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

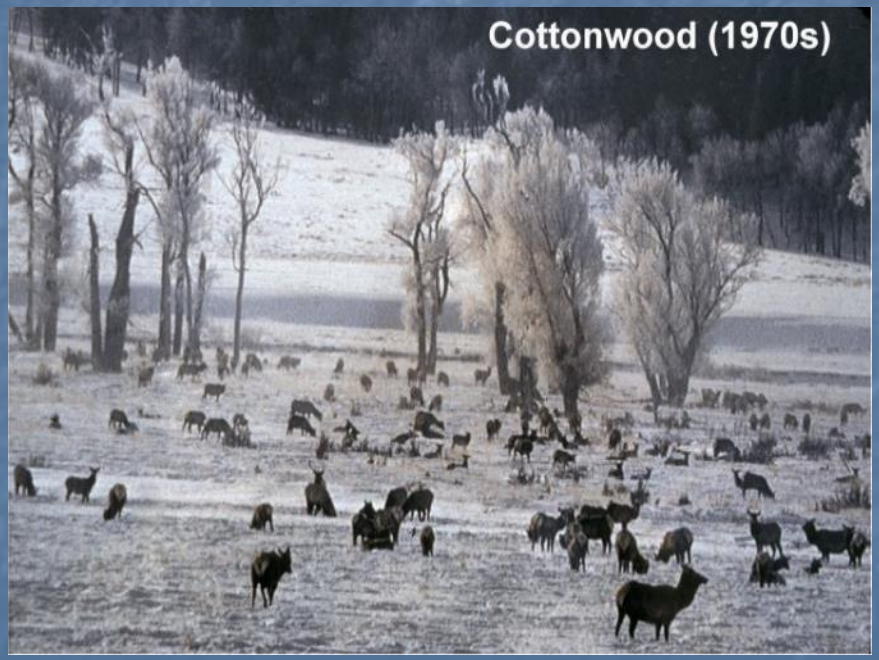
Part 2 - The Return of Wolves

Wolves reintroduced in 1995-96

(Photo – National Park Service)

Elk and Vegetation before Wolf Reintroduction

From the 1930s to the late 1960s, the park service had been culling elk to reduce the high levels of herbivory affecting plant communities. In the absence of wolves, elk can heavily browse plants in winter. Culling ceased in 1968 when elk numbered about 5,000 animals and their numbers rapidly increased. By the early 1990s the northern range population comprised nearly 20,000 elk.



(Photo – National Park Service)

The photo at left shows elk foraging in the Lamar Valley in mid-winter. Some are resting, others are feeding with their heads down, and many have their backs towards the photographer, all indicating a low level of vigilance. Others are browsing on young willow and cottonwood plants, reducing them to short stubs. Thus, prior to wolf reintroduction, young woody plants across the northern range were being suppressed by heavy elk browsing, often being held to an average height of only 50 cm (20 in), or less.

The Return of Wolves

Gray wolves, an apex predator, were reintroduced into Yellowstone in 1995-96, thus completing the park's large predator guild. Elk are the primary prey of wolves, particularly in winter when deep snow and icy conditions can impede their escape. Below, wolves are trying to bring down an elk. Because a wolf pack may not be able to entirely consume a dead elk, these kills often become an important source of food for coyotes, eagles, ravens, and other wildlife.

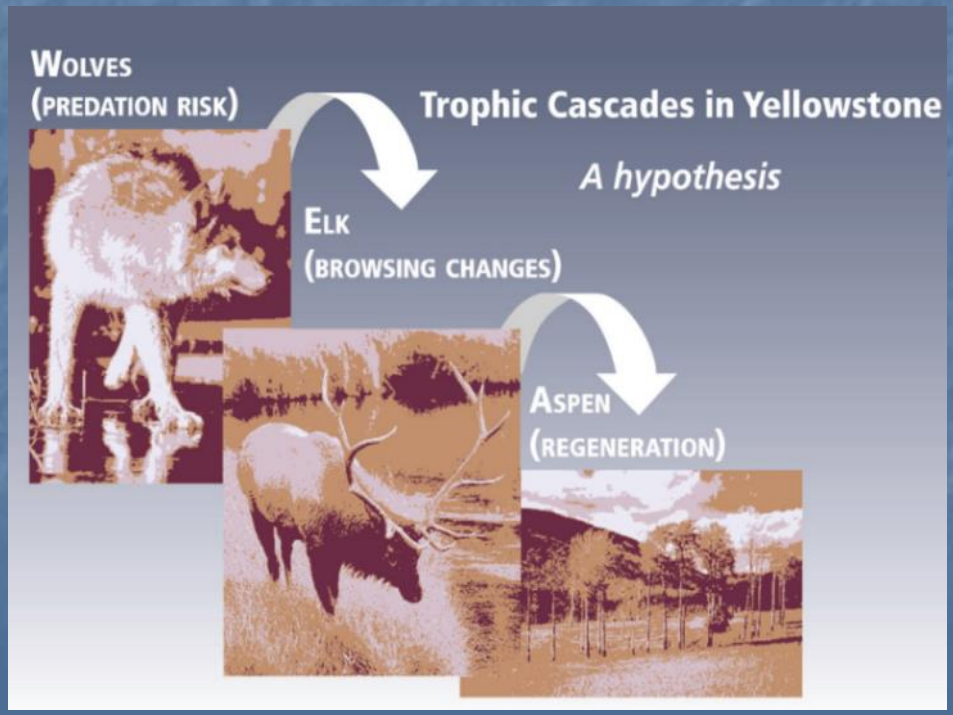
Following the return of wolves, elk behavior (e.g., vigilance, use of habitat) changed and elk numbers began to drop. As a result, young woody plants experienced less herbivory in some portions of the northern range and began growing taller.

(Photo – National Park Service)

A Trophic Cascade Hypothesis

After an absence of approximately seven decades from Yellowstone National Park, the potential ecosystem effects of reintroducing wolves in 1995-1996 were not known.

While there was concern regarding the extent to which this apex predator might affect elk populations, the capability of wolves to affect plant communities, *via* a process known as a trophic cascade, was unanticipated.



Wolves can trigger a trophic cascade by altering the behavior and number of elk sufficiently to reduce browsing levels, thus sustaining plant communities.

In Yellowstone, this trophic cascade involves three trophic levels:

(1) wolves (predators)
(2) elk (consumers)
(3) plants (producers)

Trophic Cascade and Vegetation

If a trophic cascade was occurring following the return of wolves, would it allow young woody plants in the northern range that had been suppressed by elk browsing for decades to again begin to grow taller? Species such as:

Willow

Aspen

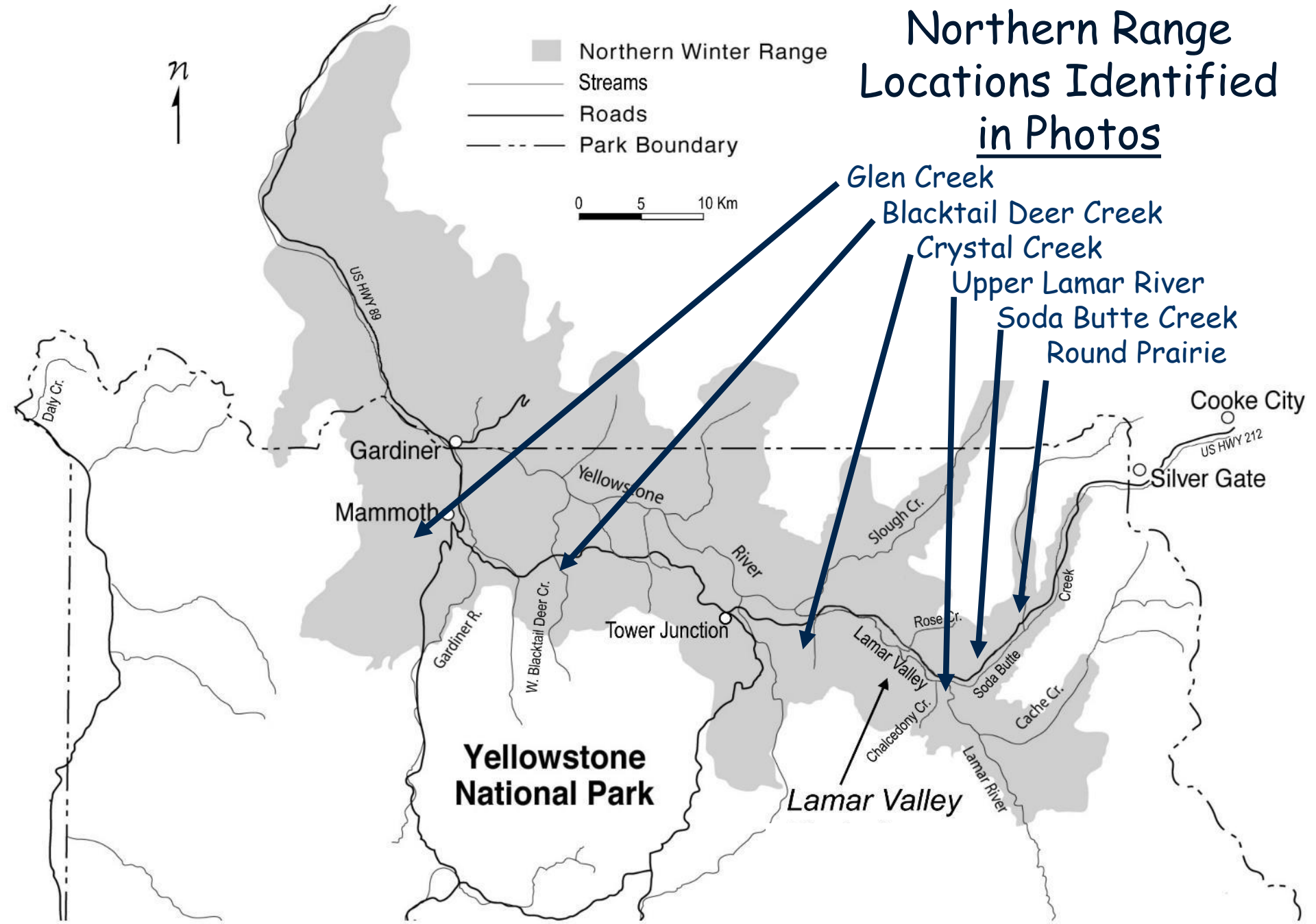
Cottonwood

Thinleaf Alder

Berry-producing Shrubs

Repeat Photographs

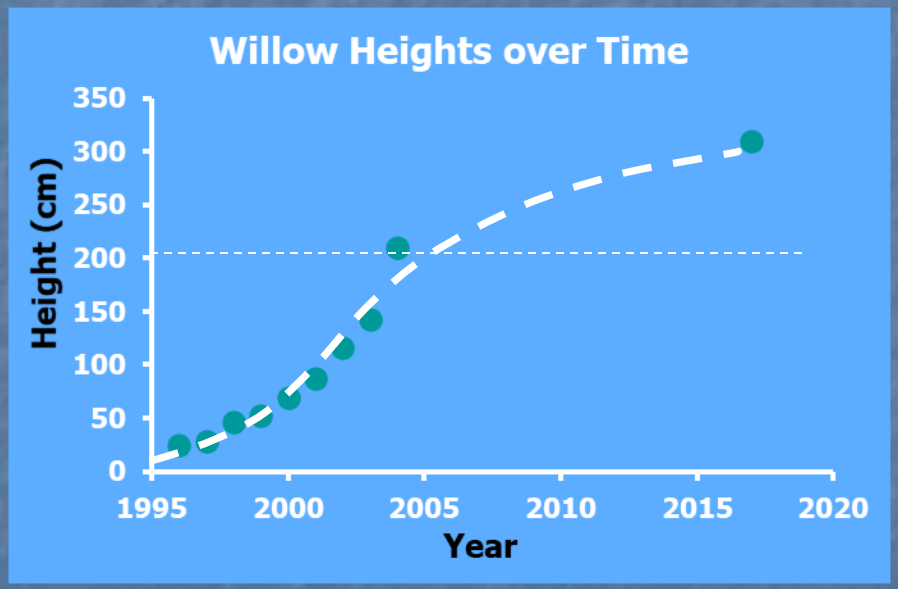
The following photographs illustrate some of the changes in vegetation that has begun to occur in portions of Yellowstone's northern range after wolf reintroduction.


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

Increasing Willow Heights

Blacktail Deer Creek

Willows are multi-stemmed woody plants that can quickly begin to grow taller if browsing is reduced, as happened along Blacktail Deer Creek. In 1996, willows along the stream had an average height of less than 50 cm (20 in). However, within a decade of wolf reintroduction, streamside willows had attained an average height of 200 cm (80 in), the normal upper browse level of elk, and they have since continued to increase in height.



(Graph - Beschta and Ripple 2019; photos – RL Beschta)

Recovering Floodplain Willows

Soda Butte Creek

In 1997, wolves had been back in the park for only two years. Even though there were young willows present across this floodplain in 1997, they were very short and not visually evident in the tall grass because they were browsed nearly to the ground each year by wintering elk.

By 2001, willows were increasing in height, a recovery that continued through 2013.

(Photos – top, National Park Service; middle, WJ Ripple; bottom, RL Beschta)

Willow Degradation and Recovery

Round Prairie

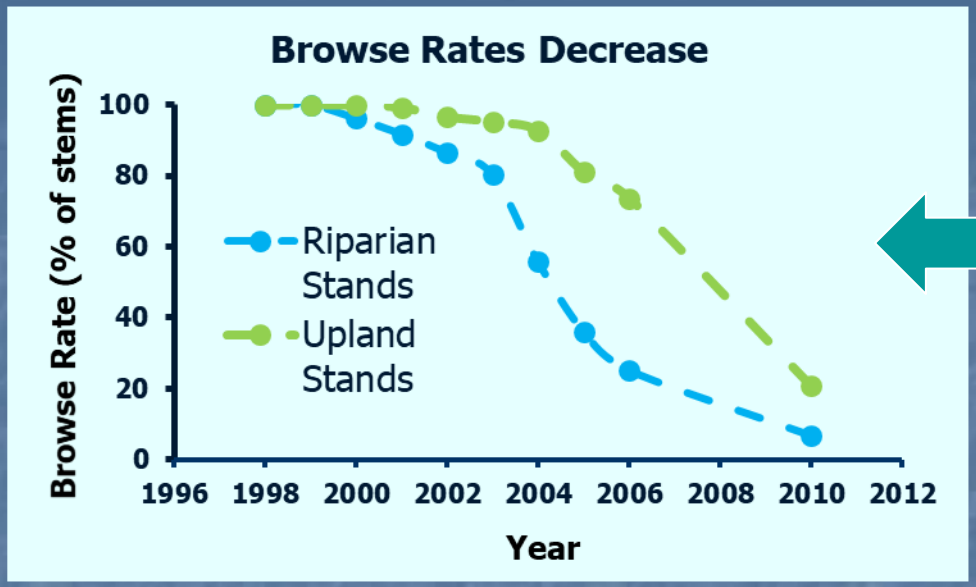
1943 - Willows were common across this meadow but beginning to show the effects of heavy elk browsing.

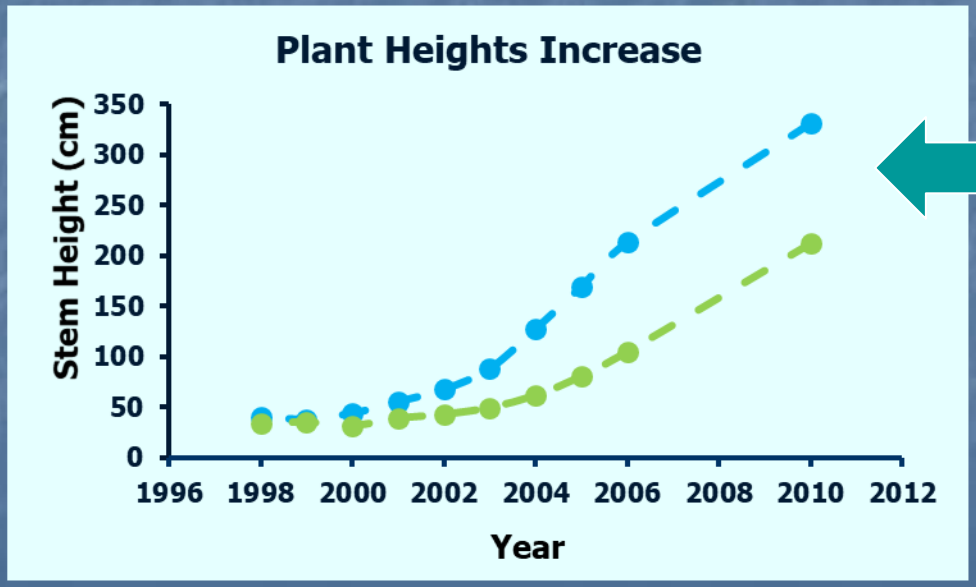
1988 – Willows have been almost completely removed due to high levels of elk browsing over many years. The few that remain are suppressed by elk browsing.

2020 – 25 years after the return of wolves, a dense stand of tall willows has re-established in this meadow.

(Photos – top, National Park Service; middle, CE Kay; bottom, RL Beschta)

Quaking Aspen: Less Browsing and Greater Heights





(Adapted from: Ripple & Beschta 2012)

Although wolves were reintroduced in 1995-1996, it wasn't until about 2004, when wolf numbers had become relatively high, that browsing rates of young aspen in portions of the northern range began to significantly decrease.

As browsing rates declined, young aspen were again able to grow taller, this effect being most pronounced in riparian stands.

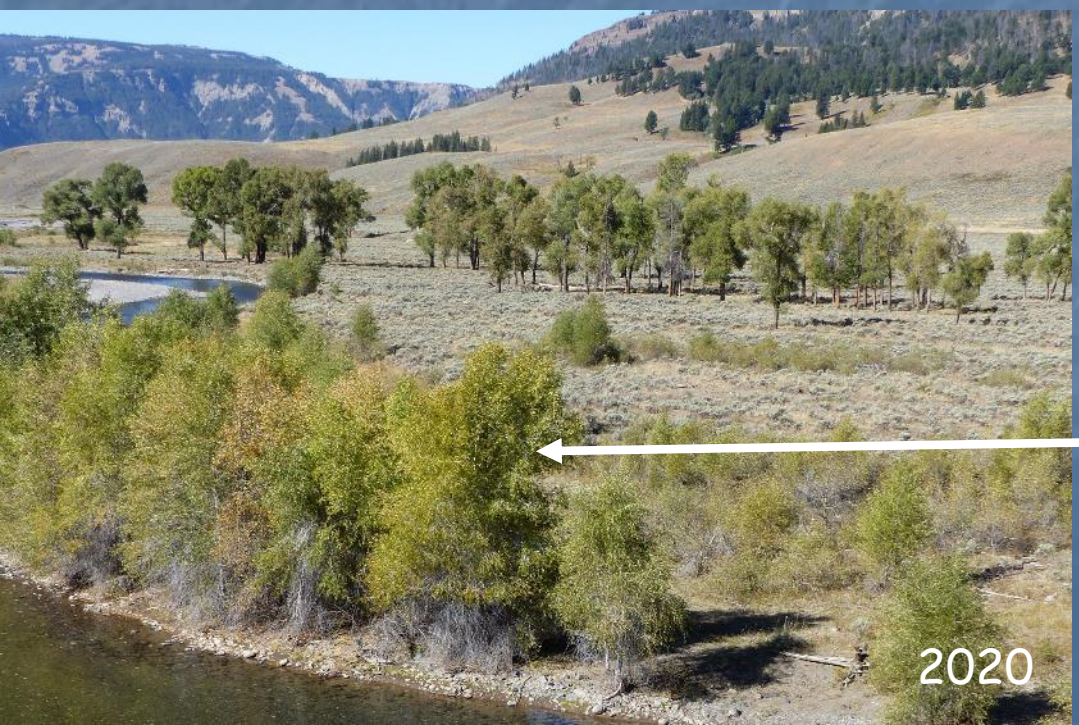
Because riparian and upland aspen stands were near each other, the more rapid decrease in browsing (and concurrent increase in plant heights) indicated that elk may have become more cautious in riparian areas, perhaps in response to the landscape of fear associated with wolves and other large predators.

Releasing Aspen

Once elk browsing began to decrease, increased heights of young aspen in northern range aspen stans have become more widespread.

(Photos – RL Beschta)

Taller Cottonwoods
Soda Butte Creek



In the background is a stand of overstory cottonwoods that had become established well over a century ago, a period when Yellowstone had a complete large carnivore guild.

Young cottonwoods were common along this gravel bar but all were less than 50 cm (20 in) in height due to persistent elk herbivory.

After wolves returned, browsing subsequently decreased and young cottonwoods along the streambank grew taller. By 2020, many of them exceeded 4 m (13 ft) in height.

(Photos – top, RB Keigley; bottom, RL Beschta)

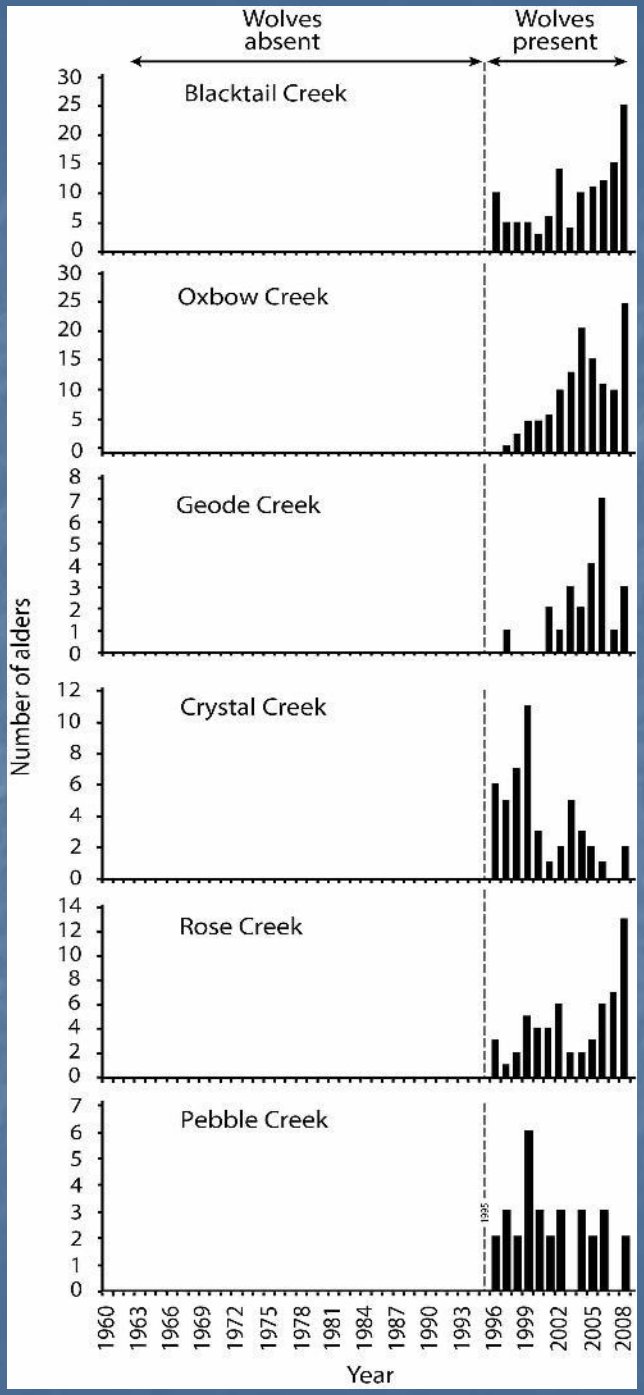
More Cottonwoods

Upper Lamar River

In the spring of 2001, the Lamar River changed course and abandoned this section of channel, leaving many thousands of cottonwood seedlings growing on the exposed gravels (dashed line) at the base of an 8 m (26 ft) high terrace.

Elk herbivory in this portion of the northern range has been light in recent years and by 2020 the tops of these young cottonwoods were nearly as tall as the surface of the terrace. With continued growth, these cottonwoods will develop into a gallery forest.

(Photos – RL Beschta)



Thinleaf Alder again Growing Tall

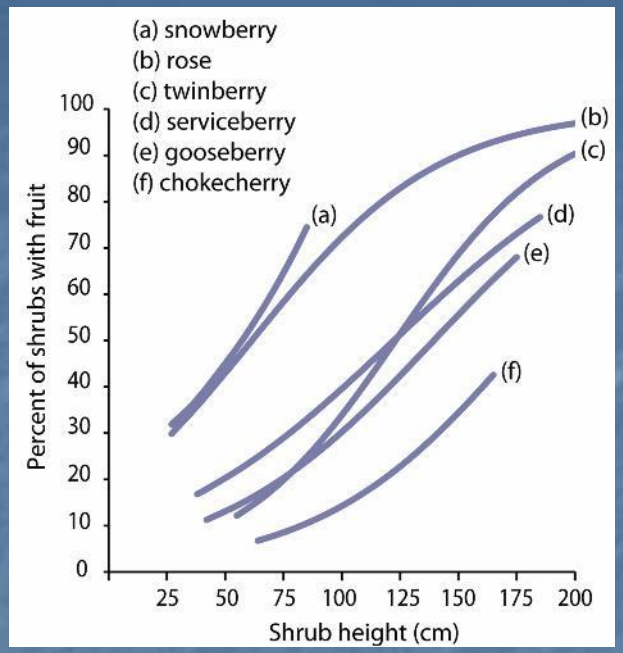
Blacktail Deer Creek

Thinleaf alder is a small tree or tall shrub, up to ~12 m (40 ft) in height, that is common in riparian areas along northern range streams. Even though it is of low palatability to ungulates, unusually high levels of elk herbivory in the 1960s-1980s prevented young alder from growing taller (see graph). Almost immediately after wolf reintroduction, however, young alders along various northern range streams were again able to grow taller, providing perhaps the clearest plant response to the return of wolves.

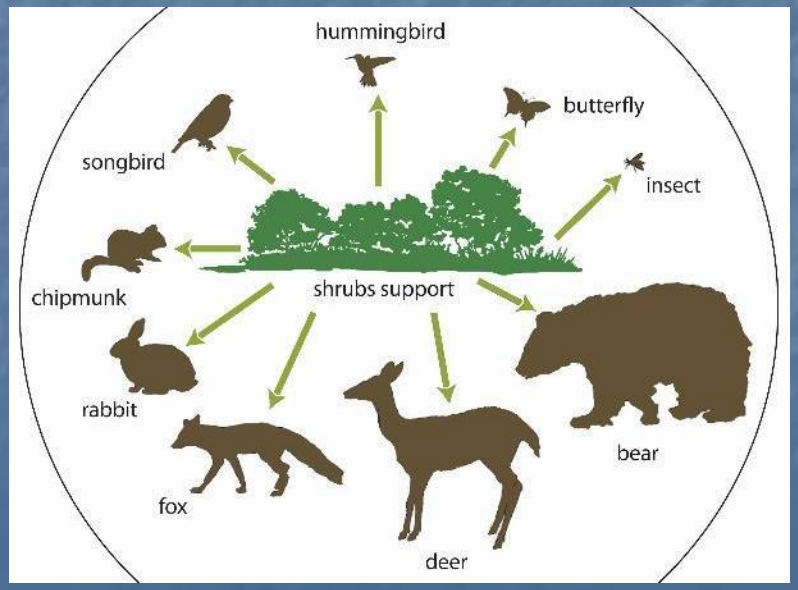
Thinleaf alder releasing along Blacktail Deer Creek.

(Graph – Ripple et al. 2015; photo - WJ Ripple)

More Shrubs with Berries



As young aspen were beginning to increase in height following the return of wolves, berry-producing shrub also were growing taller within aspen stands. With greater shrub heights, the percentage of plants with fruit (i.e., berries) increased, indicating that its availability to birds, bears, and other wildlife was beginning to expand in the northern range.



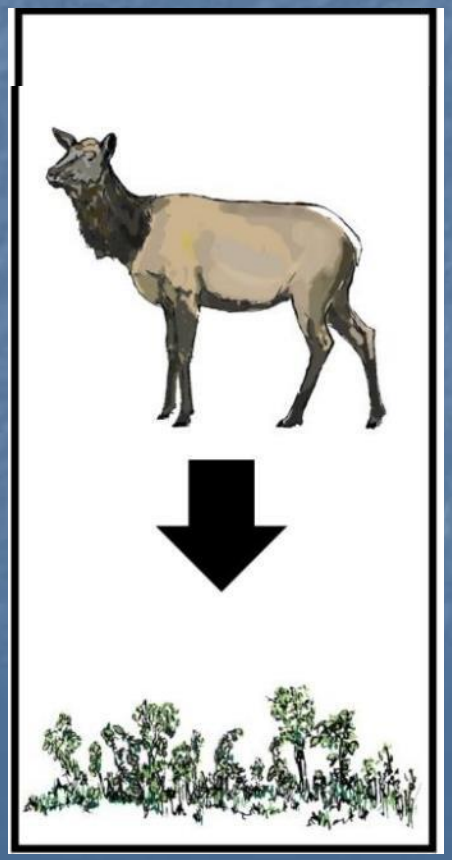
Berry-producing shrubs are an important component of many western ecosystems since the flowers and fruit they produce each year often play a crucial role in supporting an array of avian and terrestrial wildlife species.

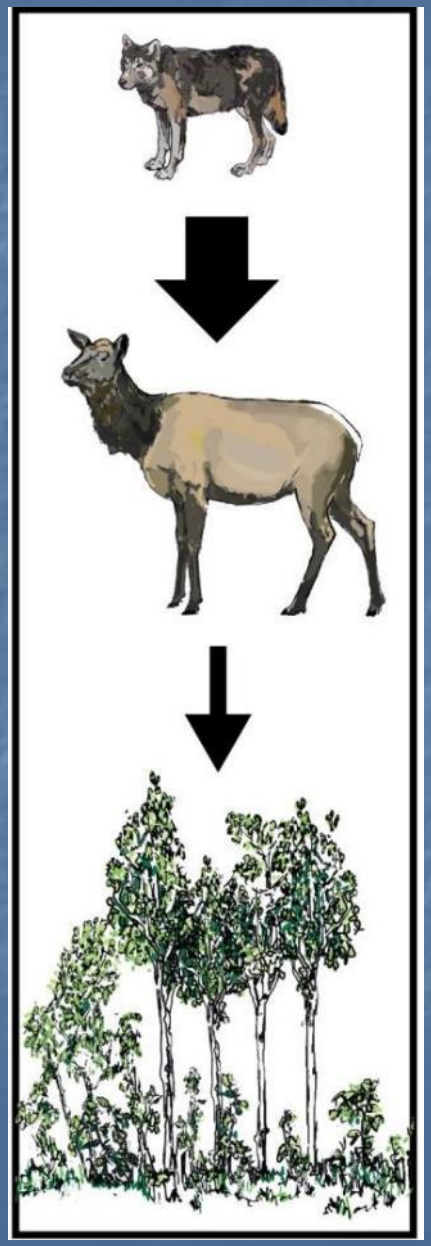
(Graphs - Beschta & Ripple 2012)

Recovering Plant Communities with Wolves

Yellowstone without Wolves

Unimpeded elk browsing prevented woody plants from growing taller.





Yellowstone with Wolves

Wolves affect elk behavior and numbers.

Elk browsing is reduced.

Young woody plants begin to grow taller and recover, a trophic cascade.

(Figures - Beschta & Ripple 2012)

Recovering Vegetation in the Northern Range: Alternative Hypotheses

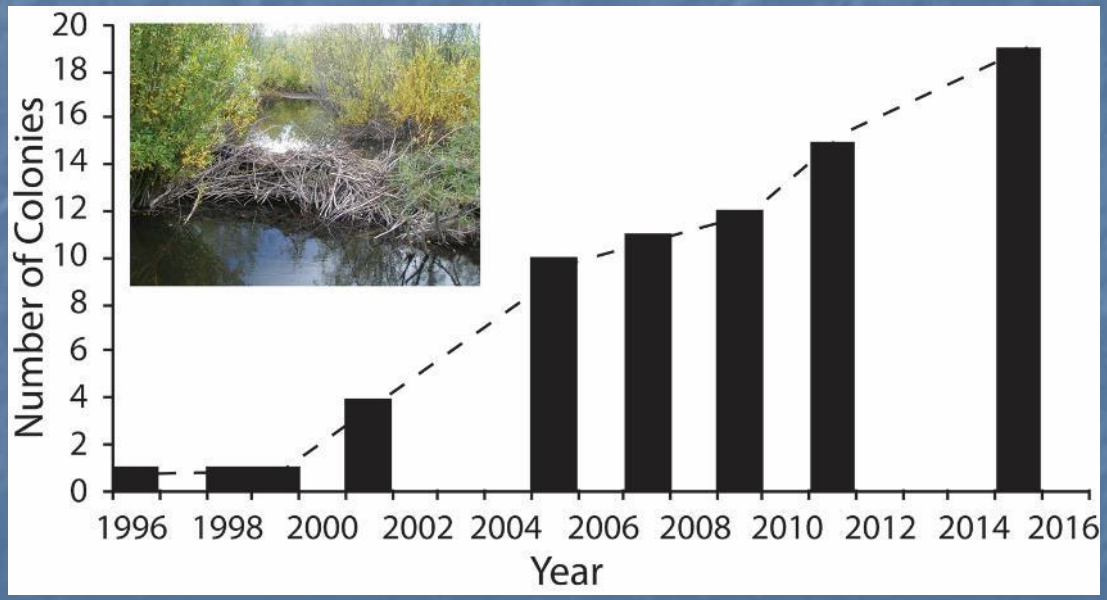
Additional explanations for the recent growth of woody plants in Yellowstone's northern range might include such factors as long-term climate change, years with abnormally large precipitation or snowmelt, the uneven history of fire control in the park, or natural variations in the pattern of plant regeneration and growth.

While some of these factors may influence the rate of vegetation recovery that is occurring, numerous studies found that young woody plants only began to increase in height once elk browsing declined, consistent with the effects of a trophic cascade following wolf reintroduction, a reintroduction that completed the park's large carnivore guild.

With reduced elk herbivory, a wide range of plant species can again establish, grow, and reach reproductive maturity, thus helping to recovery the composition, structure, and function of northern range plant communities.

Returning Beaver

Established beaver colonies have been largely absent from the northern range for nearly half a century. However, with improving riparian plant communities, beaver colonies are beginning to increase. The number of colonies is still low, and nowhere near the many hundreds of colonies, or more, that likely existed across the northern range in the early 1900s. However, their increasing presence confirms the ongoing recovery of plant communities.



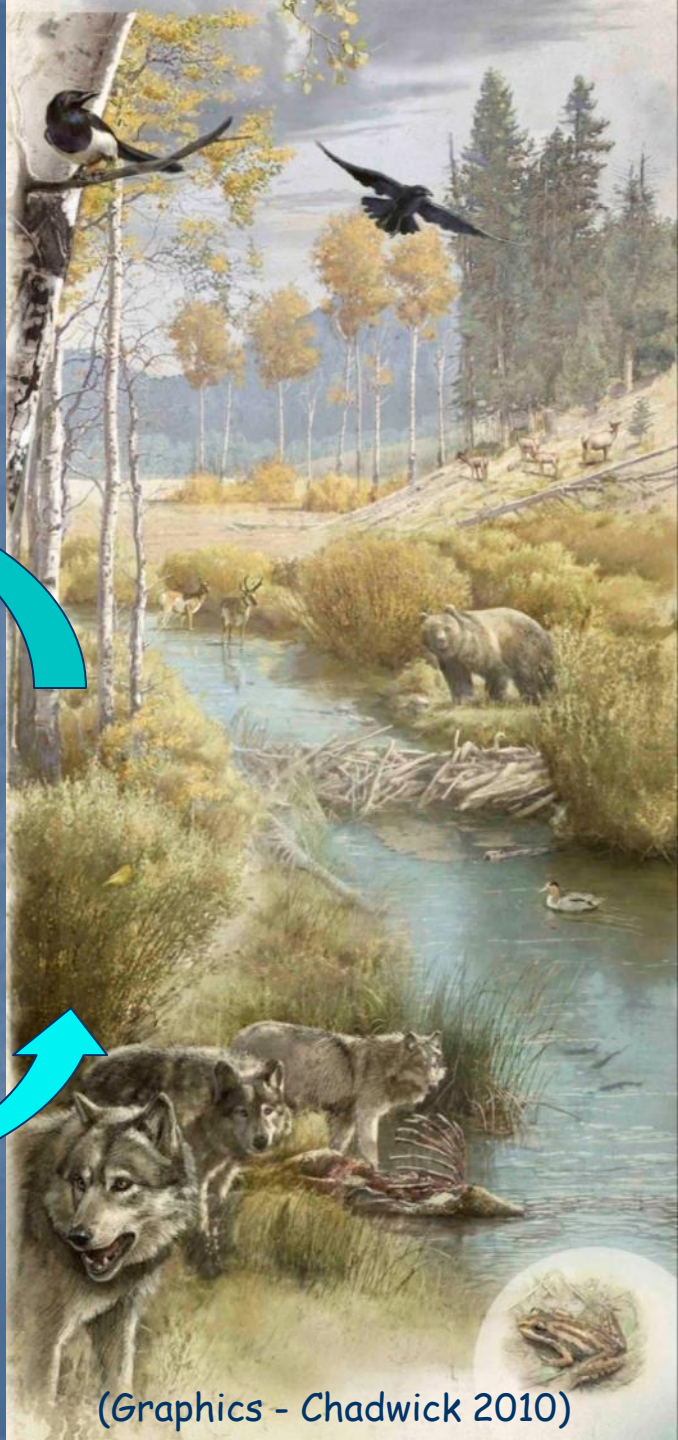
Beaver, as ecosystem engineers, dam streams and spread water onto floodplains. Doing so increases the diversity of plant species in riparian areas, thereby improving habitat for numerous aquatic and terrestrial wildlife species.

(Graph – Beschta & Ripple 2016)

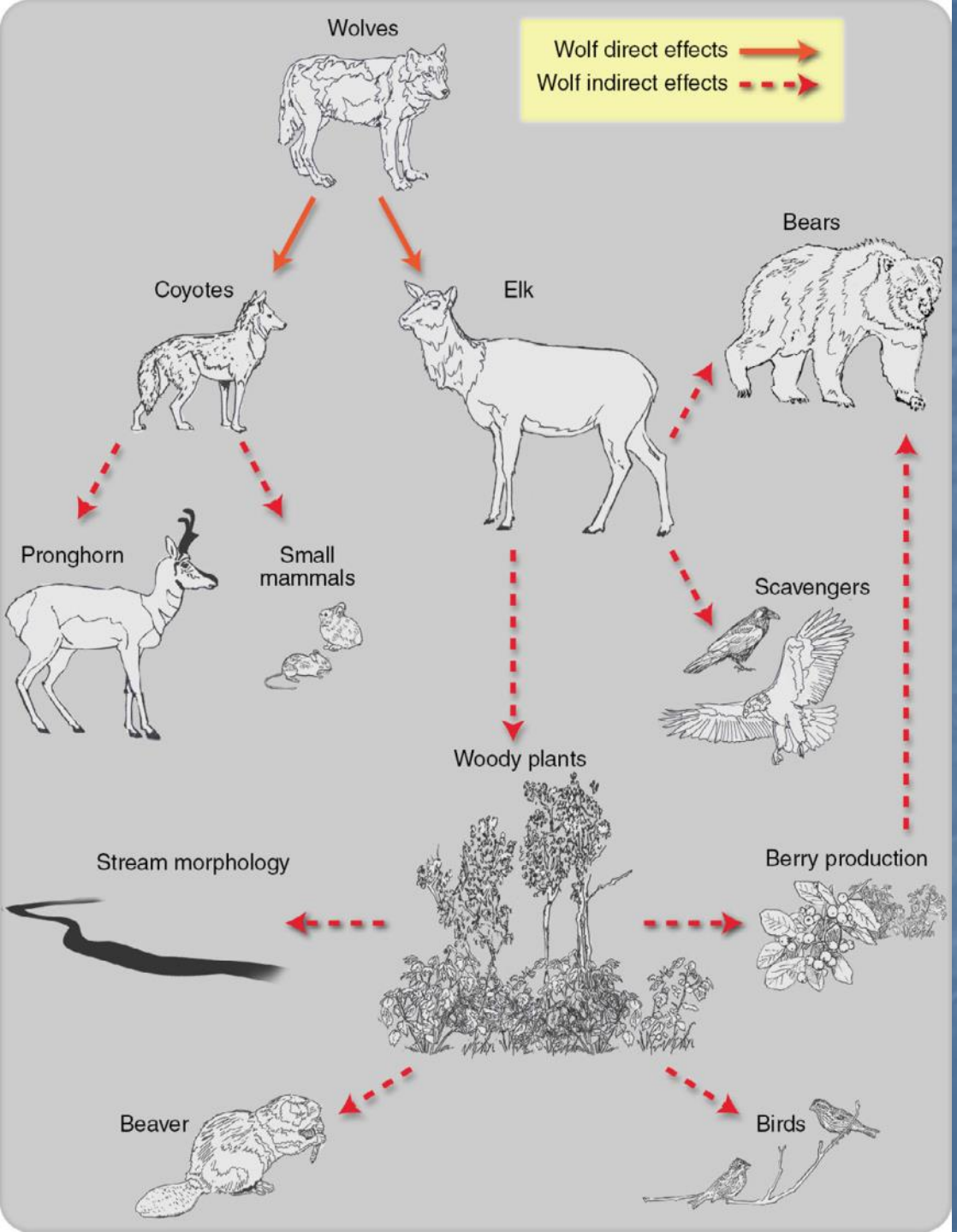
Yellowstone's Riparian Areas

Without wolves, a simplified ecosystem.

With wolves, and other large predators, an ecosystem with higher biodiversity and functionality.



(Graphics - Chadwick 2010)



A Trophic Cascade is more than Wolves, Elk, and Plants

Some of the various direct and indirect effects of a re-established gray wolf population in Yellowstone.

Many of these effects extend beyond elk and plants.

(Graphic - Ripple et al., 2014)

Summary

- Wolves - The 1995-96 return of wolves to Yellowstone completed the park's large carnivore guild.
- Elk – Elk behavior changed, and their numbers declined after 1995-96, with both wolf and elk numbers stabilizing in recent years.
- Browsing – Following the return of wolves, decreased elk browsing began to occur in various portions of the northern range.
- Plants - Because the heights of young woody plants species such as willow, cottonwood, aspen, thinleaf alder, and others had been suppressed by intensive elk browsing when wolves were absent, the recent increases in heights represent a beginning of recovery.
- Trophic Cascade – The behavioral and density changes that occurred with elk after wolf reintroduction, changes that were followed by reduced browsing and increased plant heights, are consistent with a three-level trophic cascade involving: (1) large mammalian carnivores, (2) ungulate prey, and (3) plant communities.

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Cited Literature

Beschta RL, & Ripple WJ. 2012. Berry-producing shrub characteristics following wolf reintroduction in Yellowstone National Park. Forest Ecology and Management 276: 132-138.

Beschta RL, & Ripple WJ. 2016. **Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction**. Biological Conservation 198: 93-103.

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Chadwick DH. 2010. Wolf wars. National Geographic 217: 34-55.

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Ripple WJ, Beschta RL, & Painter LE. 2015. Trophic cascades from wolves to alders in Yellowstone. Forest Ecology and Management 354: 254-260.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC. Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, et al. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science 343(6167).

Related Literature

Beschta RL, Painter LE, Levi T, & Ripple WJ. 2016. Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone National Park. Canadian Journal of Forest Research 46: 548-556.

Beschta RL, Painter LE, & Ripple WJ. 2018. Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. Forest Ecology and Management 413: 62-69.

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Painter LE, Beschta RL, Larsen EJ, & Ripple WJ. 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. Ecosphere 9: e02376.

Ripple WJ, Beschta RL, & Painter LE. 2015. Trophic cascades from wolves to alders in Yellowstone. Forest Ecology and Management 354: 254-260.

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

Chokecherry – *Prunus virginiana*
Cottonwoods – *Populus* spp.
Gooseberries – *Ribes* spp.
Quaking aspen – *Populus tremuloides*
Rose – *Rosa* spp.
Sagebrush – *Artemesia* spp.
Sedges – *Carex* spp.
Serviceberry – *Amelanchier alnifolia*
Snowberry – *Symphoricarpos* spp.
Thinleaf alder - *Alnus incana* spp. *tenuifolia*
Twinberry – *Lonicera involucrata*
Willows – *Salix* spp.

Animals

Bears – *Ursus* spp.
Beaver – *Castor canadensis*
Cougar – *Puma concolor*
Gray wolf – *Canis lupus*
Grizzly bear – *Ursus arctos*
Moose – *Alces Keighley*
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 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.