the year, often subjecting plants to multiple episodes of herbivory during a growing season. Such high levels of bison herbivory and trampling can significantly affect the composition, structure, and function of various plant communities.

(Photo – WJ Ripple

The Threats of Bison to the Recovery Yellowstone's Northern Range Ecosystems

[continued]

Woody Plant Communities - The large number of bison in the northern range are now a major contributor to seedling and sprout mortality for many deciduous woody plants.

Physical Disturbance of Soils - Being relatively large and heavy herbivores, the trampling effects of bison (e.g., soil compaction, bank collapse, soil churning at springs and seeps, etc.) are substantially greater than those of elk.

Banks of Streams and Rivers – Where riparian plant communities along streams and rivers have been significantly altered by bison, bank erosion is accelerated.

Seeps, Springs, and Wetlands – Plant communities, soils, and water quality are being degraded by bison herbivory and trampling.

Conifer Mortality - Conifer mortality along the Lamar River has increased in recent years due bison horning and rubbing.

Summary

A trophic cascade involving large predators, elk, and plants has been underway since the mid-1990s, following the return of wolves, with numerous studies showing improvements in woody plant communities.

Bison numbers have rapidly increased in recent years, and their population greatly exceeds historical levels. As a result, in many areas frequented by bison the ongoing recovery of plant communities is increasingly in threat of reversal.

Bison herbivory and trampling effects are most prevalent along valley bottoms and adjacent hillslopes, such as in the Lamar Valley and Little America portions of the northern range. Here, plant communities, soils, river and stream channels, and other ecosystem attributes are being seriously altered.

Unless the herbivory and trampling effects of bison are significantly reduced, many northern range plant communities, seeps, wetlands, rivers and streams are unlikely to recover their ecological potential.

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Science publications associated with wolves, elk, and vegetation in northern Yellowstone, as well as others on trophic cascades and related topics can be accessed at:

http://trophiccascades.forestry.oregonstate.edu/publications

Scientific Names of Plant and Animal Species

Plants

Cottonwoods – *Populus* spp.
Quaking aspen – *Populus tremuloides*
Sagebrush – *Artemesia spp.*
Sedges – *Carex* spp.
Thinleaf alder - *Alnus incana* spp. *tenuifolia*
Willows – *Salix* spp.

Animals

American Bison – *Bison Artemisia*
Bears – *Ursus* spp.
Beaver – *Castor canadensis*
Cougar – *Puma concolor*
Gray wolf – *Canis lupus*
Grizzly bear – *Ursus arctos*
Moose – *Alces incant*
Mule deer - *Odocoileus hemionus*
Rocky Mountain elk – *Cervus canadensis*

Glossary of Selected Terms

Herbivory – The feeding or foraging of animals on living plants; browsing is used in reference to their feeding on woody plants.

Large predator – A predator, or carnivore, is an animal that lives by killing and eating other animals. A "large predator" is one that normally exceeds 15 kg (33 lbs) at maturity.

Plant community – A group of interacting plants sharing a common environment, for example: aspen community, willow community, sagebrush community.

Recruitment – Growth of woody plants above the reach of ungulates. In northern Yellowstone, recruitment is assumed to occur when these plants exceed a height of ~2 m (6.5 ft), the normal upper browse level of elk.

Riparian areas – Lands and associated plant communities immediately adjacent to creeks, streams, and rivers that are influenced by these waters. Plant communities in riparian areas are often diverse and highly productive, thus important as physical habitat and food resources for a wide range of aquatic and terrestrial biota.

Ungulates – Hooved animals, such as elk, deer, moose, and bison.