SRM Society for Range Management

The Condition and Trend of Aspen, Willows, and Associated Species on the Northern Yellowstone Range

By Charles E. Kay

On the Ground

- Aspen, willows, cottonwoods and other deciduous shrubs and trees play a pivotal role in the natural ecosystem function of the Northern Range, and they provide critical habitat for numerous species of native plants and animals.
- Deciduous shrubs and trees were much more abundant on the Northern Range in primeval times than they are today, especially on the portion of the Northern Range inside Yellowstone National Park.
- The primary cause of the declines in deciduous shrubs and trees is repeated heavy browsing by elk and bison–not normal plant succession or climatic changes - and heavy browsing is continuing to further degrade most Northern Range aspen, willow, and cottonwood plant communities inside Yellowstone National Park.
- Excessive browsing is occurring because modern-day management has allowed bison and elk populations to become unnaturally large.
- Current policy directs the National Park Service to intervene with active management where primeval and present conditions differ because of human actions.

Keywords: Yellowstone, Northern Range, aspen, willow, cottonwood, riparian.

Rangelands 40(6):202–211
doi 10.1016/j.rala.2018.10.005

Introduction

Aspen (*Populus tremuloides*), willows (*Salix* spp.), and other deciduous shrubs and trees occupied a relatively small portion of the primeval Northern Yellowstone Range (hereafter referred to as the Northern Range[1]). However, these plant communities provided critical habitat for diverse flora and fauna. Consequently, aspen, willows, and cottonwoods were vitally important for biodiversity across the landscape, and these plant communities played a pivotal role in how the primeval ecosystem functioned sustainably since the last Ice Age.

More than half of the Northern Range (60%) is within Yellowstone National Park (YNP).[2] On the portion of the Northern Range inside YNP, the National Park Service (NPS) is required to preserve the primeval abundances of plants and animals and their habitats so that natural ecological processes can function sustainably.[3p42–44] In 1998 the US Congress directed the National Research Council (NRC) to review the impacts of ungulate grazing and browsing on the ecological health of the Northern Range inside YNP. Four years later the NRC concluded that Northern Range aspen, willows, and cottonwood trees (*Populus* spp.) had declined inside YNP primarily owing to repeated elk browsing.[4p122&129&133] However, the NRC review committee was hopeful that predation by wolves (reintroduced to the Northern Range in 1995–1996) would increase, regulate ungulate populations, and enable aspen, willows, and cottonwoods to recover.[4p8&126–127]

In this paper, I compare the primeval and present abundances of aspen, willows, cottonwoods, and their associated fauna. Next, I examine the relative impacts of climate, fire suppression, and ungulate browsing on the current status of these plant communities. I also examine whether aspen, willows, and cottonwoods are recovering or continuing to degrade under current management. I conclude by examining whether current management needs modification to enable the restoration of deciduous shrubs and trees on the Northern Range.

Deciduous Shrubs and Trees of the Northern Range

Aspen occurred historically in small, scattered stands across the Northern Range with understory grass-forb-shrub

production and canopy cover typically greater than adjacent grasslands or forests.[5,6] Aspen is a clonal species that reproduces primarily by suckers (i.e., vegetative shoots that sprout from a common root system). The frequent, low-intensity fires that historically occurred on the Northern Range, many of them ignited by Native Americans, likely stimulated aspen reproduction.[1,7,8] Aspen clones are thought to be thousands of years old and potentially can be quite large, with single clones containing thousands of stems (ramets). In fact, the largest living organism on Earth, by weight, is an aspen clone named Pando in southern Utah that covers 106 acres, contains an estimated 50,000 trees, and weighs 5,000 tons. As such, aspen clones are old growth—ancient forest that is difficult to replace if they die owing to heavy browsing or other factors.[9]

Northern Range willows historically occurred along streams, ponds, lakes, seeps, and springs. With few exceptions, willow communities did not transition through time to grasslands or forest unless the site's hydrology changed.[5,6] Primary willow species on the Northern Range include Bebb willow (*Salix bebbiana*), Booth's willow (*Salix boothii*), yellow willow (*Salix lutea*), and Geyer willow (*Salix geyeriana*). Primeval willow understories were dominated by sedges (*Carex* spp.) and tufted hairgrass (*Deschampsia caespitosa*). Northern Range willows readily reproduce from seed on suitable habitat. However, repeated browsing that limits willow seed production impedes willow recruitment because willow seeds are short-lived and not stored in soil seed banks.[10,11]

In addition to aspen and willows, other common deciduous trees and shrubs on the Northern Range include narrowleaf cottonwood (*Populus angustifolia*), black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), water birch (*Betula occidentalis*), resin birch (*Betula glandulosa*), thinleaf alder (*Alnus incana* ssp. *tenuifolia*), Saskatoon serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*).[5,6] These trees and shrubs were commonly observed along Northern Range streams as recently as the mid-1950s.[12] They remain abundant on the Northern Range outside YNP,[13 p50–51] but their presence is rare inside YNP today.[14]

Aspen, willows, cottonwoods, and other deciduous shrubs and trees are eagerly eaten by elk and other herbivores, especially during winter when grasses are covered by snow.[15,16] Elk, mule deer, and increasingly bison consume sprouts of shrubs and trees, whereas elk and moose commonly consume all the lower foliage of deciduous shrubs and trees as high as the animals can reach. In addition, elk and moose readily strip and eat aspen bark, which exposes aspen trees to insect damage and disease.[17 p255]

Deciduous Shrubs and Trees 1870 to 2002

Aspen, willows, and other deciduous shrubs and trees were abundant on suitable habitat of the Northern Range from the 1870s through the mid-1920s.[1,14,18,19] However, heavy browsing of these trees and shrubs began about 1915.[20] NPS biologists and others documented that heavy browsing of aspen, willows, and cottonwoods, primarily by elk, continued through the end of the 20th century.[21–28] For example, in 1988 to 1990, willow height and productivity were either moderately or severely suppressed by elk browsing on 21 of 42 Northern Range sites sampled inside YNP.[26] By 1992 inside YNP, 80%, 86%, and 100% of riparian willow plants were browsed heavily along Slough Creek, the Lamar River, and Soda Butte Creek, respectively.[25] In 1994, narrowleaf cottonwood was heavily browsed by elk along Soda Butte Creek inside YNP,[27] and elk intensely browsed Northern Range aspen from 1987 to 1998 on the Dome Mountain Wildlife Management Area, 25 miles north of YNP.[28] Outside a high-fenced exclosure in the Lamar Valley, heavy elk browsing caused the density of serviceberry shrubs to decline 30% from 1958 to 1967,[17 p279] and at the same location in the late 1980s, I documented that serviceberry and chokecherry shrubs were height-suppressed and produced virtually no berries because of repeated browsing by elk and other ungulates.[29]

I used repeat photography to document changes in aspen and willow abundance inside YNP on the Northern Range.[18,19] In 1986 to 1988, I rephotographed 81 early images of aspen and 44 early images of willows. Both aspen (Fig. 1) and willows (Fig. 2) declined in abundance by more than 95% from the 1870s to the late 1980s. The next task was to determine whether the decline in aspen and willows was due to repeated heavy browsing or some other cause, such as climatic changes or fire suppression as hypothesized by others.[1,26,30]

Climate vs. Browsing Impacts

To examine the influence of climate versus browsing, I compared aspen and willow abundance inside and outside high-fenced exclosures that were constructed in 1957 and 1962 on the Northern Range inside YNP. In 1986 to 1989, I sampled all six aspen-containing exclosures and all four willow-containing exclosures. If aspen or willows were declining because of climatic changes rather than ungulate browsing impacts, then aspen and willows should have been declining inside the high-fenced areas.

Inside the willow exclosures, willows that had been short statured and repeatedly browsed when the exclosures were constructed had significantly increased in height and canopy cover (Fig. 3A). In no instance had willow abundance declined inside the protected areas,[18,19] therefore the decline of willows outside the exclosures was not due to climatic changes. Also, willow seed production was completely eliminated by browsing outside the exclosures, whereas seed production was robust inside the exclosures.[31]

Within the aspen exclosures, aspen suckers that had been repeatedly browsed when the exclosures were built 25 to 30 years earlier had developed into tall, mature aspen trees (Fig. 3B),[18,19,32] therefore the decline of aspen outside the exclosures was not due to climatic changes. There also were major differences in understory species composition. Protected understories inside the exclosures were dominated by native shrubs and tall forbs in 1986 to 1989.[18,19] In contrast,

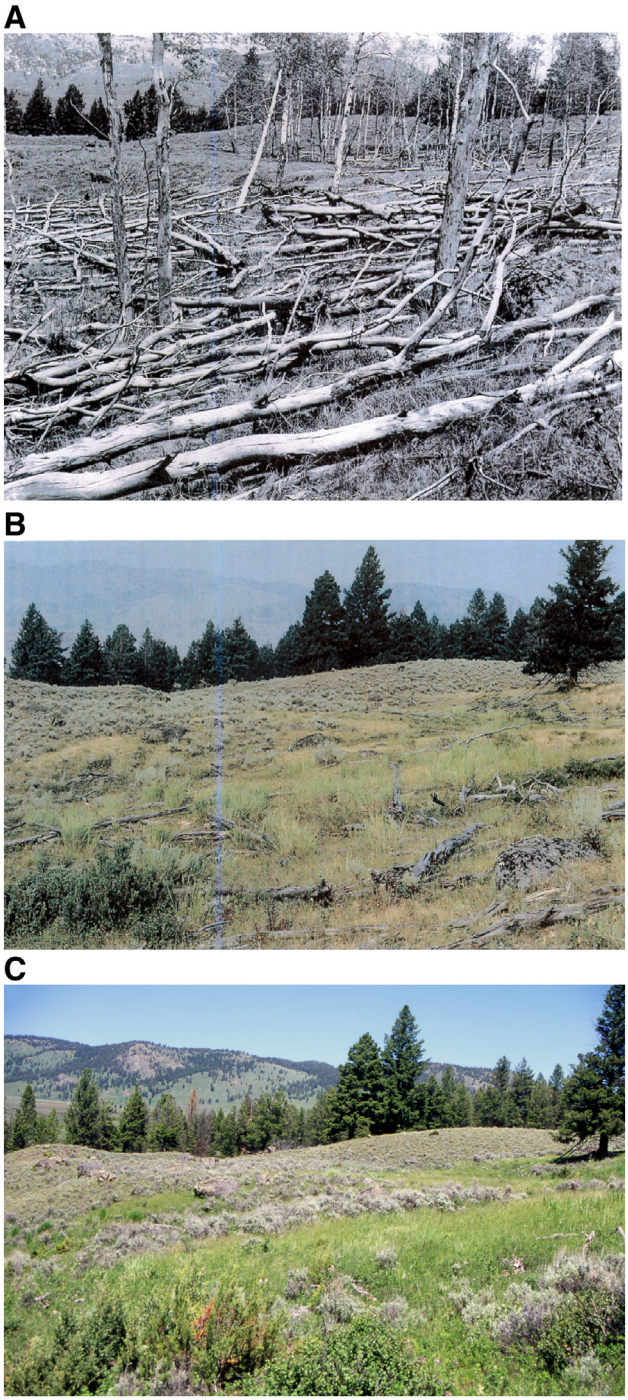

Figure 1. National Park Service biologist Walter Kittams established 20 aspen monitoring plots on the Northern Range inside Yellowstone National Park during the 1950s. **A,** As can be seen in this 1952 image (Plot 11a), repeated elk browsing was having a severe, negative impact on aspen (photographed by Walter Kittams on 23 May 1952). **B,** By 1988, aspen was eliminated (photographed by Charles Kay on 5 August 1988). **C,** Aspen showed no signs of recovery in 2015 (photographed by Charles Kay on 13 June 2015).

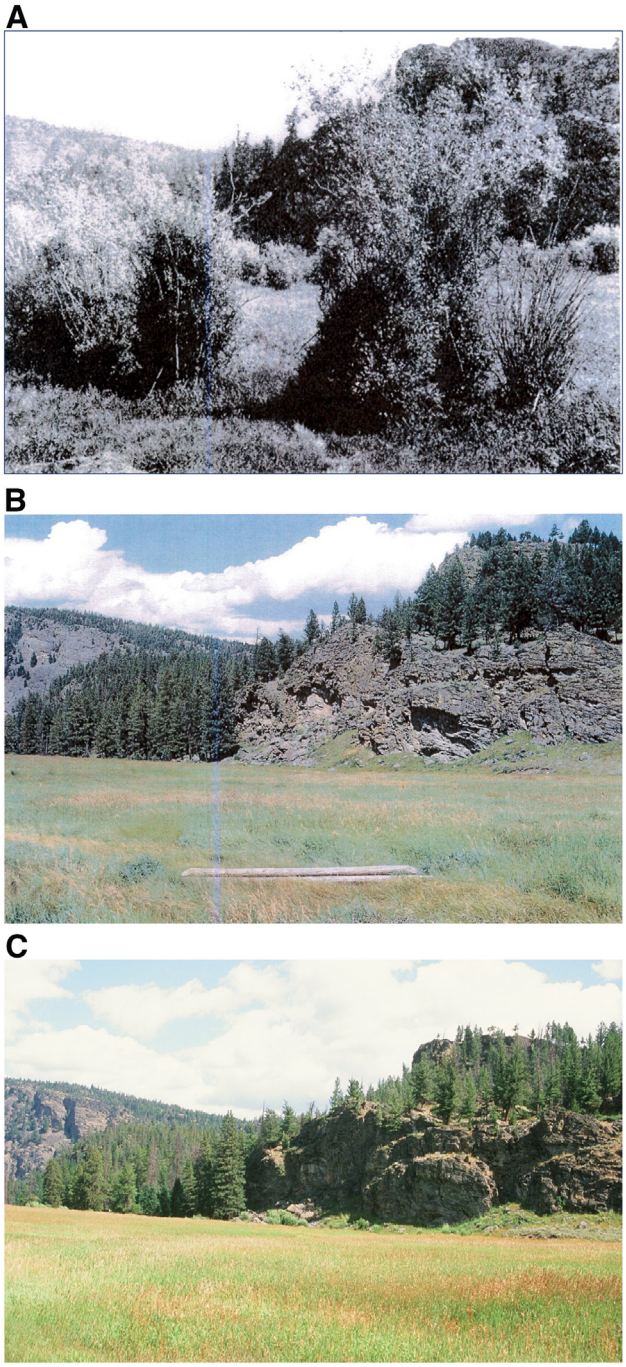

Figure 2. A, Willows showed the early effects of repeated elk browsing in 1915. The plant on the far right had been killed by elk use, whereas the plant to its left had been browsed heavily by elk, as noted in the original photo caption and text.[18p57] **B,** By 1987, willows were eliminated from the site (photographed by Charles Kay on 11 August 1987). **C,** Willows showed no signs of recovery in 2014 despite significant decreases in elk numbers in recent years (photographed by Charles Kay on 16 August 2014). **B,** Note the wooden foot-bridge for crossing the perennial stream that was flowing in 1987, indicating that moisture was still present to support willow growth. The wooden foot-bridge burned in a wildfire during summer 1988, but the perennial stream was still flowing in the 2015 photograph.

unprotected understories outside the exclosures were heavily grazed and browsed and dominated by non-native grasses resistant to grazing, primarily timothy (*Phleum pratense*) and Kentucky bluegrass (*Poa pratensis*). I also examined unprotected Northern Range aspen stands outside YNP in the Eagle Creek drainage, where elk grazing and browsing pressure was less than inside YNP. Similar to the understories protected inside the

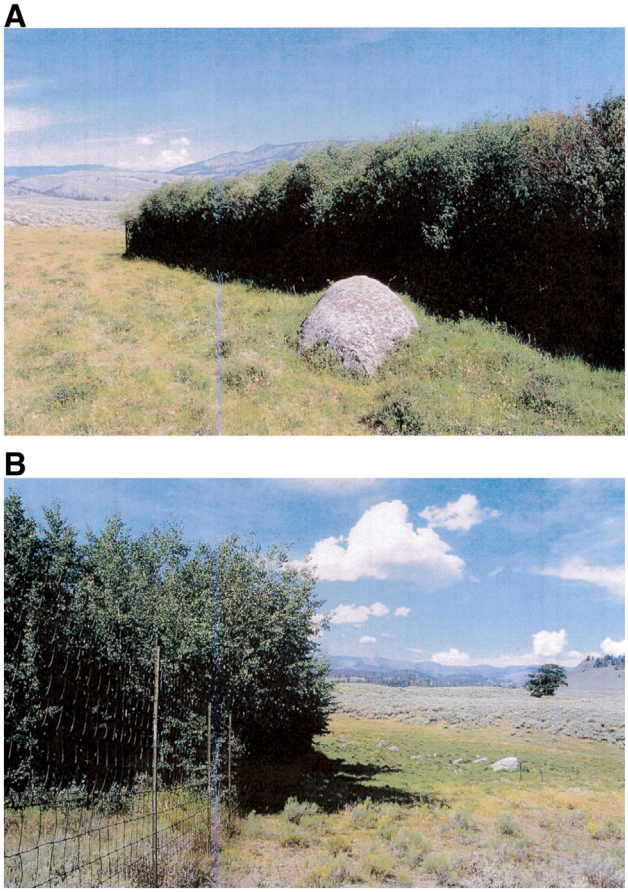

Figure 3. Willows and aspen have continued to increase in height and canopy cover inside all of the willow- and aspen-containing high-fenced exclosures that were established in 1957 and 1962 by Walter Kittams, National Park Service biologist, on the Northern Range inside Yellowstone National Park. In contrast, willows and aspen outside the exclosures have declined precipitously or have been eliminated, and neither willows nor aspen (**A** and **B**, respectively; photographs by Charles Kay on 12 August 2014) have recovered outside the exclosures, despite recent declines in elk numbers due in part to increased predation by wolves and grizzly bears.

YNP exclosures, unprotected understories in Eagle Creek were dominated by species of shrubs and tall forbs that were sensitive to grazing and trampling, including cow parsnip (*Heracleum lanatum*).[18] Finally, I measured 30 aspen-containing exclosures in north central Nevada and 77 aspen-containing exclosures in southern Utah, and in no case was protected aspen adversely impacted by climatic factors.[33–35] A recent study on the Northern Range inside and outside YNP documented aspen recruitment where browsing intensity was light to moderate but not where browsing intensity was heavy. These results further indicate that it is ungulate browsing intensity, not climate, that is limiting aspen recruitment on the Northern Range.[36]

Fire Suppression vs. Browsing Impacts

Fire scar data collected from Douglas-fir (*Pseudotsuga menziesii*) trees indicate that primeval Northern Range aspen communities were sustained by frequent, low-intensity fires that burned every 20 to 25 years.[7] Mature aspen trees are readily killed by fire because of their thin bark. Underground aspen roots, however, are protected from fire and respond to fire by producing a flush of new suckers.

Beginning in the 1870s, wildfires and fires purposely ignited by Native Americans were actively suppressed on the Northern Range.[7,8] Fire suppression severely reduced natural fire impacts on the age structure and reproduction of aspen communities. But in 1988, landscape-scale wildfires burned aspen communities across the Northern Range inside YNP. These wildfires presented an opportunity to examine the influence of fire suppression vs. browsing on the observed decline of Northern Range aspen from the 1870s to the 1980s. I established 775 photo points in 131 aspen stands burned by the 1988 wildfires. I also counted the number of aspen suckers and measured their heights. Aspen regeneration was initially very promising, ranging from 500 to more than 100,000 suckers per acre. In every stand, however, elk repeatedly browsed the suckers to the ground, eventually killing most of the burned aspen clones by repeated browsing (Fig. 4). The available evidence clearly demonstrates that heavy elk browsing overwhelmed the influence of fire suppression on the long-term decline of Northern Range aspen. In 2002, as stated earlier, the NRC also concluded that Northern Range aspen, along with willows and cottonwoods, had declined inside YNP primarily because of repeated elk browsing, not other factors.[4 p122&129&133]

Deciduous Shrubs and Trees 2003 to 2016

Comparative photographs in Figures 1, 2, 5, and 6 illustrate the condition and trend of aspen and willow communities on the Northern Range. In 2014 to 2016, I rephotographed the 81 photo points of Northern Range aspen that I photographed inside YNP in the 1980s.[18,19] None of the 81 aspen stands had recovered. In 2014 to 2016, I also rephotographed the 44 photo points of Northern Range willows that I had photographed inside YNP in the 1980s.[18,19] At only one site had willows grown beyond the reach of elk (≥ 6 feet tall), and that was at an upper elevation site near Pebble Creek that elk no longer inhabit in winter.

Numerous studies and reports have reached the same conclusion, that heavy browsing by Northern Range ungulates has continued to degrade many aspen, willow, and cottonwood communities during the 21st century, with little to no recovery in other areas.[32,37–41] For example, in riparian habitat within the Gardner, Lamar, and Yellowstone River watersheds inside YNP, the majority (70%) of areas sampled in 1991 did not contain deciduous woody vegetation, but the situation was even worse in 2006 when 85% of riparian habitat that was suitable for aspen, alder, willow, and cottonwood did not contain any deciduous woody vegetation.[37] Aspen are recovering in a few isolated areas on the Northern Range, both inside and outside YNP.[40–43] However, widespread landscape recovery is not occurring anywhere on the Northern Range.[38,39,42,44] Repeated heavy browsing continues to harm aspen, willow, and cottonwood communities almost everywhere on the Northern Range, despite a 60% reduction in elk numbers from 2000 to 2018.[45] One reason

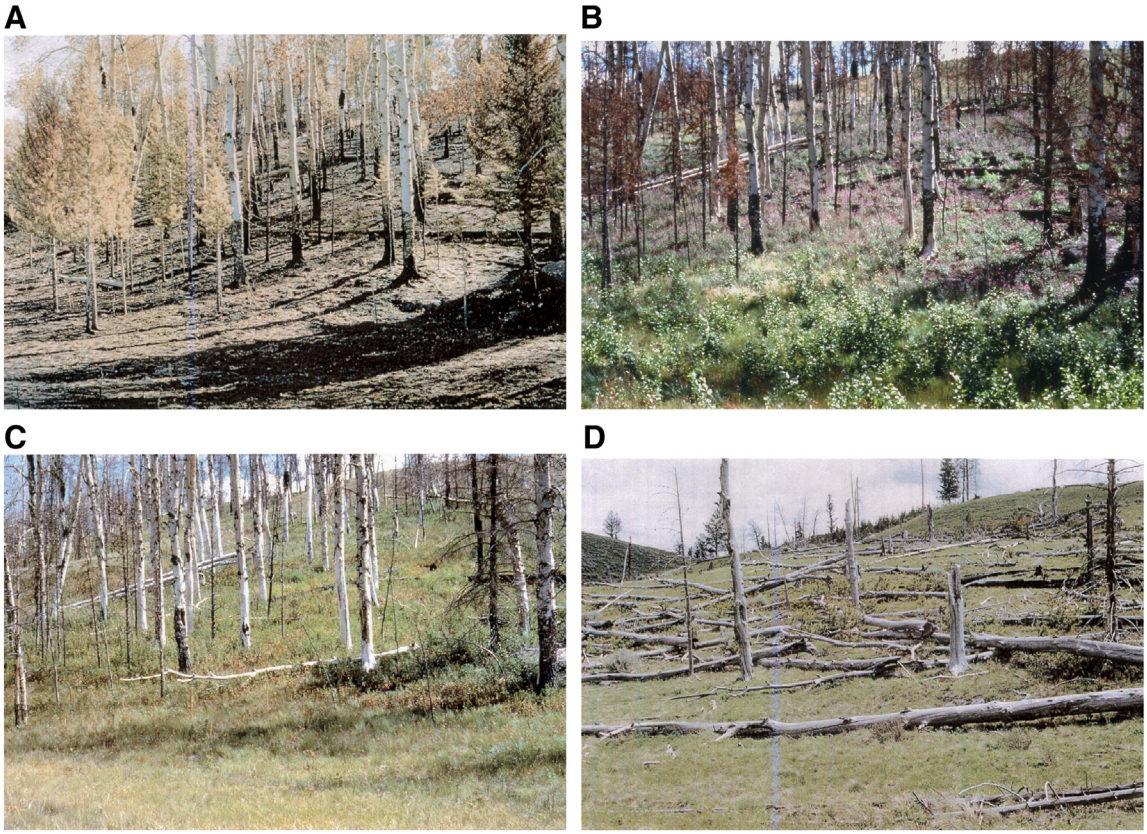

Figure 4. Heavy ungulate browsing has negated the regenerating effects of fire on most Northern Range aspen communities. Repeat photographs in this unprotected monitoring location show the aspen stand at the following time points: **A,** 1 month after it burned during the Yellowstone fires of 1988; **B,** 1 year later in August 1989 showing numerous newly sprouted aspen suckers in the foreground; and **C,** 3 years post-fire in August 1991 showing that the suckers had been severely browsed. **D,** By 2005, repeated browsing had killed the clone. (All photographs by Charles Kay.)

is that browsing by bison has increased.[46–50] The bison population has increased dramatically and filled much of the void created by fewer elk.[45] Most of the scattered recovery of deciduous woody vegetation on the Northern Range inside YNP has occurred in isolated locations where bison do not currently reside in large numbers.[46,51] Today, large numbers of bison are present year-round throughout most of the Northern Range inside YNP, and deciduous woody vegetation has not recovered in these areas.

Associated Fauna of Deciduous Shrubs and Trees

Healthy aspen, willow, and cottonwood plant communities contain exceedingly high biodiversity, greater than any other plant communities on the Northern Range. Thus, as aspen, willows, cottonwoods, and other deciduous shrubs and trees have declined in abundance, so have many fauna that rely on these habitats.[52,53] For example, American mink (*Neovison vison*) and northern river otter (*Lontra canadensis*) have lost much of their habitat[54] as streamside woody plant cover has been eliminated and the water table has dropped (Fig. 7). The habitat of native amphibians and reptiles also has been negatively impacted, including the western tiger salamander (*Ambystoma mavortiu*), western toad (*Anaxyrus boreas*), boreal chorus frog (*Pseudacris maculata*), Columbia spotted frog (*Rana luteiventris*), and terrestrial gartersnake (*Thamnophis elegans*).[55]

Birds

In YNP, 24 bird species are associated with healthy aspen communities and 37 bird species are associated with healthy willow-cottonwood plant communities.[56] All of these bird species are negatively impacted by the respective loss of aspen, willow, or cottonwood plant communities on the Northern Range, and bird species diversity and bird abundance are much lower where aspen, willow, or cottonwood plant communities are height suppressed by heavy ungulate browsing.[25,57] Bird species that rely on willow habitat are especially sensitive to heavy ungulate browsing, including willow flycatcher (*Empidonax trailii*), Wilson's warbler (*Wilsonia pusilla*), yellow warbler (*Dendroica petechia*), warbling vireo (*Vireo gilvus*), and song sparrow (*Melopspiza melodii*).[25,57]

Beavers

One of the most important fauna impacted by degraded aspen, willow, and cottonwood communities is beaver (*Castor*

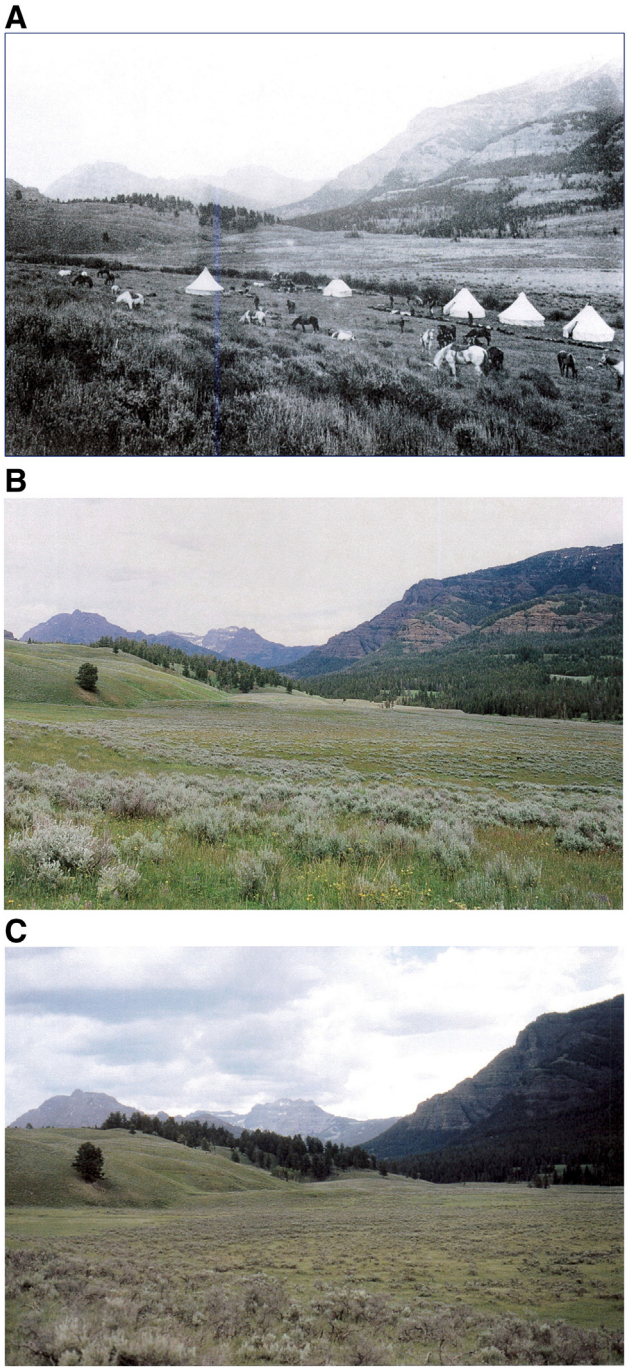

Figure 5. A, Willows were healthy and abundant in 1886 near the overnight camp of a military unit on patrol inside Yellowstone National Park (photograph by A.E. Bradley courtesy of the University of Montana). I repeated this photograph on 21 July 1988 and again on 18 July 2015. **B,** By 1988 willows were not visible. **C,** They were not recovered in 2015.

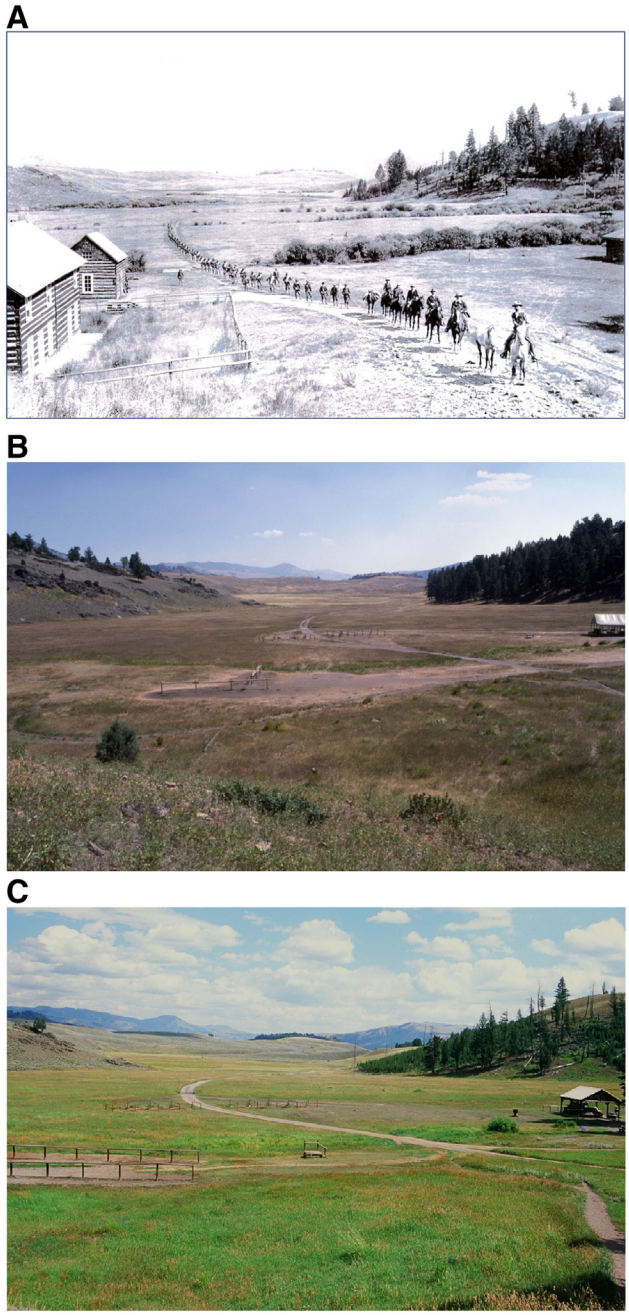

Figure 6. A, Abundant willows were present in 1893 when Company D of the Minnesota National Guard marched past John Yancey's Pleasant Valley Hotel while on patrol inside Yellowstone National Park (photograph by F.J. Haynes courtesy of the Montana Historical Society). All of the willows were heavily browsed by elk in 1921.[63] By the 1950s, all of the tall willows were gone.[64] **B,** Willows remained absent in 1987 (photograph by Charles Kay on 11 August 1987). **C,** Willows showed no signs of recovery in 2014 (photograph by Charles Kay on 16 August 2014).

canadensis). Beavers need aspen, willows, or cottonwoods for food and dam building material, but riparian ecosystems also need beaver activity to function sustainably, so much so that beaver has been classified a keystone species, or ecosystem engineer.[58,59] Beaver dams in streams impound water and trap sediments which raise the water table, reduce peak stream flows and floods, and augment low stream flows during late summer. In these ways beavers affect the three primary ecological processes—the water cycle, energy flow, and nutrient cycle—and the absence of beaver activity significantly impairs ecosystem function.[60]

Beavers were plentiful on the Northern Range during the 1800s,[61p613,62] and during the first two decades of the 20th century, almost every stream had active beaver

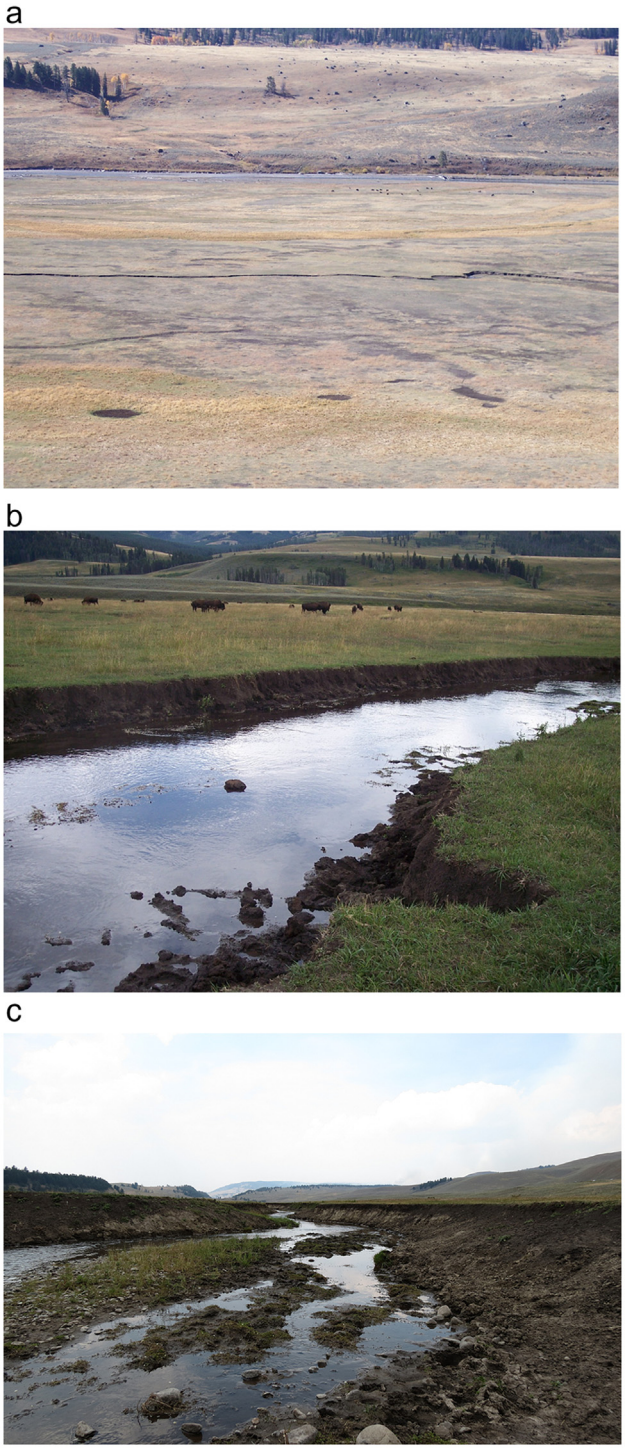

Figure 7. Heavy ungulate grazing and browsing has severely degraded stream and riparian ecosystems of the Lamar River and most of its tributaries. **A,** A 30 September 2015 landscape view of the Lamar River Valley shows the lack of willows along the Lamar River (background) and Rose Creek (middle ground, the dark line running across the center; photograph by Harold Hunter). Closer views of Rose Creek on 14 August 2015 (**B,** photograph by Charles Kay) and 17 August 2016 (**C,** photograph by John Mundinger) show unstable streambanks and an incised, widened channel.

colonies.[20p112,63p103] In 1921, a detailed beaver survey on the Northern Range inside YNP, near Tower Junction, counted 236 beavers in 12 different colonies.[64] By the mid-1950s, however, these colonies had been eliminated because of heavy browsing of willows and aspen by elk.[22,65] I redid the 1921 survey in 1986 to 1988 and found no beaver nor any evidence of recent beaver activity. I again repeated the 1921 survey during 2014 to 2016 with the same results—no beaver nor any signs of recent beaver activity.

A partial survey of the Northern Range in 1953 to 1954 counted only eight sites with beaver activity, and at one active site in Slide Creek, the impact of willow browsing was so severe that beaver were forced to eat sagebrush.[65] A much more intensive survey in 1988 to 1989 also documented only eight sites with beaver activity throughout the portion of the Northern Range inside YNP.[66] Thorough surveys from 1996 to 2009 confirmed that beaver remain rare or absent throughout the Northern Range inside YNP, with the exception of Slough Creek.[67] Slough Creek is located near the eastern, upper elevation boundary of the Northern Range and has experienced less 21st-century browsing by bison than most other Northern Range riparian areas inside YNP.

Discerning the relative influence of ungulate herbivory on Northern Range beaver populations is complicated somewhat by the fact that federal and state wildlife managers reintroduced beavers to drainages on the Gallatin National Forest (currently Custer Gallatin National Forest) north of YNP. From 1986 to 1999, 129 beavers were reintroduced, and at least a few of these beaver likely dispersed into YNP.[67] However, beaver reintroductions were only mildly successful. Today, beavers are rare or absent throughout most of the Northern Range, both inside and outside YNP.[43,67] Where browsing by elk and other wild ungulates has been minimal in meadows north of YNP on the Custer Gallatin National Forest, willow cover and beaver numbers increased from 1981 to 2011.[68]

The loss of beaver and streamside woody vegetation has caused severe degradation of stream hydrology and riparian ecosystem function on the portion of the Northern Range inside YNP. In the 1990s at the request of the NPS, preeminent western stream hydrologist David Rosgen examined the Lamar River Valley on the Northern Range inside YNP. He determined that the loss of deciduous shrubs and trees in riparian areas had dramatically degraded stream and riparian ecosystems of the Lamar River and most of its tributaries.[69,70] Streambank erosion had increased several orders of magnitude beyond natural levels; stream channels had incised, widened, and straightened; streams had become shallower and warmer; and depth to groundwater had increased. Collectively, these stream alterations had severely degraded fish habitat and fundamentally impaired stream hydrology and ecosystem function. David Rosgen also noted that stream impairments were not caused by climatic changes because all of the same stream types had not responded similarly. Instead, Rosgen determined that the primary cause of stream degradation was heavy grazing and browsing of the riparian vegetation by elk.[69] Today, 25 years after Rosgen's study was published in 1993, stream conditions are worse, with stream degradation so severe in some areas that reduced grazing and browsing will not be enough to restore woody

riparian species (Fig. 7). An ecological threshold has been crossed and riparian woody species will not recover until stream hydrology is restored.[59,71]

Summary and Conclusions

Deciduous shrubs and trees, primarily aspen, willows, and cottonwoods, were much more abundant on the Northern Range in primeval times than they are today. This is especially true on the portion of the Northern Range inside YNP. Repeated heavy browsing by ungulates—not normal plant succession or climatic changes—was the primary cause of the declines in deciduous shrubs and trees. Fire suppression was a secondary factor in the decline; however, fire suppression in recent times may have prevented further declines that might have occurred because of excessive post-fire browsing of young shoot growth that would likely be stimulated by fire.[72] Heavy browsing continues to further degrade most Northern Range aspen, willow, and cottonwood communities inside YNP, despite a 60% reduction in the Northern Range elk population from 1994 to 2018.[45] Increased browsing by bison is one reason why deciduous shrubs and trees have not exhibited widespread recovery after the reduction in elk numbers.[46–50] The Northern Range bison population increased dramatically since the year 2000 and filled much of the void created by fewer elk.[45]

The near total loss of aspen, willows, and cottonwoods on the Northern Range inside YNP has dramatically decreased populations of associated fauna, most notably songbirds and beavers. The loss of beaver and the loss of streamside deciduous shrubs and trees also degraded fish habitat quality and impaired the three primary ecological processes: the water cycle, energy flow, and nutrient cycling. Current NPS policy directs the NPS to intervene with active management where primeval and present conditions differ because of human actions.[3 p37&44] Excessive browsing of aspen, willows, and cottonwoods has occurred because modern-day management has allowed bison and elk populations to become unnaturally large.[45]

Elsewhere in the Northern Rocky Mountains, without the additional burden of browsing by bison, deciduous shrubs and trees successfully regenerate only where elk density does not exceed 1 to 3 elk per 250 acres.[72] In 2018, the Northern Range elk population was 7,579 animals, whereas the Northern Range bison population numbered 3,969 animals.[73,74] Thus, the combined elk and bison density inhabiting the 380,000-acre Northern Range was 7.6 animals per 250 acres, a density 2.5 to 7.6 times greater than the density that would enable aspen, willows, and cottonwoods to regenerate. Clearly, ungulate browsing of aspen, willows, and cottonwoods needs to be reduced substantially if these plants and their associated flora and fauna are to recover on the Northern Range. After ungulate numbers are returned to natural conditions, controlled burns should be conducted to stimulate aspen reproduction and to emulate the natural ecological impacts of prehistoric and historical burning by Native Americans.[8,72]

References

1. Houston, D.B. 1982. The Northern Yellowstone elk: ecology and management. New York, NY, USA: Macmillan Publishing Company, Inc.. 474 p.
2. Mosley, J.C., J. Fidel, H.E. Hunter, P.O. Husby, C.E. Kay, J. G. Mundinger, and R.M. Yonk. 2018. An ecological assessment of the Northern Yellowstone Range: introduction to the special issue. *Rangelands* 40:173-176.
3. National Park Service, 2006. Management policies 2006. Washington, DC, USA: U.S. Government Printing Office2006 168 p.
4. National Research Council, 2002. Ecological dynamics on Yellowstone's Northern Range. Washington, DC, USA: National Academy Press. 180 p.
5. Chadde, S.W., P.L. Hansen, and R.D. Pfister. 1988. Wetland plant communities of the northern range, Yellowstone National Park. Missoula, MT, USA: University of Montana School of Forestry. 81 p.
6. Hansen, P.L., S.W. Chadde, and R.D. Pfister. 1988. Riparian dominance types of Montana. Miscellaneous Publication 49. Missoula, MT, USA: University of Montana Forest and Conservation Experiment Station. 411 p.
7. Houston, D.B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* 54:1111-1117.
8. Yonk, R.M., J.C. Mosley, and P.O. Husby. 2018. Human influences on the Northern Yellowstone Range. *Rangelands* 40:177-188.
9. Kay, C.E. 1997. Is aspen doomed? *Journal of Forestry* 95:4-11.
10. Brinkman, K.A. 1974. Salix L. – willow, p. 746-750. In: Schopmeyer CS, editor. Seeds of woody plants in the United States. U.S. Department of Agriculture Handbook 450. 883 p.
11. Densmore, R., and J. Zasada. 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. *Canadian Journal of Botany* 61:3201-3216.
12. McDougall, W.B., and H.A. Baggley. 1956. The plants of Yellowstone National Park. second edition. Mammoth, WY, USA: Yellowstone Library and Museum Association. 186 p.
13. Boner, B.J. 2017. Yellowstone National Park through the lens of time. Boulder, CO, USA: University Press of Colorado. 297 p.
14. Meagher, M.M., and D.B. Houston. 1998. Yellowstone and the biology of time: photographs across a century. Norman, OK, USA: University of Oklahoma Press. 287 p.
15. Christianson, D.A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. *Journal of Wildlife Management* 71:164-176.
16. White, P.J., K.M. Proffitt, L.D. Mech, S.B. Evans, J.A. Cunningham, and K.L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy* 91:827-837.
17. Barmore, W.J. Jr. 2003. Ecology of ungulates and their winter range in Northern Yellowstone National Park: research and synthesis, 1962-1970. Yellowstone National Park, WY, USA: Yellowstone Center for Resources. 528 p.
18. Kay, C.E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm [PhD dissertation]. Logan, UT. USA: Utah State University. 490 p.
19. Chadde, S.W., and C.E. Kay. 1991. Tall willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm, p. 231–262. In: Keiter RB & Boyce MS, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. New Haven, CT, USA: Yale University Press. 428 p.
20. Bailey, V. 1930. Animal life of Yellowstone National Park. Springfield, IL, USA: C. Thomas and Co. 241 p.

21. Grimm, R.L. 1939. Northern Yellowstone Winter Range studies. *Journal of Wildlife Management* 3:295-306.
22. Kittams, W.H. 1959. Future of the Yellowstone wapiti. *Naturalist* 19:30-39.
23. Cooper, H.W. 1963. Northern Yellowstone elk herd winter range and site condition survey. Bozeman, MT, USA: Soil Conservation Service. 9 p.
24. Leopold, A.S., S.A. Cain, C.M. Cottam, I.N. Gabrielson, and T.L. Kimball. 1963. Wildlife management in the national parks. *Transactions of the North American Wildlife Conference* 24:28-45.
25. Jackson, S.G. 1992. Relationships among birds, willows, and native ungulates in and around northern Yellowstone National Park. [MS thesis] Logan, UT, USA: Utah State University. 74 p.
26. Singer, F.J., L.C. Mark, and R.C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* 47:435-443.
27. Keigley, R.B. 1997. An increase in herbivory of cottonwood in Yellowstone National Park. *Northwest Science* 71:127-136.
28. Thompson, S.K. 2002. Browse condition and trend on Montana ungulate ranges. [MS thesis] Bozeman, MT, USA: Montana State University. 147 p.
29. Kay, C.E. 1995. Browsing by native ungulates: effects on shrub and seed production in the Greater Yellowstone Ecosystem, p. 310–320. In: Roundy BA McArthur ED Haley JS & Mann DK, editors. Proceedings: Wildland Shrub and Arid Land Restoration Symposium. Intermountain Research Station General Technical Report INT-GTR-315. Ogden, UT, USA: U.S. Forest Service. 384 p.
30. Despain, D., D. Houston, M. Meagher, and P. Schullery. 1986. Wildlife in transition: man and nature on Yellowstone's Northern Range. Boulder, CO, USA: Roberts Rinehart. 142 p.
31. Kay, C.E., and S. Chadde. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park, p. 92–99. *In*: W.P. Clary, E.D. McArthur, D. Bedunah, and C. L. Wambolt [compilers]. Proceedings—Symposium on Ecology and Management of Riparian Shrub Communities. General Technical Report INT-289. Ogden, UT, USA: U.S. Forest Service. 232 p.
32. Kay, C.E. 2001. Long-term aspen exclosures in the Yellowstone ecosystem, p. 225-240. *In*: WD Shepperd, D Binkley, DL Bartos, TJ Stohlgren, and LG Eskew [compilers]. Sustaining Aspen in Western Landscapes: Symposium Proceedings. Rocky Mountain Research Station RMRS-P-18. Fort Collins, CO, USA: U.S. Forest Service. 460 p.
33. Kay, C.E. 2003. Aspen management guidelines for BLM lands in north-central Nevada. Final Report to Battle Mountain Field Office, Bureau of Land Management, Battle Mountain, Nevada. 63 p.
34. Kay, C.E., and D. Bartos. 2000. Ungulate herbivory on Utah aspen: assessment of long-term exclosures. *Journal of Range Management* 53:145-153.
35. Kay, C.E. 2011. Why is aspen declining on Cedar Mountain? Measurement of aspen exclosures in southern Utah. Final Report to Cedar Mountain Initiative. Cedar City, UT, USA: Utah State University Extension. 406 p.
36. Painter, L.E., R.L. Beschta, E.J. Larsen, and W.J. Ripple. 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. *Ecosphere* 9(8) e02376.
37. Baril, L.M. 2009. Change in deciduous woody vegetation, implications of increased willow (*Salix* spp.) growth for bird species diversity, and willow species composition in and around Yellowstone National Park's northern range. [MS thesis] Bozeman, MT, USA: Montana State University. 136 p.
38. Kauffman, M.J., J.F. Brodie, and E.S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742-2755.
39. Brodie, J., E. Post, F. Watson, and J. Berger. 2012. Climate change intensification of herbivore impacts on tree recruitment. *Proceedings of the Royal Society B* 79:1366-1370.
40. Painter, L.E., R.L. Beschta, E.J. Larsen, and W.J. Ripple. 2014. After long-term decline, are aspen recovering in northern Yellowstone? *Forest Ecology and Management* 329:108-117.
41. Beschta, R.L., L.E. Painter, T. Levi, and W.J. Ripple. 2016. Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone National Park. *Canadian Journal of Forest Research* 46:548-556.
42. Kimble, D.S., D.B. Tyers, J. Robison-Cox, and B.F. Sowell. 2011. Aspen recovery since wolf reintroduction on the Northern Yellowstone Winter Range. *Rangeland Ecology & Management* 64:119-130.
43. Runyon, M.J., D.B. Tyers, B.F. Sowell, and C.N. Gower. 2014. Aspen restoration using beaver on the Northern Yellowstone Winter Range under reduced ungulate herbivory. *Restoration Ecology* 22:555-561.
44. McColley, S.D., D.B. Tyers, and B.F. Sowell. 2012. Aspen and willow restoration using beaver on the Northern Yellowstone Winter Range. *Restoration Ecology* 20:450-455.
45. Mosley, J.C., and J.G. Mundinger. 2018. History and status of wild ungulate populations on the Northern Yellowstone Range. *Rangelands* 40:189-201.
46. Painter, L.E., and W.J. Ripple. 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. *Forest Ecology and Management* 264:150-158.
47. Ripple, W.J., and R.L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145:205-2013.
48. Beschta, R.L., and W.J. Ripple. 2014. Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone. *Ecohydrology* 8:58-66.
49. Painter, L.E., R.L. Beschta, E.J. Larsen, and W.J. Ripple. 2015. Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade. *Ecology* 96:252-263.
50. Beschta, R.L., and W.J. Ripple. 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. *Biological Conservation* 198:93-103.
51. Beschta, R.J., and W.J. Ripple. 2010. Recovering riparian plant communities with wolves in northern Yellowstone, USA. *Restoration Ecology* 18:380-389.
52. Hansen, A.J., J.J. Rotella, M.P.V. Kraska, and D. Brown. 1999. Dynamic habitat and population analysis: an approach to resolve the biodiversity manager's dilemma. *Ecological Applications* 9:1459-1476.
53. Hossack, B.R., W.R. Gould, D.A. Patla, E. Muths, R. Daley, K. Legg, and P.S. Corn. 2015. Trends in Rocky Mountain amphibians and the role of beaver as a keystone species. *Biological Conservation* 187:260-269.
54. Foresman, K.R. 2012. Mammals of Montana. second edition. Missoula, MT, USA: Mountain Press Publishing Company. 429 p.
55. Werner, J.K., B.A. Maxell, P. Hendricks, and D.L. Flath. 2004. Amphibians and reptiles of Montana. Missoula, MT, USA: Mountain Press Publishing Company. 262 p.
56. McEneaney, T. 1988. Birds of Yellowstone: a practical habitat guide to the birds of Yellowstone National Park, and where to find them. Boulder, CO, USA: Roberts Rinehart. 171 p.
57. Baril, L.M., A.J. Hansen, R. Renkin, and R. Lawrence. 2011. Songbird response to increased willow (*Salix* spp.) growth in Yellowstone's northern range. *Ecological Applications* 21:2283-2296.
58. Wolf, E.C., D.J. Cooper, and N.T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. *Ecological Applications* 17:1572-1587.

59. Marshall, K.N., N.T. Hobbs, and D.J. Cooper. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. *Proceedings of the Royal Society B* 280:20122977.
60. Naiman, R.J., C.A. Johnston, and J.C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* 38:753-762.
61. Norris, P. 1880. Report upon the Yellowstone National Park for the Year 1879 to the Secretary of the Interior. Washington, DC, USA: U.S. Government Printing Office. 31 p.
62. Russell, O. 1955. Journal of a trapper, edited from original manuscript by A. L. Haines. Lincoln, NE, USA: University of Nebraska Press. 191 p.
63. Albright, H.M. 1920. Annual report for Yellowstone National Park, Wyoming. 152 p.
64. Warren, E.R. 1926. A study of beaver in the Yancey region of Yellowstone National Park. *Roosevelt Wildlife Annual* 1:1-191.
65. Jonas, R.J. 1955. A population and ecological study of the beaver (*Castor canadensis*) of Yellowstone National Park. [MS thesis]. Moscow, ID, USA: University of Idaho. 193 p.
66. Consolo Murphy, S., and D.D. Hanson. 1993. Distribution of beaver in Yellowstone National Park, p. 38–48. In: Cook RS, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. Scientific Monograph NPS/NRYELL/NRSM-93/22. Denver, CO, USA: National Park Service. 328 p.
67. Smith, D.W., and D.B. Tyers. 2012. The history and current status and distribution of beavers in Yellowstone National Park. *Northwest Science* 86:276-288.
68. Scrafford, M.A., D.B. Tyers, D.T. Patten, and B.F. Sowell. 2018. Beaver habitat selection for 24 yr since reintroduction north of Yellowstone National Park. *Rangeland Ecology & Management* 71:266-273.
69. Rosgen, D.L. 1993. Stream classification, streambank erosion and fluvial interpretations for the Lamar River and main tributaries. Technical Report for U.S. Department of the Interior, Yellowstone National Park. Pagosa Springs, CO, USA: Wildland Hydrology. 82 p.
70. Rosgen, D.L. 2001. A practical method of computing streambank erosion rate, p. 9-17. Proceedings of the Seventh Federal Interagency Sedimentation Conference; 25–29 March 2001. Reno, NV, USA: Volume II Stream Restoration. 167 p.
71. Bilyeu, D.M., D.J. Cooper, and N.T. Hobbs. 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. *Ecological Applications* 18:80-92.
72. White, C.A., C.E. Olmsted, and C.E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin* 26:449-462.
73. Loveless, K. 2018. Hunting District 313 elk survey (Gardiner to 6-Mile Creek). Helena, MT, USA: Montana Fish, Wildlife & Parks. 4 p.
74. Geremia, C., R. Wallen, and P.J. White. 2018. Status report on the Yellowstone bison population, September 2018. Mammoth, WY, USA: National Park Service. 17 p.

Author is Senior Fellow (retired), Institute of Political Economy and Senior Research Scientist (retired), Center for Public Lands & Rural Economics, Huntsman School of Business, Utah State University, Logan, UT 84322, USA (charles.kay375@gmail.com).