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Conserving Yellowstone's Northern Range

Tatural resource managers in Yellowstone National Park face many challenges that will continue into the future. Visitation has doubled over the past several decades, making it more difficult to avoid disturbances to vegetation, waterways, and wild animals. A warming climate is affecting precipitation and snowmelt patterns, the frequencies of droughts, flooding, and fires, and plant and animal communities. Development of some areas surrounding the park continues to fragment habitats for wildlife and alter their movements. In addition, nonnative plants are spreading into the park and displacing native plants in some areas. As a result, managers need to continue working with residents, states, tribes, visitors, and the national public to consider a variety of ideas and find reasonable responses.

One pressing issue is how to manage grasslands and migratory ungulates in northern Yellowstone and nearby areas of Montana. Thousands of bison and elk and hundreds of bighorn sheep, deer, and pronghorn move across this "northern range," where they interact with bears, cougars, coyotes, and wolves. This area provides one of the best places in the world to watch wildlife. Since the 1920s, however, there have been concerns about too many ungulates removing too much vegetation, eroding soils, and reducing the variety of plants. In addition, nonnative plants have taken over portions of this range, raising concerns about their effects and continued spread.

There is a need to develop realistic goals and feasible approaches for managing grasslands and grazing animals on the northern range. Since 2012, park biologists and various collaborators have increased monitoring of grassland and sage-steppe communities to gauge conditions, document plant production and grazing consumption, assess soil health, and describe the composition of native and nonnative plants. In this edition of Yellowstone Science, we describe findings from these efforts and recommend future actions.





Wildlife & Aquatic Resources, Yellowstone National Park

The Great Debate: Are Yellowstone's Northern Grasslands Overgrazed?

P. J. White, Chris Geremia, Rick Wallen, Doug Frank, & Roy Renkin



any people refer to the grasslands in northern Yellowstone as America's Serengeti because they support a wide variety Lof abundant ungulates and their predators watched by millions of people each year. However, this concentration of grazing animals has been a source of controversy since the 1920s due to concerns about them removing too much vegetation, compacting soils, and reducing the diversity of plants. As a result, managers reduced numbers of bison, elk, and pronghorn during the 1930s through the 1960s by shooting or capturing and removing them from the park. Managers stopped these culls when there were about 3,170 elk, 70 bison, and 100 pronghorn in northern Yellowstone and nearby areas of Montana. Thereafter, managers allowed ungulate numbers to vary in response to forage availability, harvests outside the park, predation, and weather. Numbers increased rapidly with counts of about 18,900 elk, 940 bison, and 495 pronghorn by the late 1980s.

As their numbers increased, more ungulates began to move to lower-elevation valleys outside the park during winter, leading some people to conclude there was not enough food in the park for existing numbers of animals. This led to debates about whether overabundant elk were permanently damaging the landscape by overgrazing and compacting or eroding the soils. In 1998, the House Appropriations Committee directed the National Park Service to contract an independent review of this issue. The National Research Council (NRC) published their findings in a 2002 book entitled Ecological Dynamics on Yellowstone's Northern Range. The NRC concluded grazing had not permanently damaged the grasslands and, as a result, natural fluctuations in ungulate numbers and grassland and grazing conditions could continue. However, they cautioned that future predictions were difficult given a warming climate, wolf reintroduction from 1995 to 1997, more elk moving north of the park during winter, and the continued harvests of ungulates outside the park. Thus, they recommended park managers conduct monitoring and research over the next several decades to determine the effects of these changes.

Counts of northern Yellowstone elk decreased by 80% to 3,915 in 2013 (Figure 1) and, in turn, the debate about overgrazing by elk waned. However, bison counts in northern Yellowstone increased to 3,420 by 2014 and intense grazing in the Lamar Valley rekindled the debate about grazing effects. This change towards fewer elk and more bison was unprecedented in recent history and, as a result, the long-term effects of bison grazing on grassland communities were uncertain. Unlike elk and other ungulates, bison are constrained by surrounding states from moving much beyond the boundaries of the park due to concerns about disease transmission to livestock, competition with cattle for grass, human safety, and property

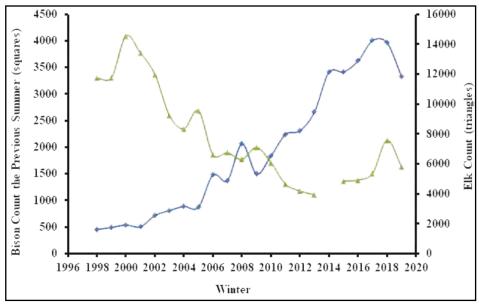


Figure 1. Winter counts of northern Yellowstone elk (triangles) and summer counts of bison (squares) in the northern portion of Yellowstone National Park from 1998 to 2019 (Geremia et al. 2018, NYCWWG 2018).

damage. Thus, the substantial increase in bison numbers led to concerns that intense grazing could damage grasslands in northern Yellowstone.

Grazing Effects

The debate about the management of grazing ungulates and grasslands in northern Yellowstone hinges on the question of what is overgrazing. Grazing usually is not destructive because it does not permanently damage plants or decrease their production and storage of energy. The growth of new plant tissue depends on obtaining sunlight and carbon dioxide from the air and water, nitrogen, and other minerals from the soil. Low to moderate grazing by ungulates can increase plant production in areas with high soil moisture and nutrients by removing some leaf tissue, which allows more sunlight to reach the plants and reduces water loss via evaporation from the leaves (McNaughton 1985, Knapp et al. 1999). In addition, ungulates increase the availability of nitrogen in the soil by depositing fertilizers in the form of feces and urine and breaking down plant litter, which helps roots and associated fungi intake nitrogen and water (Frank et al. 2013 and references therein). As a result, the amount of nitrogen in grasses is increased and, provided there is sufficient soil moisture, there is an increase in the production of new plant tissue. Through this process, ungulates can increase plant production and the quality of forage (McNaughton 1985, Frank et al. 2013). However, too much grazing can decrease plant production by removing too much leaf tissue, exposing and compacting soils, reducing available nutrients, and decreasing the variety of plants (Frank et al. 2013 and references therein). Excessively grazed areas are vulnerable to erosion and invasions by nonnative plants due to less plant litter and more bare ground (Pellant et al. 2005).

Given this background, we suggest overgrazing occurs when widespread, repeated foraging removes so much leaf tissue that plant productivity and regrowth decrease considerably and soils become unproductive and eroded (Pellant et al. 2005, Fuhlendorf et al. 2012, NRC 2013). Signs of overgrazing include changes in the variety of plants, the spread of nonnative plants, and poor body condition in ungulates. However, deciding whether an area is overgrazed is complicated and depends on a person's experiences, training, and goals. Rangeland managers usually view grazing as a tool for livestock production with substantial human involvement to maintain desirable forage plants. Thus, they focus on indicators of grassland health such as plant composition, the amount of litter, soil erosion, and whether grazing is moderate and uniform (Fuhlendorf et al. 2012). In contrast, wildlife biologists view grazing as a process that contributes to a variety of animals, plants, and conditions across the landscape. Thus, they focus on indicators such as plant production, energy and nutrients, the diversity of animals and plants, and ungulate body condition (Fuhlendorf et al. 2012). As a result. rangeland managers and biologists often evaluate the same grazed landscape and reach different conclusions regarding its condition.

Yellowstone National Park (YNP) is not a ranch with domesticated animals and human-controlled animal, nutrient, and water inputs. Rather, the park preserves a wilderness where untamed, free-roaming animals and natural processes exist in an area not dominated by humans. Since ungulate numbers vary considerably among seasons and years, quite unlike the stocking and rotation of livestock on rangelands and grazing allotments, the grasslands within the park will not look like nearby ranches. The NRC addressed this issue in their 2002 report: "For example, some people compare the northern range unfavorably with nearby ranches, but that reflects a mixing of values. Ranching seeks high production for human uses, but YNP seeks to preserve a natural environment and the species and ecological processes within it."

Today, most deer, elk, and other ungulates in the Yellowstone area move from lower elevations during winter to higher elevations during summer. They eat mostly dead, low quality forage during winter, but select newly growing, green grass in lower elevation areas during spring. They then move to higher elevations as snow melts to find more-abundant, nourishing vegetation as the growing season progresses. These movements allow grazed vegetation to regrow new tissue and store energy in their roots, which enables plants to withstand modest levels of grazing year after year (Frank et al. 2013). However, large aggregations of ungulates may graze certain areas for long periods of time if their movements are restricted, which is the case with Yellowstone bison because surrounding states have little tolerance for them and, as a result, most bison remain within the park (Geremia et al. 2015). In addition, bison tend to create grazing lawns, similar to those found in the savanna systems of the Serengeti, unlike elk that feed in a more scattered manner (McNaughton 1985). Herds of many hundreds of bison graze in the Lamar Valley through summer, whereas most elk move through this area to more distant summer ranges (White et al. 2010, Geremia et al. 2015). Intense, sustained grazing by bison in this area would subject grasses to repeated tissue loss and could affect plant productivity.

Desired and Existing Conditions

Congress established YNP in 1872 to preserve resources in their natural condition for the benefit and enjoyment of people. The natural condition for vegetation and wildlife communities in YNP would be pre-settlement, before substantial changes by colonizing Euro-Americans. However, it is impossible to recreate those conditions given ensuing changes such as the slaughter of ungulates, removal of native people, development around the park, increasing visitation, invasions by more than 217 types of nonnative plant species, and a century of a warming climate (White et al. 2013, Tercek et al. 2015, Hansen and Phillips 2018, Whittlesey et al. 2018).

Ungulates were widespread in the Yellowstone area prior to settlement during the late 1800s (Whittlesey et al. 2018). After the massive slaughter of wild ungulates by market hunters, and the

relocation of American Indians to reservations, thousands of livestock (cattle, horses, and sheep) were allowed to graze grasslands in northern Yellowstone from about 1875 to 1922 and nearby areas of Montana through the 1900s (Whittlesey 1994). After removing livestock from the park, grazing in northern Yellowstone primarily occurred during winter and spring by wild elk, bison, and other ungulates, with animals moving between higher elevations during summer and fall and lower elevations during winter. In recent years, however, more than one thousand bison have remained in the Lamar Valley and nearby areas throughout the summer (White et al. 2012, Geremia et al. 2015).

Between 1904 and 1952, about 575 acres (233 hectares) in the Lamar Valley, 530 acres (215 hectares) in the Gardiner basin, and some areas along Slough Creek and in Yancey's Hole were cleared of native vegetation and planted with nonnative grasses (alfalfa, oats, smooth brome, clover, timothy) to grow hay for bison, elk, pronghorn, and other wildlife (Figures 2 and 3; Cahalane 1944, Whittlesey 1995). Managers eventually planted nonnative crested wheatgrass in the hayfields in the Gardiner basin. Sufficient moisture in the higher-elevation hayfields allowed smooth brome and timothy to expand substantially beyond the originally planted fields. A warming climate with high nitrogen deposition from feces and urine from ungulates allowed nonnative plants to spread in the following decades (Renkin et al. 2014). For example, annual wheatgrass, cheatgrass, and desert alyssum spread through the Gardiner basin during the 1990s and 2000s, replacing crested wheatgrass on previously farmed fields and filling in spaces between native bunchgrasses (Renkin et al. 2014). In addition, nonnative plants spread along roads where soils were disturbed, in areas burned by fires, and elsewhere from feces deposited by wildlife, packhorses, and mules. This spread has changed the composition and production of some grassland communities by displacing native plants and altering productivity, soils, and nutrients (Renkin et al. 2014).

Nonnative plants now dominate plant communities in areas such as the Gardiner basin and Lamar Valley (YCR 2018).

Climate is the main factor affecting grass production because variations in precipitation and temperature strongly influence soil moisture, which can limit production (Frank et al. 2013). As a result, variations in weather among years contribute to large variations in grass production (Knapp and Smith 2001). Temperatures have warmed and precipitation has decreased over the past century, with about 80 to 100 more days above freezing at the northeast entrance of the park compared to 1985 (Tercek et al. 2015). These changes have resulted in less snow at lower elevations, earlier snowmelt and plant growth, longer and drier growing seasons, and more frequent drought (Tercek et al. 2015, Hansen and Phillips 2018, YCR 2018). Fewer green grasses may be available in late summer if green-up occurs earlier and grasses die by mid-summer. As a result, some ungulates may be unable to obtain adequate fat and protein reserves for pregnancy and survival (Middleton et al. 2017). In addition, fires that are more frequent could make grassland communities more vulnerable to the spread of nonnative grasses (Romme and Turner 2015, Hansen and Phillips 2018, YCR 2018).

The recovery of large predators such as wolves, grizzly bears, and cougars during recent decades contributed to large changes in the numbers and distribution of grazing ungulates, with fewer elk and more bison, and a much greater portion of the elk population moving to lower-elevation areas outside the park during winter. These changes occurred, at least in part, due to increased predation of elk at higher elevations where they were more vulnerable due to deeper snow packs (White et al. 2012). Today, fewer and smaller groups of elk use the grasslands in northern Yellowstone and more of their feeding occurs during nighttime when wolves are less active (Kohl et al. 2018). In contrast, bison numbers in northern Yellowstone increased from about 900 to 4,000 during 2005 to

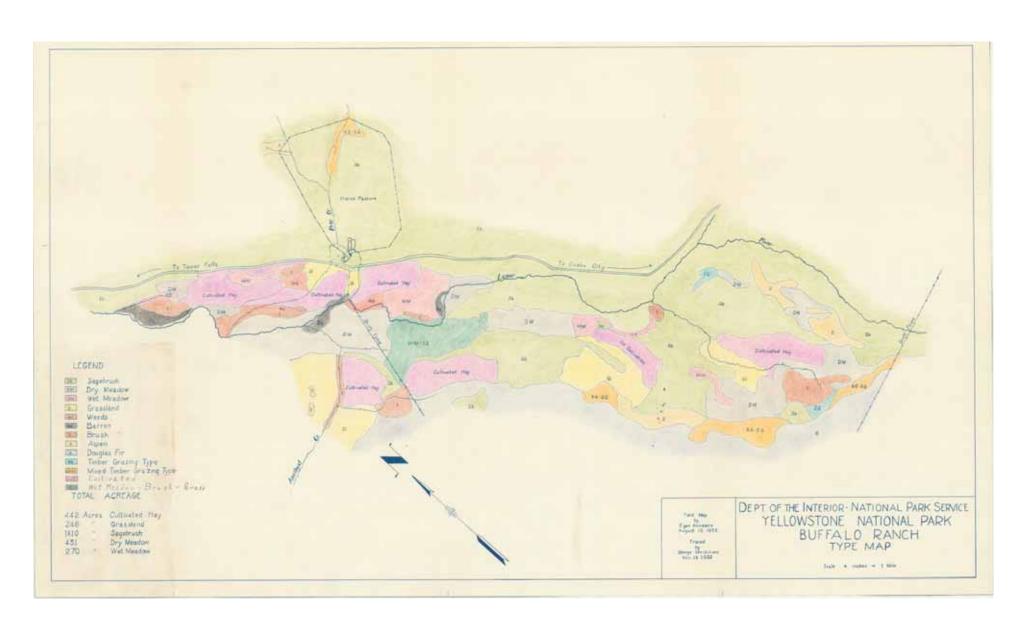


Figure 2. Map of the cultivated hayfields and other vegetation types in the Lamar Valley of Yellowstone National Park during 1932-1933.

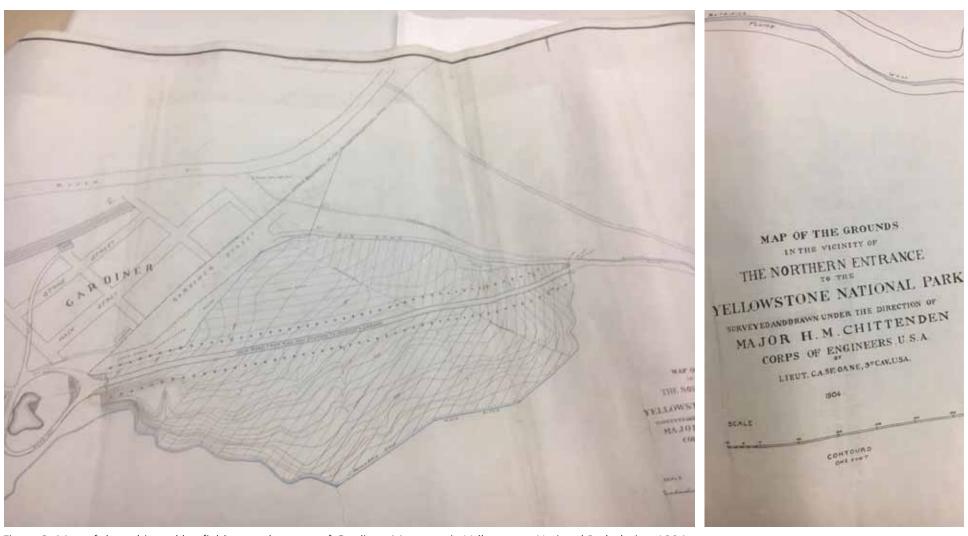


Figure 3. Map of the cultivated hayfields near the town of Gardiner, Montana, in Yellowstone National Park during 1904.

2017 due to high survival and calving combined with movements of bison from the central to the northern region of the park. As mentioned previously, these bison began using traditional winter range areas for elk in the Lamar Valley as summer grazing areas

(Geremia et al. 2015). Bison are more difficult prey for wolves than elk due to their large size and use of group defenses. As a result, they can congregate in large groups in grasslands without increasing predation risk.

Conclusion

Given all of these changes over the past century, a more realistic desired condition for grasslands in northern Yellowstone, rather than attempting to recreate the natural conditions before Euro-American colonization, is to try and maintain communities with functional groups of grasses, forbs, and shrubs, healthy soils, and functioning water, energy, and nutrient cycles. Many communities will include widespread nonnative plants due to their previous spread throughout much of northern Yellowstone. In addition, variable grazing intensities will produce an assortment of vegetation conditions across the landscape ranging from lightly to intensively grazed areas. This mosaic will support a diversity of animals and plants because some need a variety of different areas, while others rely on either disturbed or undisturbed areas (Fuhlendorf et al. 2012, NRC 2013).

Since 2012, wildlife biologists have monitored changes in plant production, consumption, soil health, and plant composition across the ranges used by Yellowstone bison. In addition, vegetation biologists have monitored plant composition in sagebrush-steppe communities to detect changes in the abundance of native and nonnative plants, bare soil and litter, and other indicators. The articles in this edition of Yellowstone Science summarize findings from these monitoring efforts and provide recommendations for the future

Literature Cited

See *Literature Cited* section of this issue on page 108.

P.J. White (see page 4) is the Chief of Wildlife and Aquatic Resources at Yellowstone National Park. He has researched many of the major mammals in the Greater Yellowstone Area and worked to find solutions that help wildlife and humans coexist. White is the author of more than 100 scientific papers and many popular books,

including Can't Chew the Leather Anymore--Musings on Wildlife Conservation in Yellowstone from a Broken-down Biologist, Greater Yellowstone's Mountain Ungulates—A Contrast in Management Histories and Challenges, Yellowstone Grizzly Bears—Ecology and Conservation of an Icon of Wildness, Yellowstone Bison—Conserving an American Icon in Modern Society, Yellowstone's Wildlife in Transition, and The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies.



History & Status of the Yellowstone Bison Population

P. J. White, Chris Geremia, & Rick Wallen

rotection and Recovery By 1900, there were only two dozen bison left in the Yellowstone area due to their widespread slaughter by Euro-American colonists during the 1870s and 1880s. To help with recovery, managers relocated 18 pregnant females from northwestern Montana and 3 males from Texas to the northern portion of Yellowstone National Park (YNP) during the early 1900s. Managers fed these bison during winter at the Buffalo Ranch in the Lamar Valley and herded them to the Mirror Plateau and upper Lamar River area during summer. The remaining native bison spent winter in the Pelican Valley in central Yellowstone, but also moved to the Mirror Plateau and upper Lamar River area during summer. As a result, some of the native Pelican bison likely mixed and bred with the introduced Lamar bison during the breeding season from mid-July to mid-August. Bison numbers increased rapidly to about 1,100 by 1930 (Figure 1). In 1936, managers relocated 71 bison from the Lamar Valley to the Hayden Valley and Firehole River area in central Yellowstone, creating the Mary Mountain herd (Meagher 1973).

Managers stopped feeding and herding bison in the Lamar Valley in 1952, after which bison moved about freely. However, managers shot or captured and shipped about 3,500 bison from this herd between 1930 and 1966 to reduce numbers and take out individuals with the disease brucellosis. For similar reasons, managers removed about 860 Mary Mountain bison and 150 Pelican bison between 1954 and 1966. These removals reduced numbers to about 70 Lamar, 160 Pelican, and 188 Mary Mountain bison by winter in 1968 (Meagher 1973). Thereafter, managers stopped removing bison and allowed numbers to vary in response to forage availability, predation, and weather. Bison numbers increased rapidly to about 1,700 during the 1970s and 3,000 during the 1980s. Some Lamar bison began spending both summer and winter in the Lamar Valley, while others pioneered winter ranges westward along

the Yellowstone River towards the northern boundary (Meagher 1989). Pelican bison began moving west to the northern shore of Yellowstone Lake and along the Yellowstone River to the Hayden Valley (Figure 2). Eventually, bison spending winter in the Pelican Valley stopped moving to the Mirror Plateau and upper Lamar River



hoto: ©Clint Parkhill

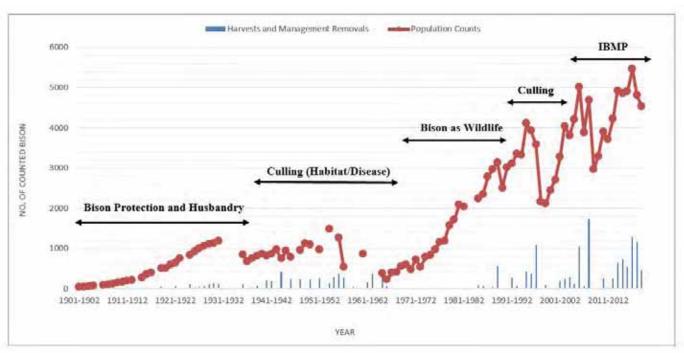


Figure 1. Counts and removals of Yellowstone bison from 1901 to 2018. IBMP refers to the Interagency Bison Management Plan.

area during summer and, instead, mostly remained in the Hayden Valley (Meagher 1998). Thus, there was likely considerable mixing of descendants from the native (Pelican) and introduced (Lamar/Mary Mountain) lineages.

In addition, some bison began moving from the Hayden Valley to the Firehole River area and along the Gibbon and Madison rivers towards the western boundary during winter. Others began moving to northern Yellowstone, likely in response to increasing bison numbers and deep snow depths that reduced forage availability (Meagher 1993, Fuller et al. 2007). As a result, there was probably further mixing of descendants from the native and introduced lineages and distinguishing between descendants of Lamar, Pelican, and Mary Mountain bison based on their location in the park

became impossible. Instead, biologists began counting and referring to bison that spent summer in the central and northern regions of Yellowstone as the central and northern herds.

Interagency Bison Management Plan

When bison began moving outside YNP during the mid-1980s, managers began hazing, capturing, and shooting them due to concerns about the transmission of brucellosis to cattle in Montana. By 1994, bison numbers increased to about 4,100, with almost 3,000 bison in central Yellowstone and larger winter movements towards the park's northern and western boundaries. Managers captured and shipped more than 1,000 bison to slaughter during the severe winter of 1997. There were a series of lawsuits because bison moving outside the park allegedly put Montana's ranching economy

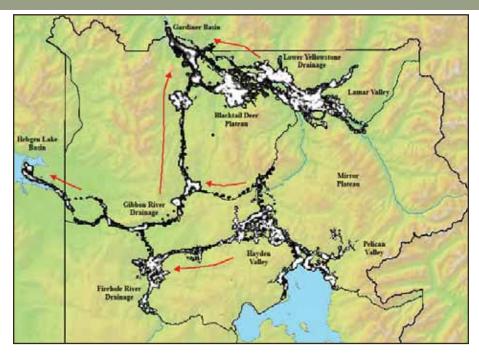


Figure 2. Winter (December-February) distribution of locations from radio-collared, adult, female bison during 2004-2012, with white areas showing increased use and arrows showing the direction of most movements (Geremia et al. 2015).

at risk from brucellosis outbreaks and trade restrictions. By December 2000, managers developed a management plan that allowed a few hundred bison to move into small, adjacent areas of Montana during winter, provided they did not mix with cattle.

Through the mid-2000s, bison tended to move from central Yellowstone to the western boundary of the park during winter. As a result, hazing actions to keep them within the park were more common at this boundary than in the north. There were about 3,500 bison in central Yellowstone and 1,500 bison in northern Yellowstone during the summer of 2005. Since then, there has been a large decrease in the number of bison in central Yellowstone, a rapid increase in the number of bison in northern Yellowstone, and more movements of bison from central to northern Yellowstone

(Wallen and White 2015). These movements were likely in response to high bison numbers in central Yellowstone, intense hazing along the western boundary, and groomed roads that allowed bison to rapidly travel to the north during winter (Meagher 1993). In addition, there was a decrease in numbers of elk in northern Yellowstone from about 19,000 in the mid-1990s to 3,915 elk by 2013 following the restoration of predators such as bears, cougars, and wolves. As elk numbers declined, the number of bison in northern Yellowstone increased from about 1,500 in 2005 to 4,000 in 2016-2017. In contrast, the number of bison counted in central Yellowstone decreased from about 3,500 in 2005 to about 1,200 in 2018. Hunters and managers removed more than 1,000 bison in 2006, 2008, and 2017-2018, primarily females and young that tend to move to the park boundary more than males.

In recent years, most bison in central Yellowstone have spent summer in the Hayden Valley. Many of these bison spent winter along the Firehole, Gibbon, and Madison rivers and nearby areas of Montana (Hebgen Basin), while others moved to northern Yellowstone. Most bison in northern Yellowstone have spent the summer in the Lamar Valley and adjacent areas, but then moved downslope to the Blacktail Deer Plateau and the Gardiner basin during the winter (Geremia et al. 2015). Since 2014, captures and shipments of bison to slaughter have occurred only near the northern boundary of the park, while harvests in Montana occur outside the western and northern boundaries (although hunters shoot more bison near the north boundary).

Genetic Diversity

Yellowstone bison have high genetic diversity (Halbert and Derr 2007, Hedrick 2009). The introduction of bison into the Lamar Valley from different genetic lineages than the native Pelican bison contributed to this diversity and, at least initially, created genetic differences between bison living in the central and northern

regions of the park. Bison sampled near the western and northern boundaries of the park during winters from 1997 to 2003 had somewhat different genetic make-ups (Halbert et al. 2012). These differences were a bit surprising given the mixing of descendants from the native and introduced lineages for many decades. Bison wintering in the Pelican and Lamar valleys used the same areas during the summer beginning in the 1920s and, in the mid-1930s, managers relocated descendants from the introduced Lamar lineage in northern Yellowstone to the Hayden Valley and Firehole River area in central Yellowstone. Bison from this Mary Mountain herd began mixing and breeding with bison from the Pelican Valley with the native lineage during the 1980s (Meagher 1998).

Regardless, since the mid-2000s there have been increasing movements of bison between central and northern Yellowstone that have further mixed descendants of the introduced and native lineages throughout the central and northern regions of the park. For example, two-thirds of adult females fitted with radio-collars in central Yellowstone during 2004 to 2017 moved in groups with hundreds of other female and young bison to northern Yellowstone during winter. About half of these collared females remained in northern Yellowstone at least through the breeding season the following summer. In addition, bison sampled in central and northern Yellowstone during 2011-2012 did not have distinct genetic make-ups. Rather, the native and introduced lineages were found in both areas in about equal proportions (Forgacs et al. 2016). We are continuing studies to further evaluate genetic diversity and the distributions of the historic bison lineages.

Literature Cited

See Literature Cited section of this issue on page 108.

In 2018, **Rick Wallen** retired from a career in the National Park Service. For 17 years, he was the team leader for the Bison Ecology and Management Program in the Yellowstone Center for Resources. He worked to gain more space for bison to occupy the greater Yellowstone landscape, so they could play their ecological role at a more meaningful scale. Rick collaborated with many colleagues to show bison could be allowed more freedom of movement without quickly transmitting brucellosis to nearby livestock. His work with NPS staff and cooperating agencies has led to a reduction in heavy handed management practices of the past and opened up doors for quarantine and relocation of live surplus bison to tribal nations through a partnership with the Assiniboine and Sioux tribes of Fort

Peck. During his tenure at Yellowstone the bison population increased from 2,000 to 4,500 individuals.

Rick initiated efforts to study the ecological influence of bison grazing on Yellowstone grasslands as the population doubled in size following the implementation of the Interagency Bison Management Plan in December 2000.



How Do Yellowstone's Ungulates Make a Home on the Range?

Lauren McGarvey & Chris Geremia

rellowstone National Park is home to many ungulates, including bison, bighorn sheep, elk, mule deer, and pronghorn. These ungulates are herbivores (only consume plants) and depend on grasslands for food. They move across the landscape in search of food, but grasslands are a limited resource. Biologists have long been interested in how similar species (types) of animals coexist when food resources are limited. Species may compete with one another if they use limited resources similarly, resulting in decreased nutrition, body condition, survival, and reproduction. However, species may lessen competition and coexist by partitioning food resources, such as consuming different plants and using areas at different times. We are studying the movements and diets of different ungulates in Yellowstone to determine how they make a home on the range – do they compete with one another or partition resources to coexist? This article provides our preliminary findings.

Migration and Ranges

Migration is the seasonal movement between two distinct, and often distant, ranges. Biologists have proposed several theories to explain why ungulates migrate, such as enhancing access to high quality forage, avoiding predation, and preventing grasslands from being overgrazed (Fryxell and Sinclair 1988). In Yellowstone, ungulates migrate along elevation gradients in response to snow accumulation or melting. In spring, ungulates follow a green wave of new, highly nutritious vegetation growing as snow melts from low-elevation winter ranges to high-elevation summer ranges. In fall, ungulates return to low-elevation winter ranges where less snow accumulates and food is more accessible.

We use global positioning system (GPS) collars to document ungulate movements. Collaring ungulates requires a tranquilizer gun and immobilization drugs (Figure 1). Once we immobilize an animal, we fit it with a GPS collar and release it. The newly collared



Figure 1. Biologists fitting a female pronghorn with a GPS collar.

animal continues its natural movements, and now we know its daily locations. We use these locations to create a detailed map of the animal's migration and ranges.

Bighorn sheep, elk, mule deer and pronghorn have similar migration strategies. These species tend to have distinct ranges they migrate between during spring and fall. When these species migrate, they take a direct path between ranges with a few stops along the way to "refuel." The individual bighorn sheep, elk, mule deer, and pronghorn migrations illustrated in Figure 2 lasted between 3-21 days. Once these animals reached their seasonal range, they stayed in a relatively small geographic area for the rest of the season.

Bison migrate differently than other ungulates in Yellowstone. Bison are more nomadic and stop to graze areas while they migrate. For example, the individual bison illustrated in Figure 2 migrated from Blacktail Deer Plateau to Lamar Valley, up the Lamar River drainage, returned to the Lamar Valley, and then moved to the Hayden Valley. Her migration from Blacktail Deer Plateau to Hayden Valley lasted 77 days. Instead of having distinct ranges, bison wander throughout their migration. The article titled "Give Bison Room to Roam" in this volume explains why bison migrate differently than other ungulates.

During summer, most ungulates use high-elevation areas where new, highly nutritious vegetation grows. Bison and pronghorn use grasslands in Lamar Valley, while bison also use grasslands on the Mirror Plateau and in the Pelican and Hayden valleys (Figure 3). Bighorn sheep use meadows on the mountain ridges surrounding Lamar Valley and in the Gardiner basin. Elk and mule deer use meadows and forests throughout Yellowstone. The most overlap in summer range occurs between bison and pronghorn (Table 1). Bison summer range overlaps with 76% of pronghorn summer range, whereas pronghorn summer range overlaps with 26% of bison summer range. The percentage of overlap varies between bison and pronghorn because bison collectively have a very large summer range, whereas pronghorn have a very small summer range.

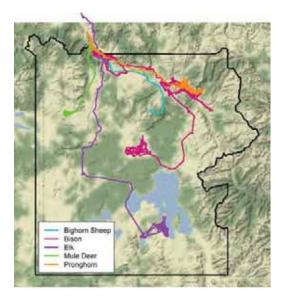


Figure 2. Migration routes of individual bison, bighorn sheep, elk, mule deer, and pronghorn in Yellowstone National Park.

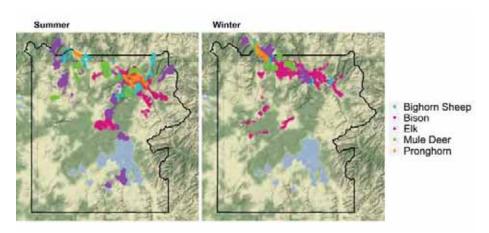


Figure 3. Daily locations of GPS-collared bighorn sheep, bison, elk, mule deer, and pronghorn by season. Each point represents a GPS location. Summer locations are from July to September; winter locations are from December to March.

Table 1: Proportion of summer range overlap between species. For example, pronghorn summer range overlaps with 26% of bison summer range and bison summer range overlaps with 76% of pronghorn summer range. The numbers of radio-collared animals are in parentheses.

Species	Bighorn Sheep	Bison	Elk	Mule Deer	Pronghorn
Bighorn Sheep (6)	1.00	0.06	0.05	0.12	0.10
Bison (7)	0.12	1.00	0.08	0.13	0.76
Elk (6)	0.08	0.06	1.00	0.10	0.00
Mule Deer (5)	0.13	0.07	0.08	1.00	0.04
Pronghorn (4)	0.08	0.26	0.00	0.03	1.00

During winter, most ungulates use low-elevation areas where less snow accumulates in northern Yellowstone and north of the park (Figure 3). The most overlap in winter range occurs between pronghorn and bison (Table 2). Bison winter range overlaps with 83% of pronghorn winter range. Bison overlap with the majority of pronghorn winter range because pronghorn use a very small winter range in northern Yellowstone and the Gardiner basin. Bison winter range also overlaps with 71% of mule deer winter range and 72% of bighorn sheep winter range. As with pronghorn, these species use small winter ranges in northern Yellowstone and the Gardiner basin. In addition to northern Yellowstone, bison also use areas in the Hayden Valley and the Firehole and Madison River drainages during winter.

Diet Composition and Overlap

Diet composition is the proportion of different plant species consumed by ungulates. Biologists have found diet composition varies considerably among ungulates, especially those that primarily

Table 2: Proportion of winter range overlap between species. For example, mule deer winter range overlaps with 6% of bison winter range and bison winter range overlaps with 71% of mule deer winter range. The numbers of radio-collared animals are in parentheses.

Species	Bighorn Sheep	Bison	Elk	Mule Deer	Pronghorn
Bighorn Sheep (6)	1.00	0.05	0.10	0.07	0.26
Bison (8)	0.72	1.00	0.36	0.71	0.83
Elk (6)	0.23	0.06	1.00	0.01	0.06
Mule Deer (5)	0.09	0.06	0.01	1.00	0.13
Pronghorn (4)	0.30	0.07	0.03	0.12	1.00

browse and those that primarily graze (McNaughton and Georgiadis 1986). Browsers primarily consume forbs (flowering plants), conifers, and shrubs, while grazers primarily consume grasses. There also are ungulates that consume both browse and grass. Browsers and grazers typically vary in body size, morphology, and digestive physiologies. Large-bodied ungulates typically graze low quality vegetation, such as grass, because it is plentiful enough to meet their energetic demands and digests efficiently in their large, 4-chambered stomachs. Small-bodied ungulates typically browse high quality vegetation, such as forbs, because these plants digest quicker in their smaller stomachs.

We study diet composition by collecting fresh fecal samples from groups of ungulates with at least one animal wearing a GPS collar that provides spatial information. Laboratory technicians analyze fecal samples using a technique called microhistology in which they place a portion of the fecal sample on a microscope slide, examine it under a microscope, and identify species of plant fragments. We analyze diet composition seasonally because it varies with the

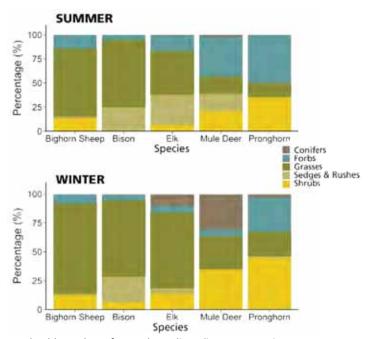


Figure 4. Stacked bar plot of ungulate diets (i.e., vegetation type consumed) determined by examining fecal samples.

availability of plants. Grasses and forbs are abundant and easily accessible during the summer. These plants become dormant and covered by snow during the winter, making them scarcer and less accessible. As a result, some ungulates consume shrubs and conifers that are more accessible.

During the summer, bighorn sheep, bison, and elk primarily consumed grasses (Figure 4). Bighorn sheep and bison preferred bluebunch wheatgrass, bluegrass, and Idaho fescue. Elk preferred bluegrass as well, but also consumed a high proportion of reed grass. Mule deer and pronghorn primarily consumed forbs. Both species preferred geranium, but mule deer also preferred lupin. In addition to forbs, pronghorn preferred shrubs such as big sagebrush. Bison, elk, and mule deer also consumed a considerable amount of

sedges during the summer.

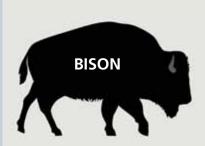
During the winter, bighorn sheep, bison, and elk consumed grasses (Figure 4). Elk and mule deer consumed more conifers in the winter, such as juniper and Douglas fir. Unlike the other ungulate species, pronghorn consumed a high proportion of forbs, such as phlox, during the winter.

We assess diet overlap by comparing how similar diet compositions are among different ungulates using ordination (Kartzinel et al. 2015). Ordination creates a simple plot from very complex diet data. Diets plotted closer together are more similar than diets plotted further apart. Diet variation within a species depends on the closeness of individual diets. Species with individual diets that cluster together in plots (smaller ellipses) have less variation in diet than species with individual diets spread apart (larger ellipses).

There was less overlap in diet among ungulate species during the summer (Figure 5). Bison and elk, which graze on grasses, have the most overlap in diet. However, bison are more similar in diet to other bison (indicated by the tight clustering of their points), whereas elk have more variation in diet (indicated by the spread of their points). Pronghorn, which primarily browse forbs and shrubs, have the least overlap in diet with the other ungulate species. Pronghorn also have the most variation in their diet compared to the other ungulate species.

There was more overlap in diet during the winter, especially among bighorn sheep, bison, and elk, which primarily graze on grasses (Figure 6). As in the summer, bison are more similar in diet to other bison whereas elk have more variation in their diet. Instead of primarily grazing grasses as in the summer, elk browse more conifers in the winter. Mule deer and pronghorn also have more overlap in diet with the other ungulate species during the winter.

What Do Yellowstone's Ungulates Eat?



Summer

- 1. true sedges
- 2. bluebunch wheatgrass
- 3. Idaho fescue

Winter

- 1. bluebunch wheatgrass
- 2. true sedges
- 3. Idaho fescue



Summer

- 1. true sedges
- 2. lupine
- 3. cranesbill or geranium

Winter

- 1. big sagebrush
- 2. juniper
- 3. Douglas fir needles



Summer

- 1. true sedges
- 2. annual meadow grass
- 3. reed grass or smallweed

Winter

- 1. bluebunch wheatgrass
- 2. annual meadow grass
- 3. Idaho fescue



Summer

- 1. forbs
- 2. big sagebrush
- 3. geranium

Winter

- 1. big sagebrush
- 2. whitlow-grass
- 3. bluebunch wheatgrass



Summer

- 1. bluebunch wheatgrass
- 2. annual meadow grass
- 3. Idaho fescue

Winter

- 1. bluebunch wheatgrass
- 2. feather grass/needle grass
- Idaho fescue

Discussion

We observed the greatest overlap in summer range among bison and pronghorn. Many bison and pronghorn use the Lamar Valley during summer. Bison primarily graze on grasses whereas pronghorn primarily browse on forbs. Because bison and pronghorn consume different foods, there is little potential of competition between the two species even though they use similar spaces. Pronghorn may even benefit from using similar summer range as bison. Bison preferentially graze on grasses and avoid forbs, which make up a very small percentage of their diet (Knapp et al. 1999). By preferentially grazing on grasses, bison enable forbs, the primary food of pronghorn, to flourish (Knapp et al. 1999). Biologists observed a similar relationship in the Serengeti of east Africa. Over one million wildebeest, a grazer that aggregates in large groups like bison, migrate across the Serengeti Plains following rainfall.

Wildebeest graze and remove the majority (up to 85%) of plant biomass as they migrate (McNaughton 1976). A month later, substantial numbers of Thomson's gazelles begin using these areas (McNaughton 1976). The intense grazing of migratory wildebeest promotes grass growth and creates a dense lawn of nutritious grass that Thomson's gazelles feed on during the dry season (McNaughton 1976). Instead of competing, Thomson's gazelles use the same area as wildebeest for their benefit.

We observed the most overlap in winter range among bighorn sheep, mule deer, and pronghorn with bison. Bison have a very large winter range, whereas bighorn sheep, mule deer, and pronghorn have much smaller winter ranges. Bison are able to use a greater area of Yellowstone during winter because they do not migrate as early to avoid deep snow (Kauffman et al. 2018). Instead, bison

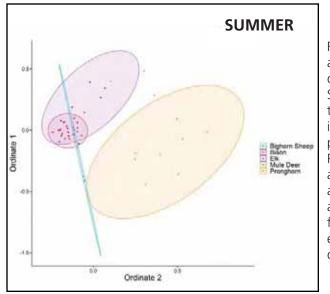


Figure 5. Diet overlap among ungulate species during the summer. Species plotted closer together are more similar in diet than species plotted farther apart. Points are individual diets and ellipses are drawn around all the diets within a species. There were too few points to draw an ellipse around mule deer diets.

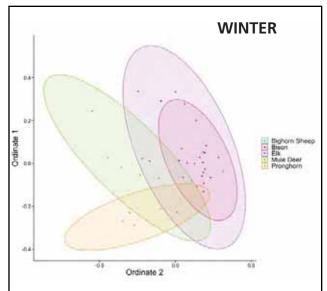


Figure 6. Diet overlap among ungulate species during the winter. Species plotted closer together are more similar in diet than species plotted farther apart. Points are individual diets and ellipses are drawn around all the diets within a species. There were too few points to draw an ellipse for bighorn sheep diets.

use their massive heads like shovels to access forage beneath deep snow. If snow conditions become too harsh, bison will migrate to the low-elevation areas used by other ungulates. This accounts for the large overlap of bison winter range with bighorn sheep, mule deer, and pronghorn winter ranges. Even though these species use similar winter ranges, there is little potential for competition among bison, mule deer, and pronghorn because they consume different foods. Bison primarily graze on grasses, whereas mule deer and pronghorn primarily browse on conifers, forbs, and shrubs. There may be potential for competition between bighorn sheep and bison because they consume similar foods, but we need more data before we can make this determination. Biologists suspected competition between bighorn sheep and elk when almost 20,000 elk used northern Yellowstone (Singer and Norland 1994). Now that bison numbers have increased and elk numbers have decreased. bison may be competing with bighorn sheep when range is limited during the winter. However, it is important to note that competition

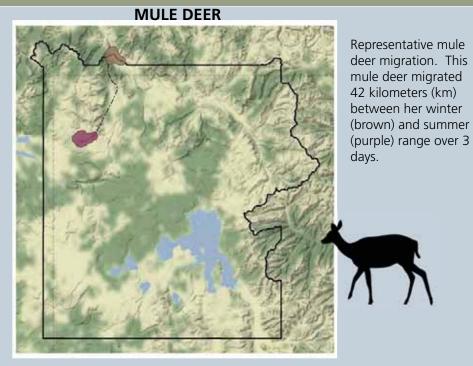
does not occur simply because there is spatial overlap in ranges. For competition to occur, resources must be limited. Numbers of bison, elk, and pronghorn have increased over the past few years, suggesting resources are not currently limited. Bighorn sheep abundance has remained stable, but this does not indicate they are competing with other ungulates because there may be other factors limiting their abundance. For example, bighorn sheep may be competing with each other for the limited amount of steep terrain they depend on to escape predators.

We observed the greatest overlap in diet between bison and elk, both of which are large grazers, but little overlap in range. A previous study of ungulate relationships in Yellowstone indicated overlap in winter range between bison and elk (Singer and Norland 1994). However, this study occurred before managers reintroduced gray wolves and there were more than 20,000 elk using northern Yellowstone. Ten years after the reintroduction of wolves, the elk population numbered 6,500 individuals. Elk are the primary prey of

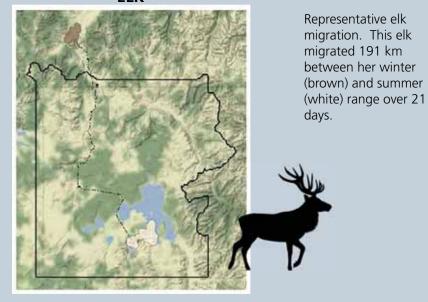
Yellowstone Ungulate Migration Patterns



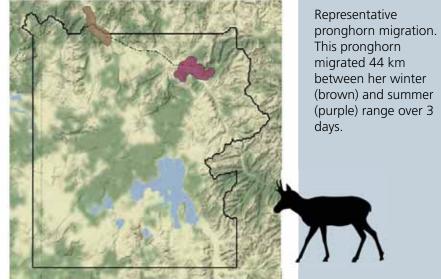
Representative bison migration. This bison roamed throughout her migration instead of having a distinct route or completely separate winter (brown) and summer (purple) ranges.



ELK



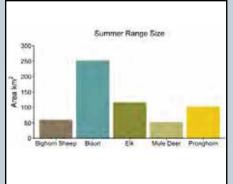
PRONGHORN

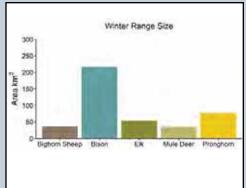


BIGHORN SHEEP



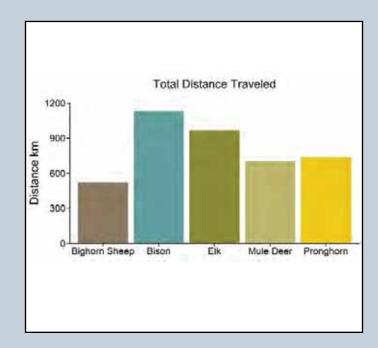
Representative bighorn sheep migration. This bighorn sheep migrated 54 km between her winter (brown) and summer (purple) range over 7 days.





In Yellowstone National Park, ungulates migrate following elevational gradients to access forage. Ungulates move from higher elevations where nutritious vegetation grows during summer to lower elevations where less snow accumulates during winter. We typically think of ungulates having distinct summer and winter ranges they migrate between each spring and fall. However, not all ungulate migrations are this simple.

Bison wander throughout their migration instead of having distinct summer and winter ranges. This results in bison traveling farther and utilizing greater areas than other ungulates. The bighorn sheep, elk, mule deer, and pronghorn had geographically small summer and winter ranges they migrated between. The bison, however, utilized much larger summer and winter ranges with no distinct migration between them.



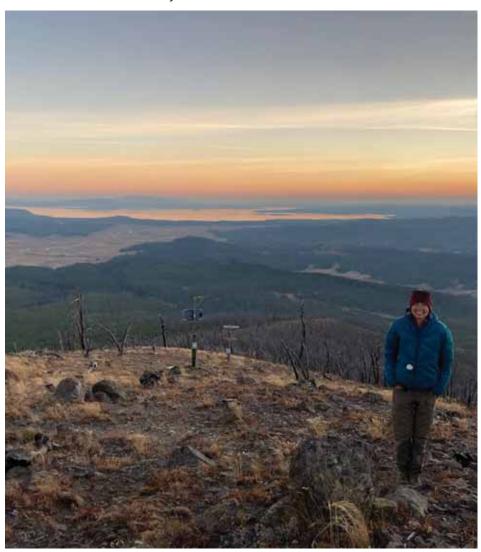
wolves, and wolf predation has resulted in fewer elk wintering in the Lamar Valley where wolf abundance is high (White et al. 2012). Bison experience far less wolf predation because of their large size and group defense strategies (bison group up to defend themselves instead of running away) which enables them to use areas of Lamar Valley during the winter that elk no longer use (White et al. 2015). Elk now primarily use winter range north of Yellowstone in the Gardiner basin and Paradise Valley where predator abundance is lower (White et al. 2012). Bison also use winter range in the Gardiner basin, but the State of Montana does not allow them to access winter range in the Paradise Valley because of concerns about disease transmission to cattle (White et al. 2015). Consequently, bison and elk have less overlap in winter range than previously reported.

Overall, our results suggest competition is not currently limiting the abundance of ungulates in Yellowstone. During the summer, ungulate species use different areas, with the exception of bison and pronghorn, which alleviates potential competition among them. Because bison increase plant biomass and diversity, pronghorn may benefit from using similar summer range as bison. During the winter, ungulates are concentrated in low-elevation areas of northern Yellowstone and beyond the northern boundary. However, variation in winter ranges, timing of migration, and diets alleviates potential competition among ungulate species. It appears that Yellowstone's ungulate species make a home on the range by partitioning resources to coexist with each other.

Literature Cited

See Literature Cited section of this issue on page 108.

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Citizen Science

Collecting fecal samples from radio-collared ungulates (up to 75 animals) takes a lot of effort. To accomplish this task, biologists from the National Park Service work collaboratively with citizen scientists through Ecology Project International, Yellowstone Conservation Corps, and Yellowstone Forever. Citizen scientists locate collared animals throughout Yellowstone to collect group demographic information on sex and age composition, and fecal samples. Our partnerships with citizen scientists enable us to implement a large-scale research project and teach students about ungulate ecology and conservation in Yellowstone.



Citizen scientist using radio telemetry to locate collared bison (Photo: Ecology Project International)



Citizen scientists classifying bison by sex and age (Photo: Ecology Project International)



Bison fecal sample collected by citizen scientists (Photo: Ecology Project International)

Are Northern Yellowstone Rangelands Healthy or Degraded?

Chris Geremia & Bill Hamilton



We are studying soil health and plant community productivity to evaluate concerns that bison degrade grasslands in northern Yellowstone.

here is no shortage of opinions about the numbers of bison and elk in Yellowstone and their effects on the vegetation. There is an ongoing scientific debate about what defines healthy rangelands and whether there are too many bison in the park.

We began a landscape-level study of grazing in northern Yellowstone in 2012 and have completed 10 years of field research. The core

of our work revolves around 30 sites in non-forested meadows where there is frequent grazing. Each site is about 1 acre (4,047 square meters) in size and includes different types of small grazing exclosures. We measure soil health, plant growth, grazing intensity, and plant community composition.

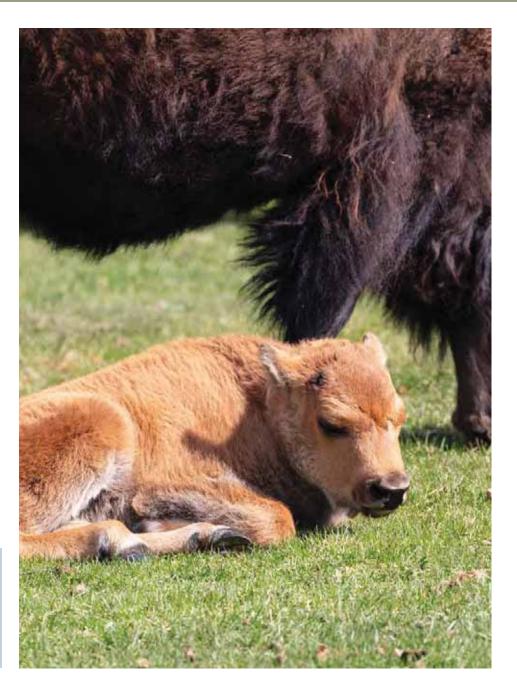
We are hoping to add clarity to a long debate over whether abundant herbivores (plant eaters) have negatively affected or permanently damaged the vegetation in northern Yellowstone. Decades of disagreement culminated in a congressionally mandated assessment of the health of northern Yellowstone during the late 1990s. The conclusions, published in 2002, indicated northern Yellowstone was not facing imminent ecological collapse. Some riparian and lower elevation sagebrush habitat had fundamentally changed in response to high browsing by elk. However, these independent scientists recommended park managers continue the policy of minimal management of elk, bison, and pronghorn within the park. They highlighted changing climate as the greatest threat to the integrity of northern Yellowstone and recommended park managers reassess the grazing system in 10 to 15 years (NRC 2002).

Grazing ecosystems are places where wild grazers and plant species have lived together for thousands of years. They are the most imperiled ecosystems on the planet. Slowly evolving, finely tuned relationships among soils, plants, and grazers make these ecosystems healthy even when they are grazed (Frank et al. 1998). By healthy, we mean these systems can sustain nutrient, energy, and water transfer (Holechek et al. 1989, Briske 2011).

If the question is whether grazers, previously elk and currently bison, reduce ecosystem health, how do you determine if nutrients, energy and water are being transferred properly? The answer is to look at the soils and plants, because they create a nutrient and energy supply that can be transferred to all other organisms in the ecosystem (Pyke et al. 2002, Pellant et al. 2005). It boils down to two simple questions: are soils sustainable and are plant communities maintaining productivity.

Are there too many bison?

Bison are ecosystem engineers that move and graze across the land to intentionally create hotspots, areas of high grazing, which improves their own food quality. Some areas are grazed more intensely than they would be if we intrusively controlled grazing in the park.



Overgrazing or Over-browsing?

Elk dominated conversations about the health of Yellowstone for decades. During the 1930s, photographs of the quintessential Yellowstone valleys, like the Lamar Valley, showed narrow swaths of willows, aspens, and cottonwoods that stretched along riverbanks. Increasing elk populations during the second half of the twentieth century coincided with the decline and eventual loss of these communities. This abrupt change became the fodder for debates over whether elk overgrazed Yellowstone.

Those claiming overgrazing pointed to the disappearance of woody vegetation. Others rebutted those claims by equating ecosystem recovery with predator recovery, and testing if wolf recovery could alter elk abundance, movements, and feeding behaviors, thereby allowing willow, aspen, and cottonwood to regrow (Peterson et al.2020).

However, we might not be looking at the right measure of overgrazing. It's flowering plants, not woody riparian vegetation, that underpin the Yellowstone grazing ecosystem. Grasslands dominate northern Yellowstone. Flowering plants, including grasses, grass-like plants, and showy flowers dominate grassland plant communities. Flowering plants not only make up the overwhelming bulk weight of vegetation in northern Yellowstone, particularly compared to riparian woody vegetation, but they also make up the majority of large herbivore diets.

Elk primarily feed on flowering plants, which make up more than 95% of summer and 75% of winter diets. On the other hand, woody riparian vegetation makes up less than 1% of summer and about 2% of winter diets. Bison also prefer flowering plants, making up about 97% of diets.

Make no mistake, riparian areas are very important to ecosystems. So is the massive amount of research dedicated to figuring out the extent to which wolves and other predators indirectly contribute to woody plant growth. However, if the question is whether or not the grazing ecosystem of northern Yellowstone is stable, grasslands and shrublands should be the focus of assessments moving forward.



If we managed Yellowstone like a ranch, the first thing we would do is figure out how many animals northern Yellowstone could support without diminishing the productivity of the plant communities. This takes estimating the amount of plant material produced within northern Yellowstone and the food requirements of each animal. Standard practice is to have enough animals to eat about 50% of the plant material. Some plant material is unavailable for grazing because it is lost to trampling, defecation, and bedding. Thus, the "take half, leave half" approach, which was long considered the preferred strategy for sustainable grazing, equates to having enough animals to eat about 25 to 50% of the total plant material produced each year.

We used state-of-the-art technology to analyze satellite images and estimate the amount of plant forage produced across northern Yellowstone. In an average year, northern Yellowstone produces about 165 to 172 million pounds (74 to 78 million kilograms) of plants. The entire park produces around 426 million pounds (193 million kilograms), almost two and half times that amount. Moreover, our estimates are conservative. We could only estimate plant production in non-forested areas, because satellites cannot see through trees. Plants growing in partly forested areas were not included, which provide an unknown additional amount of forage.

It is hard to believe, but an adult female bison eats between 400 and 1,000 pounds (180 to 455 kilograms) of plants each month, which equates to about 9,600 pounds (4,355 kilograms) of plants each year – 4.8 tons (4,355 kilograms) of plant material for each adult female each year. Bison of different ages and sex eat different amounts of forage. Calves, for example, eat very little forage while they are nursing. Larger males eat upwards of 5.5 tons (4,990 kilograms) of forage each year.

The age and sex composition of bison in northern Yellowstone is about 35% adult males, 35% adult females, 13% juveniles, and

17% calves. Given this age and sex structure, northern Yellowstone can support at least 5,000 bison based on "take half, leave half" approach. That is just in northern Yellowstone. The entire park can support at least twice that number.

When looking across all grazing animals in northern Yellowstone, there are about 3,500 bison, 7,500 elk, 500 pronghorn, 2,000 mule deer, and 500 bighorn sheep, equating to about 3 to 4 million pounds (1.3 to 1.8 million kilograms) of grazers. When considered together, all these animals still do not make up enough grazer biomass to take half and leave half of the plant material produced.

However, Yellowstone is not a ranch. The above discussion is premised on the idea of uniform grazing, by the right animal at the right time. In Yellowstone, animals get to decide where and when they graze. They have developed finely tuned migrations to move and graze across the land to get the essential foods they need to raise young, survive harsh winters, and avoid predators. Nature decides who lives and dies and the best moving and grazing strategies are passed on among generations. Take bison for example, who migrate with the green wave in early spring, before slowing their movements and letting it pass them by. They create grazing lawns, areas of particularly intense, repetitive grazing, which resets plant growth allowing them to continue to eat high quality foods (Geremia et al. 2019).

We used radio-collars to map the intensity of bison use across northern Yellowstone each month of the year. We adjusted intensity maps by the number and composition of bison, which created monthly estimates of the numbers and types of animals using each area of northern Yellowstone. From these estimates, we extracted the number of used Animal Unit Months and compared them to available Animal Unit Months. When you give bison room to roam, they do not uniformly graze areas in northern Yellowstone. Instead they use about 81% of the area at lower intensity, 9% at equal

How We Determine Carrying Capacity



An ANIMAL UNIT (AU) is a 1,000 pound animal. Age and body size is used to determine animal unit equivilents (AU). A 2,000 adult male bison is 2 AU.

This information is used to calculate **AUMs (ANIMAL UNIT** MONTHS).

An AUM is 800 pounds of plants - the amount of food required to sustain a 1,000 pound bison over the course of a month.





section of the northern range.

To estimate the number of bison that the northern range could sustain, we collected Yellowstone-specific data. To determine **AU**, we weighed bison across age and sex classes. To determine **PLANT PRODUCTION**, we used satellite imagery to estimate plant composition and ground-truthed our estimates by creating grazing plots where we collected plant growth and analyzed it's nutritional content. We also used GPS-collared bison to track grazing activity across a grid and quantified how much time bison spent in each

A 2,000 pound bison (2 **AU) requires 2 AUMs** each month and 24 AUMs each year.

Blson decide where and when to graze. They develop finely tuned migrations to move and graze across the landscape to get essential food needed to raise young, survive Yellowstone's harsh winters, and avoid predators.

Bison graze different parts of the landscape differently. Unlike livestock, whose grazing is controlled by rotation through fenced pastures, bison do not graze following a "TAKE HALF-LEAVE HALF" strategy. This strategy, considered ideal by cattle producers, removes about 50% of available plant production from their ranchlands.

Yellowstone is NOT a ranch. Across the northern range, bison graze about 81% of areas lighter, 9% of areas near, and 10% of areas more intensely than a take half-leave half management strategy.

How Many Bison Can Northern Yellowstone Support?

Bison Population Status

Three thousand to 4,000 bison migrate across the northern range. The population is made up of about 35% adult males, 35% adult females, 13% juveniles, and 17% calves.

Using all the data gathered and what we know from overflights about the composition of the northern herd, we reached the following conclusion: the northern Yellowstone produces enough herbaceous plant material each year to support more than 5,000 bison.

Number of bison	Percent (%) of AUMs used
1,000	9-19%
2,000	19-38%
3,000	28-56%
4,000	38-75%
5,000	47-93%
10,000	>99%

intensity, and 10% at higher intensity. Our challenge is to evaluate these areas of high use and determine whether bison grazing is sustainable.

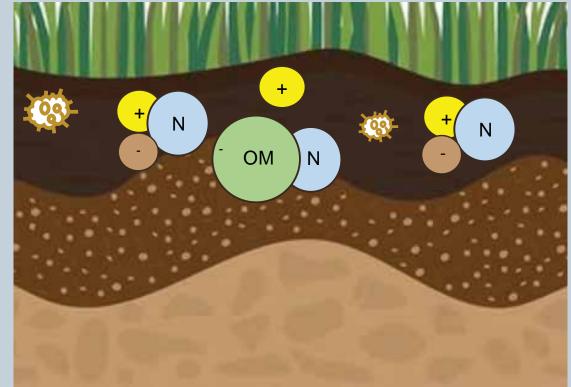
We analyzed soils by studying the top 4 to 8 inches (10 to 20 centimeters) inside and outside of small exclosures set up at each grazing site. We evaluated soils every month of each growing season to account for seasonal effects on soil nutrients, water holding potential, and microorganisms.

Soils in our grazing study sites contain approximately equal proportions of sand, silt, and clay. These names refer to particle size. The smallest particles are clay, larger particles are silt, and the largest are sand. Soils that have relatively equal proportions of sand, silt, and clay best support plant growth. The different sized particles leave spaces for air and water to flow and roots to penetrate, with enough sand to drain, and enough clay and silt to hold moisture and retain soil nutrients.

We did not detect soil compaction based on bulk density, which is less than 1.2 grams per cubic centimeter in all sites. Soil cores taken within wallows showed differing levels of compaction. Wallows are bedding areas, devoid of plants, that animals use to dust themselves for cooling, avoiding insects, and scent marking.

Soil pH ranges from slightly acidic to slightly basic and is less than pH 8 at all sites. Nutrients enter the soil in organic forms that are unavailable to plants. Microbes convert nutrients from organic to plant-friendly inorganic forms. Some inorganic forms such as nitrate and phosphate are negatively charged and either immediately absorbed by plants or leached away because soil particles also are negatively charged and like charges repel each other. Most inorganic nutrients are neutral or positively charged such as ammonia and ammonium, respectively. Positively charged inorganic nutrients bind to negatively charged soil particles, which retains them in the soil for plants. Soils with lower than pH 8 facilitate changing neutral (ammonia) inorganic nutrients to positively charged (ammonium) inorganic nutrients, which then allows them to be retained as well.

Soil microbial biomass averages 72 grams of carbon per square meter suggestive of abundant microbial populations. Different types of microbes feed on different types of soil organic matter. It is important to not only have diverse microbial populations, but soil nutrients in relative concentrations that balance microbial populations that feed on different soil components. Percentages of carbon and nitrogen in soil organic matter fall within desired ranges to support nitrogen and carbon consuming bacteria, which releases both nutrients in relative abundances necessary for plant growth.



SOIL ORGANIC MATTER (SOM) is the part of soil composed of decaying plant and animal parts.

Why is it important? It links the physical, biological, and chemical properties of soils as a general indicator of soil health. SOM supports microbes, improves water-holding capacity, and is the entry route of nutrients to the soil.

In agricultural, the goal is to maintain SOM above 2-3% and use fertilizer to support lands with less than 8%.

Grazing Site Averages:

- SOM averages 13% and ranges from 7-22%
- Plant production increases with SOM
- Short-term 3-year removals of bison grazing had no effect on SOM
- Comparisons inside and outside 60-year permanent exclosures show long-term stability
- Bison change the source of SOM from dead plant matter to animal waste

Soil organic matter is a single measure of soil health that captures the physical (particle size, bulk density, water holding capacity), chemical (pH, nutrient concentration), and biological (microbial populations) properties (Briske 2011). It is the fraction of the soil made up of decaying plant and animal tissue. Soil organic matter is the sponge of the soil, soaking up and holding water, microbes, and nutrients. In agriculture, fertilizer is used to augment soil organic matter when levels fall below 2 to 3%. Soil organic matter exceeds this level in northern Yellowstone, averaging 13% across sites.

Soil organic matter provides a quantitative assessment of erosion. Wind and water runoff hold the potential to remove the top soil horizons, which contain the greatest proportions of soil organic matter. Healthy soils show long-term stability in organic matter. Short- and long-term exclosure experiments show soils are in a nutrient-rich equilibrium. Short-term rest does not affect soil organic matter. We installed 3-year exclosures and detected no differences in soil organic matter inside or outside exclosures during the entire experiment. We also analyzed soil organic matter inside permanent exclosures set up nearly 60 years ago. It was the same as soil organic matter measured outside those exclosures today.

Bison and Elk Dung

Bill Hamilton

t is a common practice in agriculture to spread manure on fields to increase soil nutrients, primarily nitrogen and phosphorous, which then improves plant productivity. Migratory animals such as bison and elk do the spreading on a much broader scale and seasonal variations in snowpack and rainfall influence their migratory patterns. In 2016, my students and I collaborated with students from Ecology Project International to conduct transect surveys for bison and elk dung across their migratory ranges. At each site, we established at least ten 1-meter by 100-meter transects in which dung was collected and weighed. The total sample size was more than 400 transects for bison and 50 transects for bison and elk combined. We only collected dung that was not bleached and still contained moisture. A "freshness scale" was assigned to dung and samples were taken across the scale for analysis of water content, extractable nitrogen, phosphorous, and total carbon and nitrogen. We found the only difference between samples in the freshness scale was moisture content.

Carbon to nitrogen ratios in organic matter control the fate of carbon and nitrogen during decomposition. Organic matter with ratios higher than 30 to 1 are nitrogen limited and, therefore, decomposers immobilize nitrogen while breaking down carbon bonds. When carbon to nitrogen ratios are less than 25 to 1, nitrogen can be mineralized and become available in inorganic forms that primary producers can use for growth. Our sampling showed that the carbon to nitrogen ratio of bison and elk dung varied through the season and that bison and elk dung differed across all sampling points except during April and May (Figure 1). The carbon to nitrogen ratio of dung is correlated with the carbon to nitrogen ratio of the forage entering an animal. As ruminants, elk are classified as grazers and intermediate feeders because they consume grasses, forbs, and browse, and the composition of the diet varies with season. Bison are classified as grazers because most of their diet

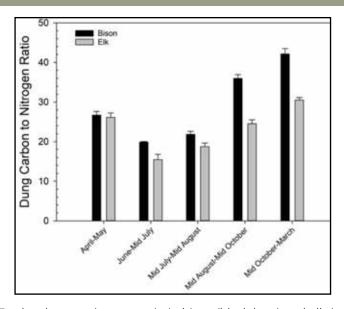


Figure 1. Total carbon to nitrogen ratio in bison (black bars) and elk (gray bars) dung across five time periods in a calendar year.

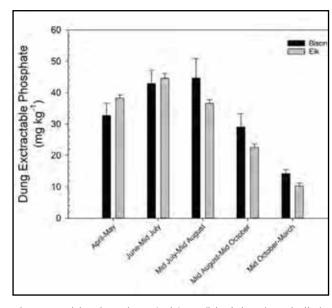


Figure 2. Total extractable phosphate in bison (black bars) and elk (gray bars) dung across five time periods in a calendar year.

is grasses with minimal forb and browse consumption (Vallentine 2001). Based on the carbon to nitrogen ratios of dung in elk and bison, both species generate dung during April to September that is favorable for providing nitrogen to plants for growth.

Phosphorous is an important plant macronutrient and exists in soils in forms that are not readily available to plants. Analysis of water extractable phosphate, which is the oxidized inorganic form of phosphorous taken up by plants, in elk and bison dung showed there is seasonal variation in dung phosphate levels. Bison and elk dung have similar seasonal trends, but elk dung has less phosphate from mid-July to March (Figure 2). The differences are likely the result of diet selection.

More than 300 transects for collecting bison dung were at seven sites across northern Yellowstone. Using the transect data, we estimated the density of bison dung patties at each site during the growing season (April-September) and found it ranged from 145 to 462 patties per hectare. From this estimate, the amount of cumulative extractable phosphate and nitrogen in dung can be estimated across the seven sites. Phosphate ranged from 1.1 to 4.8 kilograms per hectare and nitrogen ranged from 7.2 to 26.2 kilograms per hectare. Dung deposition is a major contributor to these values, but seasonal variation in dung quality (Figures 1 and 2) also contributes to the differences across sites. The Lamar Valley and slopes between Cache and Calfee creeks are sites with high productivity that have higher grazing intensities, while sites in the Gardiner basin, Blacktail Deer Plateau, Hellroaring Mountain slopes, and Crystal Bench near the base of Specimen Ridge are lower in productivity and used during migration in spring and fall (Figure 3.)

This snapshot in time of bison and elk dung provides interesting results about the importance of herbivore dung as manure in

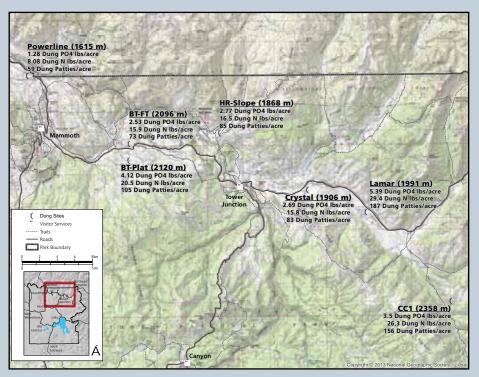
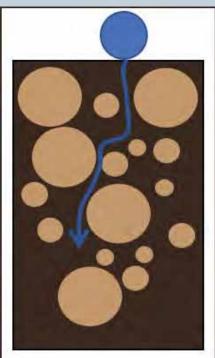


Figure 3. Bison and elk dung transects on the northern range of Yellowstone National Park.

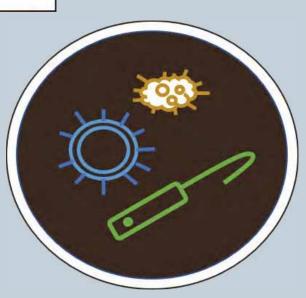
Yellowstone grasslands and suggests more work needs to be done. My students will be observing bison and elk dung deposition behavior to understand the frequency and mass of dung production. In the laboratory, we will conduct soil incubation experiments to investigate the effects of dung on decomposition of organic matter and the microbial communities responsible for decomposition.

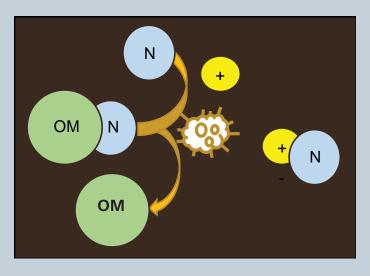
Why Does Soil Matter?



PHYSICAL PROPERTIES of soils can promote plant growth. Soils with large (sand), moderate (silt), and small (clay) particle sizes are LOAMY SOILS which allow water and root infiltration while holding water and nutrients for plant uptake.

- Grazing Site Averages:
 Loam (44%), Sandy-Clay-Loam (44%), Clay-Loam (8%), and Sandy-Loam (4%)
- Bulk density: < 1.2 grams per cubic centimeter indicating soils are not compacted.





CHEMICAL PROPERTIES

Soils with less than pH 8 promote plant growth by positively charging inorganic nutrients, which bind to negatively charged soil particles. Binding nutrients to soil particles minimizes their leaching.

Grazing Site Averages:

- pH ranges 5.2-7.7 which is well within ranges of optimal growth for existing native plants
- Plant available nitrogen averages 40 milligrams per kilogram

BIOLOGICAL PROPERTIES

Diverse and abundant microbial populations convert organic matter into inorganic nutrients. It is important to maintain balanced microbial populations that feed on different sources of organic matter and break down different types of nutrients.

Grazing Site Averages: Microbial biomass carbon averages 72 grams per square meter. Soil carbon to nitrogen ratios are well within a range of 5-18 which supports carbon and nitrogen feeding microbes.

Habitat Types

oil properties and weather create four habitat types for grassland and shrubland plants in the areas used by bison in northern Yellowstone. The habitat types vary by elevation and topographic position and we refer to them as mountain meadow, valley floor, valley slope, and low-elevation range.

Plant communities are arrangements of plants that typically grow together. Plants must absorb soil nutrients, water, and sunlight to grow. Different plants have unique rooting depths, leaf area, height, life form, lifespan, growing season, and ways to reproduce. These attributes are called functional traits. Healthy plant communities contain a wide range of functional traits, which enables them to optimize productivity across the community (Funk et al. 2017).

Each habitat type supports its own set of plant communities, because plants are adapted to grow best under certain conditions. Nature makes plant communities dynamic. Forces like drought, disease, grazing, and fire slightly modify conditions making them better for certain plants. Some species grow better under the new conditions and proliferate while others decline; a process called plant succession. Plants that grow better after disturbance are called early successional stage (early seral); those that grow best long after disturbance are called late seral. Changes do not tend to be dramatic or permanent. They shift the relative abundance of species.

Too much disturbance can fundamentally change everything. It can push plant communities across a threshold. By doing so, the existing communities disappear and are replaced by entirely new, undesired ones. Thresholds are one-way roads. It is very difficult to return to the original plant communities once a system passes a threshold.

In concept, the theory of plant community dynamics we just described (Pyke et al. 2002, Stringham et al. 2003, Briske et al. 2005) sounds very simple. In practice, it is very difficult to apply. It takes monitoring systems for a long-time, including observing systems as they cross thresholds.

What are sustainable soils?

Soils store massive amounts of nutrients. Roughly 10 times the concentration of important nutrients exist in soils rather than plants. For soils, sustainability means long-term stability of the nutrient bank. For this to happen, soils must be able to let nutrients in and hold on to them to prevent their leaching or erosion. Nutrient absorption and retention require certain soil particle sizes, sufficient aeration, and the correct chemistry and soil organisms to latch onto nutrients.

What is sustainable productivity?

Plants uptake soil nutrients and convert them into leaves and roots using water and sun energy. For plants, sustainability means sustained plant community productivity. Net primary production is the amount of new plant tissue made over the course of a growing season. Plant communities optimize productivity by obtaining soil nutrients in different ways. Plants have different functional traits, which set how they extract and use nutrients for growth. To maintain optimal production, plant communities must include a broad arrangement of functional traits among the individual plants that make up the community.

These models do not exist for northern Yellowstone, which is part of the reason why there is so much debate. Two people can look at the same habitat and speculate whether it is approaching a threshold. They can base their opinions on their own expert knowledge, but not really have any data to support it. We are just now beginning to create plant community models for northern Yellowstone to give scientists a common lens to look at rangeland health.

Typically, one starts by measuring the same sites for long periods of time and tracking plant community shifts with changes in grazing intensity. We did not have this chance, because we only monitored plant community conditions in sites starting in 2016. That led us to substitute time for space, by comparing plant communities across sites with similar soil conditions, but with different grazing intensities. In other words, we looked at areas where we expected the same plant communities, determined they were different, and asked how grazing related to those differences.

We measured plant composition by recording species abundance in sixty 20-by-50-centimeter (8-by-20-inch) plots within each grazing site. We used four traits to determine the functional grouping of 225 plant species we identified. We used life form – graminoid (grass, rush or sedge), shrub, or forb (showy flower); life span – annual or perennial; growth form – bunchgrass or rhizomatous (rootstalks); and rooting depth – shallow, moderate, or deep. Combinations of traits identified 21 different functional groups. We looked at plant communities by seeing how they were composed of these 21 functional groups (Lavorel et al. 1997).

We first tested if each habitat type (mountain meadow, valley floor, valley slope, low-elevation range) had their own unique set of plant communities. It turns out they did. We also tested the similarity of plant communities within each habitat type. It turns out they were more similar to each other than they were to communities found in other habitat types. This is what you would expect in a healthy system that has not experienced thresholds and undesired changes.



Otherwise, we would have found some communities within a habitat type that were very different from the others within the same habitat type.

The one exception was a single site in the Gardiner basin that likely has passed a threshold. The site located near the North Entrance station is the low-elevation range habitat type. It is dominated by the warm-season nonnative desert alyssum. The time frame of our analyses cannot identify the trigger or cause for the plant community to cross a threshold. However, it confirms that areas in the low-range habitat type can transition from bunchgrass/shrub to warm-season, winter-annual communities.

As expected, the plant communities within each habitat type naturally varied. Grazing generally increased rhizomatous growth forms and forbs, and decreased moderate and deep-rooted perennial bunchgrasses and shrubs.

Similar to how repeated grazing by bison makes plants younger by removing older plant tissue and stimulating the growth of new shoots (Geremia et al. 2019), grazing made plant communities younger by reducing their stage of plant succession. Plant communities changed from deeper rooted, taller growing plants to more diverse communities of shallow-rooted plants of different life-, growth- and rooting-forms. Four of our grazing sites were monitored during the 1980s (Frank and McNaughton 1992). These sites showed similar successional changes.

We did not detect strong differences among the producitivity of plant communities based on successional stage. If anything, plant communities within each habitat type with highest grazing intensities had higher productivity. In other words, grazing slightly modified plant communities and those communities were more productive than others in the same habitat type. Three of the four grazing sites monitored during the 1980s confirmed this, showing similar to slightly higher productivity today.

Northern Yellowstone has four distinct habitat types used by bison. Each supports it's own set of related plant communities.

A. MOUNTAIN MEADOW

- Soils: nitrogen-rich, clay-loam
- Climate: cold and wet
- Productivity: 200-300 grams per square meter, 1,700-2,600 pounds per acre
- Plant Communities: shrubs, grasses and showy flowers
- Dominant Functional Groups: shallow rooted perennial forbs; shallow and moderate rooted perennial bunchgrasses; perennial rhizomatous sedges; moderate rooted perennial forbs
- Example Habitat: high meadows above Lamar Valley
- Dominant Plants: timothy grass, dandelion, Idaho fescue, tuftedhairgrass, cinquefoil, oatgrass, brome, creeping clover, dandelion

B. VALLEY SLOPE

- Soils: nitrogen-available, sandy
- Climate: cool and dry
- Productivity: 50-150 grams per square meter, 450-1,300 pounds per acre
- Plant Communities: bunchgrasses, shrubs, and showy flowers
- Dominant Functional Groups: shallow and moderate rooted perennial bunchgrasses; shallow, moderate, and deep rooted perennial forbs; perennial rhizomatous grasses and sedges; shrubs
- Example Habitat: slopes around the Lamar Valley
- Dominant Plants: Idaho fescue, blue-bunch wheatgrass, June grass, Sandberg's bluegrass, needle-and-thread grass, lupine, phlox, milkvetch, sagebrush, rabbitbrush



C. VALLEY FLOOR

- Soils: nitrogen-rich, loamy
- Climate: cool and wet
- Productivity: 200-450 grams per square meter, 1,700-4,000 pounds per acre
- Plant Communities: grasses and showy flowers
- Dominant Functional Groups: perennial rhizomatous grasses; shallow and moderate rooted perennial forbs; shallow and moderate rooted perennial bunchgrasses; annual forbs
- Example Habitat: floor of the Lamar Valley
- Dominant Plants: Kentucky bluegrass, timothy grass, smooth brome, creeping clover, dandelion.

D. LOW ELEVATION

- Soils: nitrogen-poor, loamy
- Climate: warm and dry
- Productivity: 50-150 grams per square meter, XXX pounds per acre
- Plant Communities: bunchgrasses and sagebrush with winter annual infestations
- Dominant Functional Groups: XX
- Example Habitat: previously cultivated areas in the Gardiner basin
- Dominant Plants: crested wheatgrass, desert alyssum, annual wheatgrass, big sagebrush, XX



How Do Different People Come to Different Conclusions?

Cattle thrive on landscapes not recently disturbed by grazing or fire. Rangeland management developed in response to excessive livestock grazing and farming that led to wide-scale habitat destruction during the early twentieth century. The principles of rangeland management are still applied to managing most public lands today: manipulate grazing by managing the number of animals using an area for set amounts of time, evenly distributing use, grazing the right type of animal, and grazing the plants at the right time. The goal is to protect soils by minimizing disturbance to plant communities (Holechek et al. 1989, Briske 2011).

Back when bison roamed North America their grazing likely completely changed ecosystems. The story of North America was likely one of disturbance driven by massive fires, massive herds and intense grazing. In the wetter, eastern Great Plains, studies on small bison populations show that animals follow fire. Bison move to areas after fire to eat nutrient-enriched plants and the combination of fire and grazing changes plant communities (Knapp et al. 1999). In the western foothills of the Great Plains, bison in Yellowstone set up grazing lawns so large that satellites from space detect grazing effects on plant growth patterns and their grazing changes

Are Nonnative Plants Bad? It Depends.

plant community consisting of a wide range of native plants that collectively has a wide range of functional traits is healthy.

Communities with nonnative plants can be just as healthy. We do not mean that weeds are good. We mean that it is more important that plant communities maintain species representing broad sets of functional traits rather than species of just native origin. While some nonnative plants can fulfill functional roles, others can be devastating, fundamentally changing the integrity of plant communities.

Cool-Season Nonnative Invasions: Cool-season nonnatives replaced native plants throughout the cool, wet, nitrogen-rich habitats of northern Yellowstone. These species include Kentucky bluegrass, timothy grass, smooth brome, creeping-clover, and dandelion. Valley floor habitat type plant communities are primarily made of cool-season nonnatives. Mountain meadow habitat types contain smaller infestations with mixtures of native and exotic plants. Cool-season nonnatives are well adapted to live in the higher elevations and wet areas of northern Yellowstone. They inefficiently use water to grow, which requires them to live in wet areas. Cool-season nonnatives were originally introduced to the park to support bison restoration. They thrive when grazed, which likely contributes to their displacing of native plants. Cool-season nonnatives also tend to be more productive than displaced native plants. As a result, some grasslands in northern Yellowstone are likely more productive today than they were when the park was established.

Warm-Season Nonnative Invasions: Warm-season nonnatives, including desert alyssum and cheatgrass, are gradually invading the warm and dry low-elevation range habitat type. They hold potential to displace native plants and unbalance the functional integrity of plant communities. These plants grow in dry soils, where there is intense competition for moisture. Winter annuals can gain the upper hand on native plants by sprouting in the fall. Already germinated winter annuals can monopolize early spring pulses of water and outcompete native plants. The abundance and distribution of winter annuals will likely depend on how much northern Yellowstone warms and dries in the future. Under some climate scenarios, these plants could disrupt plant communities throughout the low- and mid-elevation valley slope habitat types in northern Yellowstone.

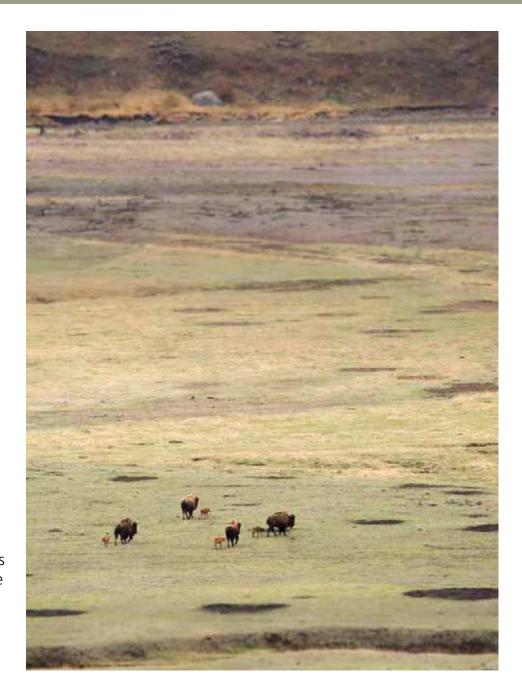
plant communities and nutrient flows between plants and animals (Geremia et al. 2019).

Therein lies the cause for debate about the health of vegetation in northern Yellowstone. When grazing changes plant communities, is it success or catastrophe? For decades, many have looked at northern Yellowstone in the context of whether the right plant communities are still there. The original lens through which we looked at rangeland health were tools like the Similarity Index and Trend Analysis. They measured how far existing plant communities differed from hypothetical climax communities, which were the plants likely present in precolonial time. We determined early seral communities were unhealthy and referred to them as rangelands in poor condition. Those lenses have changed over time as we recognized that plant communities are more complicated than we originally thought. Today, the standard is to use something called Rangeland Health Assessment. However, we still compare existing conditions to some form of idealized plant community, which still tends to be late seral communities.

The more we understand grazing ecosystems, the more we realize it is time to let nature decide which plant communities exist. Relationships among plants and grazers protect these systems, stabilizing nutrient supplies within soils and enabling plants to be productive in the face of grazing.

National Park Service policies provide enough flexibility to manage for preserving natural processes, like nutrient cycling, plant succession, migration, competition, and predation. However, the debate over northern Yellowstone always drifts back into discussions of values. Rather than looking at the health of northern Yellowstone through the lens of whether natural processes are playing out, it turns into discussions of whether we should let them happen.

People define their values by the time they are teenagers. Values affect our interpretation of the world. Values are that inner voice



Plant Communities

SOILS and WEATHER determine the types of plant communities that could live in an area.

FUNCTIONAL TRAITS of plants determine their growth potential.

PLANT COMMUNITIES are groups of plants that grow together with each plant type having unique functional traits such as rooting depth, lifespan, growth form, and life form.

Identify soil **PHYSICAL**, **CHEMICAL**, and **BIOLOGICAL** properties to classify habitat types for plants.

- 1. Evaluate the top 10-20 centimeters
- 2. Identify microbial diversity, nutrient mineralization rates, bulk density, particle composition, and pH

SOIL ORGANIC MATTER is the amount of decaying plant and animal materials in soils and a general indicator of nutrient and water holding capacity.

1. Maintain similar soil organic matter levels over decades.

SOIL NUTRIENT POOLS are the concentration of limiting nutrients (nitrogen, carbon) in soils.

1. Stabilize soil nutrient concentrations over decades.

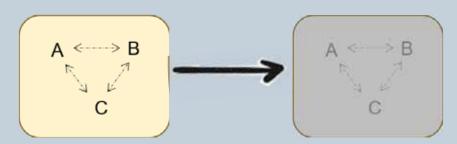
Track the functional integrity of **PLANT COMMUNITIES**

- 1. Evaluate plant community composition according to functional traits.
- 2. Maintain similar plant communities in areas with similar soils.
- 3. Support plant communities across seral stages.

PLANT PRODUCTIVITY is the amount of herbaceous material made each year.

- 1. Maintain similar productivity of plant communities in the same area, even with shifts in plant community composition.
- 2. Track plant production using empirical methods, which includes measuring conditions throughout the growing season in actively grazed areas.

Too much disturbance can cause plant communities to cross a **THRESHOLD**.



PLANT COMMUNITIES naturally shift back and forth due to mild disturbance.

Plant communities in this **ALTERNATIVE STATE** are entirely different.



speaking to you as you read our article reminding you "wow, of course bison grazing improves the park," or "wow, that's another case of bad science."

When you visit the park, ask yourself if the areas are overgrazed. Values may lead you, at the sight of bison, to think of the icon of the American west and presume they are a natural part of the ecosystem that can do no harm to the land. On the other hand, your values may make you see short plants, dirt wallows, habitat destruction, and ornery versions of cattle. Most of you are likely somewhere in between.

For too long this debate has been about gotcha moments: look what we just found, clearly northern Yellowstone is (or is not) overgrazed. Science is not meant to be point and counterpoint. Science is supposed to be about presenting observations for assessment by our peers, while also providing methods to repeat those observations. Rather than figuring out the next gotcha moment, it's time to move on from this gamesmanship.

What is at stake is our national mammal, how we manage it, and its' home. We need to stick to less of our individual values and start making assessments based on the principles of the National Park Service, which are to create a place for these natural processes to play out. If we can agree that is our goal, almost everyone that is looking at what we are looking at would come to the same conclusion. Habitat across northern Yellowstone is predominantly stable. Soils are healthy and nutrient-rich. Plant communities are productive in the face of grazing. The biggest challenge we have is a changing climate because warmer and drier weather may allow certain nonnative plant invasions that could break the balance of the grazing ecosystem.

Literature Cited

See Literature Cited section of this issue on page 108.

Chris Geremia (see page 52).

Bill Hamilton has worked on how grasses regrow in response to herbivory since he was an undergraduate. His interest in aboveground and belowground interactions in grazing systems began late in graduate school working with Doug Frank on Yellowstone grasses. Since 2004 he has been working with his undergraduate students on a variety of Yellowstone Projects relating to restoration, soil health and grass-grazer interactions. Since 2013, he has been collaborating with the grazing project, analyzing physical, chemical, and biological properties of soil as well as conducting greenhouse studies on grasses collected in Yellowstone.



Give Bison Room to Roam

Chris Geremia, Bill Hamilton & P. J. White

hen park visitors imagine the world-renowned grasslands of northern Yellowstone, many see the idyllic scene of a Thomas Moran painting. A river slowly wanders across the valley floor, lined with pockets of willows and cottonwood trees. Tall, waist-deep grasses and mountain wildflowers wave in the wind. Snowcapped mountains backdrop the valley. Small, widely scattered groups of deer, pronghorn, and elk graze where the grasslands meet the forests.

The scene today does not disappoint, but it is probably different from what many visitors expect. It is a relic of North America prior to European settlement when bison dominated the continent. Make no mistake; there is nothing wrong with this scene. In fact, allowing large groups of bison to naturally migrate and graze improves the health of grasslands in northern Yellowstone.

Up to four thousand bison graze across northern Yellowstone. Measured by sheer body size and numbers, there is more bison 'mass' than any other large grazing animal. Unlike deer, pronghorn, or elk, bison immediately include their young into their large traveling groups. As spring turns to summer, traveling groups become larger, reaching hundreds to thousands of animals. Aggregation concentrates grazing and creates a mosaic of dense mats of short-statured plants that look like golf course fairways interspersed with small islands of waist-high, yellowed, dried-up grasses. Dung piles pepper the land like pieces on a checkerboard. Wallows, bison-sized depressions devoid of plants created from them rolling on the ground, pit the dense mats of grazed plants.

Most large grazers follow the "green wave" of sprouting plants and grasses during spring because young plants are highly nutritious (Merkle et al. 2016). For example, mule deer move up to 200 miles (322 kilometers) in southern parts of the Yellowstone ecosystem, tracking highly nutritious foods that are vital to their surviving winter.



Bison migrate and graze in Lamar Valley during spring. Bison are a true force of nature acting as ecosystem engineers that improve the grazing ecosystem of northern Yellowstone.

Migrating bison begin surfing the green wave early in spring. Many bison stop and let the green wave pass them by, not reaching their final summer ranges until weeks after green-up occurred. As it turns out, bison can move out-of-sync with forage green-up because they engineer the ecosystem as they migrate and graze. Rather than just moving to find the best foods, bison create high-quality foods by how they move and graze (Geremia et al. 2019). They walk and graze, back and forth, across nearly 20 miles (32 kilometers) of the Lamar River as the green wave continues up into the mountains. Their behavior creates grazing lawns, a term popularized during the 1980s to describe intense, broad-scale grazing by millions of wildebeest in the Serengeti (McNaughton 1984). As bison let the green wave go by, they become a massive fleet of lawnmowers moving back and forth across northern Yellowstone. At a time when plants are actively growing, they form aggregations of hundreds to thousands of animals. This behavior sets bison apart from other large grazers in Yellowstone.

The aggregations are dynamic. Bison do not tend to stay in the same group or location for very long. State-of-the-art radio collars show that animals cyclically move across the land, returning to the same areas about every two to three weeks. Nearly the entire herd in northern Yellowstone, which numbers up to 4,000 animals, uses many of the same areas although not necessarily at the same time. It may look like the same bison are always in the same place, but that is not the case. Bison are always on the move.

To think bison are just aimlessly eating grass is not correct. Plants that regrow after intense grazing provide similar food quality to newly emerging spring shoots. In other words, regrowing grazed plants are more nutritious than more mature plants left ungrazed. By grazing en masse and returning to the same areas, bison modify plant growth to get the same types of high-quality foods they would get if they surfed the green wave (Geremia et al. 2019).



Bison set the terms of spring in Yellowstone. Without several thousands of bison moving freely on the landscape in sync, the springtime season of plant growth would be shorter, the land would not be as green, and the plants would not be as nutritious. Bison constantly hit reset on springtime by intensely grazing and returning to the same areas. Their intense grazing does not weaken plants but stimulates plants to regrow after being partially eaten. As bison graze on these newly re-growing shoots, they obtain a similar diet to what other grazers, like elk and mule deer, get by migrating in sync with plants as they emerge in spring.

Grazing preserves soil moisture by improving plant water-use efficiency (Frank et al. 1998, 2018). Plants face a trade-off. Plants lose water to the air when they open small pores called stomates on their leaves to suck up water from the soil and absorb carbon dioxide from the air. Plants require both water and carbon dioxide to make new plant tissue through a process called photosynthesis. Short dense plants with less leaf surface area lose less water, which prolongs moist soils.

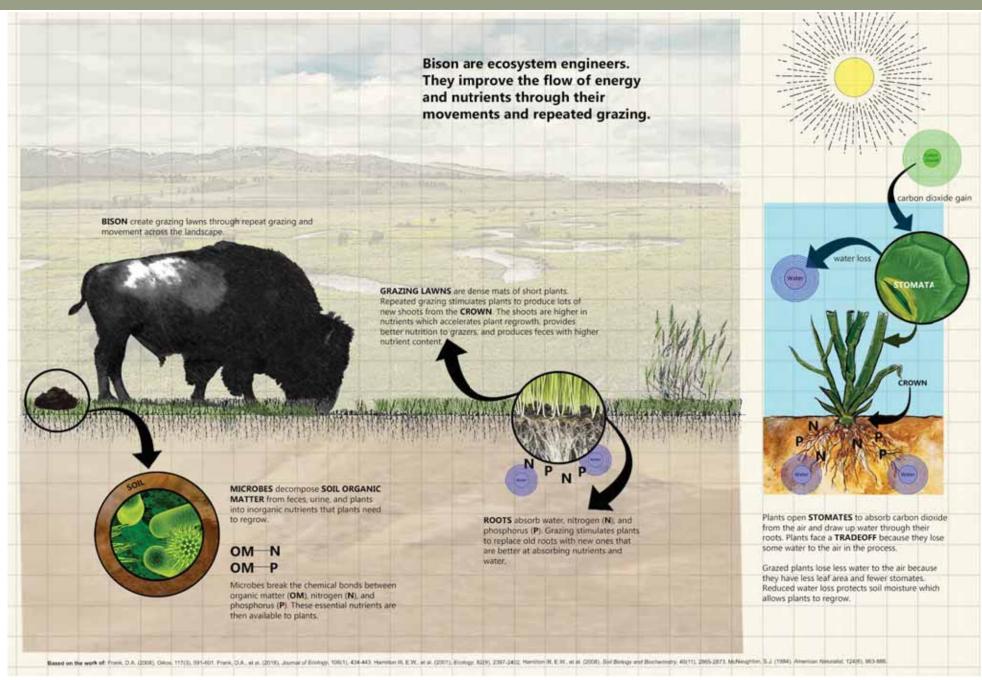
Grazing improves soil nutrient availability. Animals deposit carbon-based organic matter on the soil surface in the form of dung and urine. Organic matter is critical to soil health. It acts like a sponge absorbing water. Organic matter also provides habitat to soil microbes that are the link to plants obtaining nutrients. Plant roots cannot immediately absorb soil nutrients stored in organic form. Soil microbes must first break them down into simpler inorganic structures. Intense grazing leads to more animal-based organic matter on the soil surface, which leads to robust soil microbial populations, and creates a bountiful supply of soil nutrients in forms available to plants (Hamilton and Frank 2001). Grazing also causes older roots to die and replaces them with younger roots that are better at absorbing nutrients (Hamilton et al. 2008).

Through these mechanisms, grazed plants have soil, water, and nutrients available for them to regrow. Plants do not just regrow from the bitten off grass tips. They also produce entirely new shoots off the root crown, the part of the plant immediately below the soil surface (Frank et al. 1998). This process of tillering, growing new shoots from the crown, creates the short, dense mats of vegetation that characterize grazing lawns. New, young tillers are high in nutrients and low in indigestible matter. When bison return to bite off the new tillers, they eat the equivalent of newly growing spring vegetation.

Nutrient-rich shoots lead to nutrient-rich dung, which results in nutrient-rich soils. Grazing accelerates the turnover of nutrients back to plants. Nitrogen and phosphorus are recycled through the ecosystem as they move back and forth among organic and inorganic forms. Grazing reduces tying up these essential nutrients in decaying plant matter and litter. This means that bison change the sources of phosphorus and nitrogen from plant (litter) to animal (dung) origins (Hamilton and Frank 2001). Microbes break down animal-based sources of organic material faster than plant-based sources, making phosphorus and nitrogen more readily available to growing plants.

One might think all this grazing reduces plant growth, particularly because plants exist in low, dense mats. To get the full picture, imagine doing a science experiment on your lawn. On one-half, you let the plants grow for the entire summer. Then you mow them one time, collect the plant clippings, and place them in a pile. On the other side, you mow the lawn every week. Each time you mow, you collect the plant clippings and place them in a second pile. Which pile will have more plant material? The short story is that the pile generated from mowing each week weighs more.

If grazing increases plant growth, it just might improve the health of grassland ecosystems. Plants play the crucial role of harnessing the sun's energy and converting it into forms useable by all other organisms. Plants do this by fixing carbon, which means to store the sun's energy in carbon-to-carbon bonds that make up the basis of sugar. From plants, energy flows up through the ecosystem as herbivores graze plants and predators consume herbivores. Creating more plant material means harnessing more of the sun's energy. Grazed grasslands, more productive than ungrazed grasslands, hold more energy and a greater potential to support a more energized and robust ecosystem.



Grazing accelerates nutrient flow and creates a healthier and more productive ecosystem.

Can there be too much grazing? A complete answer to the lawn mower experiment depends on how frequently you mow the lawn, how often you water, and the nutrient richness of the soils. The theory of grazing optimization predicts that the relationship between grazing intensity and plant growth is hump-shaped. That is, compared to no grazing, plants grow a little more under low and high grazing, a lot more under moderate grazing, and less under extremely high grazing (Hilbert et al. 1981).

Doug Frank (see Interview, this issue) and his colleagues tested grazing optimization in northern Yellowstone when elk populations were high during the 1980s. They discovered that elk moderately grazed areas by migrating in sync with plant greenup. They ate about 20% of plant growth on wintering areas, 47% along migration routes, and 28% in summering areas (Frank and McNaughton 1992). Plants had time to recover after grazing because elk moved

to higher elevations in pursuit of the green wave (Frank et al. 1998). As a result, grazing increased production of leaves and stems by as much as 43% and roots by 35% (Frank et al. 2002).

Elk were the perfect Yellowstone grazer. The landscape looked like they bit every blade of grass. However, elk never took too much grass. Their migration led elk to graze sites near an idealized level of 30 to 40%, which maximized positive effects on plant growth (Frank and McNaughton 1992, Frank et al. 2016).



Measuring plant production. A citizen scientist partnership with Yellowstone Forever and Ecology Project International called 'Home on the Range' supports hundreds of high school students working alongside Yellowstone biologists.

From the 1980s to the mid-2010s, northern Yellowstone changed from being dominated by elk to being dominated by bison. Elk numbers declined 70% while bison numbers increased by nearly 700%. Since 2012, we set out to retest grazing optimization in a bison-dominated system.

We needed a way to measure plant growth. We took pictures of small 1.5 feet by 1.5 feet (0.5 meter by 0.5 meter) plots using a camera adjusted to record only red and near-infrared bands of light, the bands reflected by green vegetation. We used computer software to extract the greenness of each image. At the same time, we used small wooden frames to pass a long pin through the frame at different locations and counted the number of times the pin touched plant material. We cut all the plant material within test plots, dried it in an oven, and weighed it. Over hundreds of test plots, we developed calibration curves that related the dried weight of plant material to either photo greenness or the number

of pin hits. This enabled us to estimate the weight of plant material within other plots without cutting and weighing it.

Once we had a way to estimate plant material within a plot, we still needed to figure out how to account for what grazers ate and removed. We modified methods originally developed by Sam McNaughton and Doug Frank (see Interview, this issue), two scientists who spent decades studying grassland ecosystems in Yellowstone and the Serengeti (McNaughton 1984, Frank and McNaughton 1992). We installed several plots within each site just

as snow melted. We placed a fence around half of the plots to prevent grazing. We left the other plots unfenced. We measured the amount of plant material when we set up each plot and again after 30 days. The fenced plots told us the amount of plant growth during each 30-day period. The unfenced plots told us how much grazers ate during the same time. We moved these paired plots after every 30 days, which enabled us to measure plant production and consumption for the entire summer. We also set up permanently fenced plots to measure plant production under no grazing.

Bison did not diminish the productivity of grasslands in northern Yellowstone. Grazing of less than 5% of plant growth had no effect on productivity. Moderate grazing of up to 30% tended to make areas 20 to 30% more productive. For grazing intensities up 50%, most sites showed no difference between grazed and

ungrazed areas. Low and moderately grazed sites occurred in the less productive areas of the northern Yellowstone. These were the drier, sagebrush-dominated hillsides and highest elevation grasslands with very short growing seasons. In a way, our findings suggest the effects of bison in these areas were very similar to those of elk. However, bison are not big elk. Bison set up their grazing lawns in the highly productive, wet habitats like areas you would see if you stood alongside the road in the Lamar Valley and looked out towards the immense flat grasslands surrounding the Lamar River. Bison mowed up to 80% of the plant material that grew there.



Bison increased productivity through their grazing by as much as 20 to 30% under moderate grazing.

Ironically, park rangers replaced many of the native plant species of the Lamar Valley with cultivated grasses during bison recovery efforts in the early twentieth century (see Introductory Article this issue). These introduced cultivars included timothy grass. Kentucky bluegrass, and smooth brome. They are cool season exotics that grow best when the weather is moist and cool. These cultivars stop growing when it is warm because they inefficiently use water. They are perfectly adapted for the climate of the mid-elevations of northern Yellowstone. As a result, these cultivars displaced native plants in wet areas across much of northern Yellowstone. Today they dominate plant communities and grazing lawns from Tower Junction to the Lamar Valley to Specimen Ridge and to the origins of the Lamar River.

The cultivars are grazing beasts. We grew them in a greenhouse to test their grazing tolerance and discovered that it takes

clipping them to 2 inches (5 centimeters) in height every 15 to 30 days for six months to reduce productivity. For grazing to inhibit plant growth, bison would need to graze areas so intensely that plants never exceed 2 inches in height over the course of the entire growing season. Bison eat a lot of plant material and, at times, areas of the Lamar Valley and some of their other grazing lawns consist of mats of plants around 2 inches tall. This tends to happen late in the growing season after plants have stopped growing for the year. The current numbers of bison in northern Yellowstone do not come close to grazing plants to these levels every two weeks over the entire summer.

Our sites in the bison lawns showed variable effects of grazing on plant production. Some areas of the Lamar Valley suggested grazing approached, but did not reach, levels that reduced productivity. Wetter areas were the most resilient to high grazing and produced more plant material even when grazed at 70 to 80%.

Plants are limited by whichever runs out first, soil water or soil nutrients. On their lawns, bison increased soil nutrient availability so much that it relaxed nutrient limits on plant growth (Frank et al. 2018). Water became the primary limiting factor. While that seems like an eccentric scientific finding, it has profound implications on the health of grasslands in northern Yellowstone. Production increases in both grazed and ungrazed areas during wet years. It increases much more in grazed areas because nutrient limitation eventually takes control in ungrazed areas. That additional growth results in more root mass, which helps plants further resist the negative impacts of grazing and allows plants to grow even more during the next wet year. The ability of bison to engineer the control of plant growth from nutrients to water is likely a key mechanism underlying grazing lawns in Yellowstone.

Grazing lawns beget more grazing lawns. Bison change the plant composition in the wet areas they use the most. More showy flowers develop, which thrive in nitrogen-rich soils. Not all plants must reproduce by creating and dispersing seeds. Some can also produce a root off the root crown that travels underground and pops up above ground away from the mother plant. Over time, the clone develops its own root crown and the process repeats. Clonal, otherwise known as rhizomatous plants, thrive under intense grazing, because they form the dense mats of plants that characterize grazing lawns. Bison improve their own grazing hotspots by transitioning areas into the types of plants that make their lawns.

Ecosystem engineers are organisms that significantly modify their habitat. They are critical to ecosystem health because they construct

a more diverse landscape. By manipulating some areas a lot, some not at all, and some in between, ecosystem engineers create local habitats suitable for a much broader association of plants and animals that thrive in the extremes and in-betweens.

When we give bison room to roam, they become engineers. They change plant phenology and the timing and movement of spring green-up across the land. They manipulate plant productivity through increasing nutrient recycling and change the factors limiting plant growth to produce vegetation explosions during wet years. They also alter the composition of plant communities. Intense grazing by bison is concentrated in relatively small areas, which means they only lightly graze most of the rest of the park. This pattern of variation is the fabric that underlies a more biodiverse Yellowstone. The movements and grazing of bison provide habitat for a much broader suite of animals, songbirds, small mammals, insects, and microbes, to name a few. As a result, bison mean much more to the Yellowstone ecosystem than the sense of awe that visitors feel when they encounter bison for the first time.

Through their actions, people choose the animals they conserve and those they do not. Some of our greatest conservation successes are animals we have recovered from near extirpation, like wolves and grizzly bears. With bison, we decided to prevent their extinction at the turn of the 20th century, but their conservation story is still unveiling in front of our eyes and the ending is unwritten.

Bison conservation and restoration began in Yellowstone at the turn of the 20th century. It took nearly 90 years for bison to recover in the park. During 1980s and 1990s, when bison were relearning migration routes and attempting to move out of the park, society decided to keep them in the park. Managers began shooting animals that migrated out of the park or rounding them up and shipping them to slaughter. People drew lines on the map beyond which bison could not roam—unlike any other wild animal in the area. The



In Yellowstone, the last remnant of bison exist where nature decides who lives and dies, behaviors are passed on between generations, and large roaming populations engineer a better ecosystem. Yellowstone bison have been, and will continue to be, a source of controversy because managing such a large roaming population is difficult in modern society. That controversy is worth the trouble because it helps to rebuild bison as an American icon while restoring missing parts of ecosystems.

State of Montana established laws to prohibit the transfer of live bison from the park to anywhere but slaughter because these bison potentially were exposed to the disease brucellosis. Through these actions, society constrained bison to the park.

Across North America, bison occupy less than 1% of their historic range. We manage only about 20,000 bison for conservation on public lands. Only about 8,000 of those bison roam without fences, about 5,000 of which live in Yellowstone. Ranching is the standard model for the rest of the nearly 500,000 bison in North America. Fence a plot of land, figure out how much grass it produces, determine a light grazing intensity, and manage for a herd size that eats about 25% of the grass. Move them between pastures like cattle and round them up each year to keep a predetermined and unnatural age and sex structure that facilitates easier management.

We continue to struggle to articulate why we need to restore bison and what successful bison conservation looks like. Too many current conservation efforts involve maintaining bison in small numbers and artificially manipulating their genetics to reduce inbreeding by moving animals on trucks. Most people do not realize the individual groups of bison they encounter while visiting Yellowstone, particularly in summer, are larger than most other conservation populations. Most bison preserves are small and could fit within the seasonal ranges used by Yellowstone bison, such as the Lamar Valley. The precolonial force of bison migration is gone because tens of millions of animals no longer roam across much of North America.

Yellowstone's bison provide a sense of hope of what is possible when we bring back large bison herds and find ways to allow them room to roam. We should strive to protect more large bison populations where they can roam across large landscapes and engineer the land. We should also strive to rethink managing grazing of smaller, spatially constrained bison herds in ways that allows them some opportunity to enhance their ecosystems.

Literature Cited

See *Literature Cited* section of this issue on page 108.

Chris Geremia is the program coordinator of the bison team in Yellowstone National Park. He leads a Bison Conservation Transfer Program returning Yellowstone bison to Native American Tribes, assists in resolving conflicts when bison migrate out of the park and studies the most ecologically and culturally valuable bison herd left on the planet. The program's research is used to advise bison conservation. He received his doctorate from Colorado State University and has studied Yellowstone bison since 2002.



Sagebrush Steppe Monitoring

Stefanie D. Wacker



National Park, I read a story of geology, climate, and wildlife that has walked these lands through the ages. I can read this story using plants as the words, as they represent what can grow where, how much it rained, and who stopped for bites of grass. Plants feed us, help us to breathe, and create beauty wherever I look. I love this about plants—they have a quiet power worthy of admiration. Wonderful landscapes are covered in blankets of plants, each community so complex in the intricate details that its significance is often lost to the casual observer. Vegetation is the foundation to so much life here in the park; from our largest mammals to our smallest insects, plants play a vital role. Gaining an appreciation of this amazing resource emphasizes our duty to

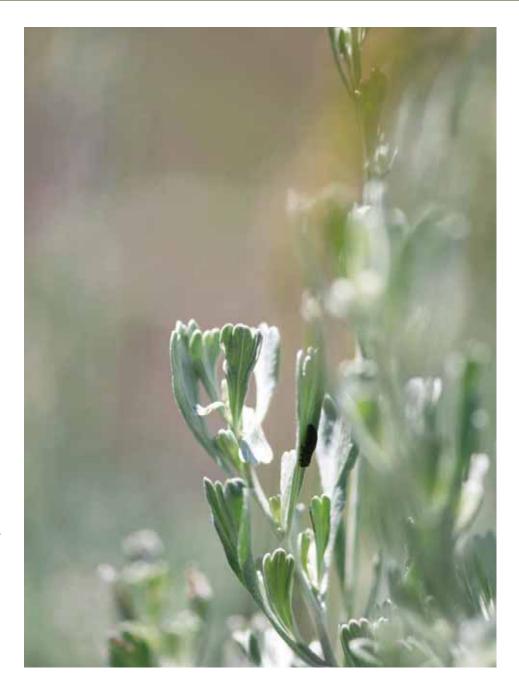
be good stewards, a role that requires us to gain knowledge and understanding of the complex relationships and how we can use this knowledge to protect and preserve the native flora and all that depends upon it.

The northern portion of Yellowstone National Park is critical winter habitat for large herbivores such as bison and elk, and top predators such as cougars and wolves. It also supports small mammals, birds, and insects. This breadth in wildlife species is supported by plant communities for food and brood habitat. All habitat types within northern Yellowstone contribute to ecosystem services such as carbon and nitrogen cycling, water cycling, and supporting a myriad of soil microorganisms. This highly connected web illustrates how the plants serve as the foundation of the trophic pyramid, which

depicts how productivity (or energy) passes from producers through consumers in an ecosystem. Because of the importance vegetation plays in the overall quality of habitat, it is critical scientists monitor for changes in the health and function of the sagebrush steppe, which is predominant in northern Yellowstone.

In the western United States, there has been an enormous loss of big sagebrush habitat due to cultivation and cattle grazing, invasions by nonnative species, mineral and gas extraction, and other development that fragments habitats. Additionally, areas of the intermountain west have seen expansive sagebrush die-offs due to drought. Other areas have seen loss of sagebrush in the form of wholesale plant community shifts due to the nonnative invasive cheatgrass, which not only displaces native species but also has significant impacts to the natural fire cycle and ecosystem function. In other areas, sagebrush has been removed by physically pulling shrubs from the ground or by herbicide to stimulate grass growth for domestic grazers. Mineral and energy extraction have reduced the land base that supports sagebrush required for food and brood habitat by sage grouse. Because so many of these shifts in land use are permanent, sagebrush habitat is considered one of the most threatened ecosystems in the west, with roughly half of lands formerly occupied by big sage now gone (Noss et al. 1995, Welch 2005).

Because Yellowstone National Park has been a protected area since 1872, it has not seen significant land use conversion; however, it is not without some human disturbance. In the early years of the park, the Army needed to feed themselves and their stock, so some lands were turned into hay fields and horse and stock corrals. As more people came to see the park's natural wonders, the need for visitor services increased developed areas, and roads and trails began to expand into areas formerly covered with sagebrush. Current-day visitation and infrastructure maintenance has had an impact on the sagebrush, as have natural disturbances such as drought, wildfires,



and persistent native ungulate grazing. It is unknown to what degree these historical and ongoing disturbances impacted the sagebrush steppe community. The best way to measure our impact is through a quantitative examination of these plant communities.

Research is used to gain basic biological information, understand roles in ecosystem function, and inform management decisions. Scientists also use research to answer specific questions and track changes across landscapes; hypotheses testing addresses the former, long-term monitoring the latter. The value of a long-term monitoring program is that it can address many goals with the same dataset. For example, monitoring can simultaneously track increases and decreases of species or communities in peril, movements of populations across a landscape, provide species inventories, note fluctuations in composition, and detect new species or extinctions. Baseline data describes the landscape, and subsequent data tracks the status and changes. The longer the duration of monitoring, the more information scientists gather, which increases our ability to understand ecological interactions and patterns and processes.

Of enormous concern in Yellowstone is the alteration of the patterns and processes of our native flora when invasive species enter the system. Invasive species are detrimental to the native plant communities because they alter plant composition and abundance, resource allocation, and usable habitat. Any life form of nonnative plant can become invasive, but in Yellowstone, they primarily are annual or perennial grasses and forbs. Perennial invasive plants tend to become established in patches, then expand either vegetatively or by seed dispersal. Invasive annual plants can have considerable spatial and temporal fluctuations, which is part of what makes them so detrimental to native plant communities. The life strategy of all annual plants is to produce as much viable seed as possible during their sole year of life. This abundance of highly viable seed creates a large population of plants, which creates large amounts of seed, and so on. This becomes problematic to native plant communities when





the species are nonnative and without natural enemies, allowing the invasive population to expand at a rate much greater than the native species. This cycle is exacerbated by winter annuals. Winter annuals are plants that germinate in the fall of the year when native species are beginning to senesce. They over-winter with actively growing root systems allowing them to green-up in the spring before the native species are active. They flower and set seed early, producing viable seed by early to mid-summer. This seed then germinates in the fall and the cycle continues out of synchrony with native flora. Often times, these species use many of the water and nutrient resources; hence the common name cheatgrass—it "cheats" the other plants of the resources and flourishes while the other species struggle. Across the western United States, cheatgrass has had considerable deleterious effects on the sagebrush steppe that likely will continue under the warmer, drier conditions expected with climate warming.

In Yellowstone, there are about 150,000 acres (607 square kilometers) of land where the dominant species is sagebrush, largely big sage and silver sage. These species occur in northern Yellowstone, as well as the Gallatin Range and Madison, Hayden, and Pelican valleys. Big sagebrush has representatives from three subspecies: basin, mountain, and Wyoming. Silver sage is represented by a single subspecies. Yellowstone has small populations of other sagebrushes, but the sagebrush population is largely mountain big sage.

Sagebrush is a long-lived member of the Aster family. In Yellowstone, sampled plants averaged 35 years old with a range of 2 to 88 years (Wambolt and Hoffman 2001). Sagebrush occupies spaces that get most of their precipitation in the form of snow during the non-growing season. Its large, shrubby stature captures snow, which usually melts slowly, allowing water to move through the soil column. The extensive taproot can use this water, which allows it

to be tolerant to drought. Smaller roots near the surface allow the plant to use surface water. Big sagebrush subspecies are generally restricted by soils, but they can occur side by side. Basin big sage is the largest in stature, and can be found in areas with deep, welldrained soils. Flat-topped in form, mountain big sage has the widest range of elevations and is found on hillsides and valley bottoms. Silver sage is also found in the valley bottoms, near streams, and in other places with wetter soils. There are places in the valley bottoms where silver and mountain big sage occur side by side. Wyoming big sage has the smallest stature and occurs only in the very arid part of the park, the Gardiner basin. Sagebrush blooms in the late summer and seeds are mature by late fall or early winter. Silver sage is the only one of these sage species that can sprout from roots following disturbance, whereas big sage is reliant upon regeneration by seed. Seeds are very small, and do not generally disperse far from the parent plant. Seed production depends on climatic conditions and competition for water and sunlight. Limited viable seed and seed predation by insects and rodents are factors limiting plant recruitment (Jacobs et al. 2011).

The sagebrush community type is characterized by grass and forb understory, with occasional other shrubs. Other species of native shrubs found in the area are green and rubber rabbitbrush, greasewood, fringed sage, rose, juneberries, mountain mahogany, winterfat, Oregon grape, white coralberry, and shrubby cinquefoil. Each of these species can be locally abundant, but none of them dominate the landscape like big sagebrush. The common native grasses and forbs are Idaho fescue, Sandberg's bluegrass, bluebunch wheatgrass, slender wheatgrass, Columbia needle grass, oatgrass, various upland sedges, field chickweed, sticky geranium, lupine, slender-leaf collomia, and western yarrow. Common nonnative species are dandelion, salsify, cheatgrass, desert alyssum, annual wheatgrass, spotted knapweed, houndstongue, and dalmation toadflax, to name a few.

Understanding that sagebrush and associated communities play an important role in the park, Yellowstone adopted the sagebrush steppe monitoring protocols developed by the Upper Columbia Basin and Greater Yellowstone Inventory and Monitoring Networks (Yeo et al. 2009). These data collection protocols and methods of analysis are conducted by a combination of Network and Park staff in eight parks in the west. Adopting these protocols allowed us to readily implement a protocol already tested and in use by other parks that have large amounts of sagebrush. These protocols addressed several aspects of the sagebrush steppe, namely the changes in frequency and occurrence of native plants, the spatial and temporal distribution of invasive plants, the community response to climate change, and the response to disturbances such as wildfire and grazing.

Sagebrush steppe is sagebrush plus numerous species in the understory—often so many that information collected on all of them becomes difficult to interpret. The protocol uses an abbreviated list of species to monitor. Species were selected to provide the most information about the sagebrush communities, balanced with the ability to read a large number of plots annually. Scientists also decided to monitor species indicative of recent disturbance, susceptible to the effects of climate warming, or that increase or decrease under heavy grazing (Figure 1).

Sites selected for sampling represent a range of density and abundance of sagebrush. Areas of highly degraded flora due to significant past disturbance or long-term nonnative plant infestations, such as the Lamar Valley floor, roadsides, and the Mammoth area, are avoided. Biologists collect data in specific locations categorized by slope, aspect, and elevation. The exact locations where data is collected are determined by running a computer program that generates locations in a statistically robust, spatially distributed manner. In addition to recording the occurrence of the species, biologists also record the abundance of each species,

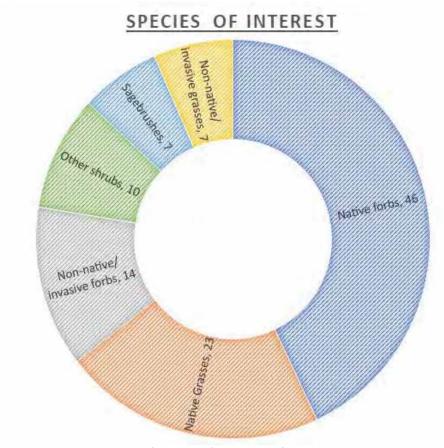


Figure 1. The breakdown of species of interest by functional group.

referred to as "cover." This measures the percentage of the sampling area underneath the canopy of each species. Since there can be many layers of plant canopies, the total cover is often greater than 100%. Correctly determining the exact percentage of the area covered is nearly impossible, so data is collected using classes (or bins) to record the percentage of area covered by each species such as zero to 5%, 6 to 25%, and so on (Daubenmire 1959). This data is used to tell which species occur where, how often, and how much.

Determination of change is done with analyses that detect when a species demonstrates significant change over time. In addition to species data, biologists also estimate the cover of bare soil and litter. Bare soil could be populated by native or invasive species, areas that were covered but now are not (plant loss), potential erosion, or non-productive soils. Litter is an indicator of production and potential soil organic matter. It can be a barrier to seed-soil contact, and when

really deep, can impede water infiltration

There are 43 plots read on a 5-year rotation and 6 "sentinel" plots read annually. Biologists selected the plots to represent various locations in the park, densities of sagebrush, and a variety of plant communities. The project started in 2015, so we have collected five years of data on some of the sentinel sites and one visit to all other sites. Biologists used baseline data to describe each site, and they will assess trends with data collected in upcoming years. They will also use the data to create detailed site descriptions and assess the value of each study location.

in Yellowstone. While the protocol does not count dead shrubs specifically, a significant decrease in cover estimations, as well as observations by staff would alert us to changes. There are new recruits at every location, with the exception of plots that burned in 2016 and biologists sampled in 2017. There is no reason to think there would not be new shrubs at these locations given enough time for seeds to germinate and establish.



The boundaries for the sampling frames are all created in Geographical Information

Systems (GIS), as are all the specific sampling quadrats. On the landscape, the black line shows the area in which sagebrush is the dominant plant, and where the quadrats are concentrated. Photo by NPS/Shulstad.

Gopher burrowing activities bring soil to the surface, which creates trails of bare soil. Other

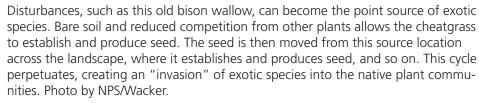
Both big sagebrush and silver sagebrush populations appear to be healthy at all our sampling locations. Since sagebrush die-offs have occurred in the southern part of Wyoming, it is of concern here

Bare Soil—There is no one soil type, slope, or aspect that has a consistent amount of bare ground. The only thing that is consistent is that bare ground is highly variable, even within a study location. The understory vegetation of sagebrush steppe can be either locally dense or sparse on all soil types. Although one could assume that highly productive soils would have minimal amounts of bare ground, these loose soils also support a high level of pocket gopher activity. Pocket gopher burrowing activities creates trails of bare soil. Other examples of soil disturbances are bison wallows, fire, animal trails,

and erosion which leave patches of bare soil of varying size.

Litter—The sites with the highest litter are also those with the lowest bare ground; they have high leaf cover from grasses, forbs,





and shrubs. Some of these sites have not only a flora of native grasses and forbs, but also a high abundance and frequency of nonnative grasses, such as Kentucky bluegrass and timothy. As one would expect, there is a negative relationship between litter and bare ground: the higher the litter, the lower the bare ground. In most locations in the study, there is not an abundance of litter, indicating that there is not high vegetation production and/or that it decomposes readily.

Native Plants—The most frequently occurring native plants across the study are upland sedges, rockcresses, Idaho fescue, junegrass, and pussytoes; the most abundant are Idaho fescue, mountain big sage, lupine, bluebunch wheatgrass, and upland sedges. All of these species are perennial. Species such as the rockcress are very small,



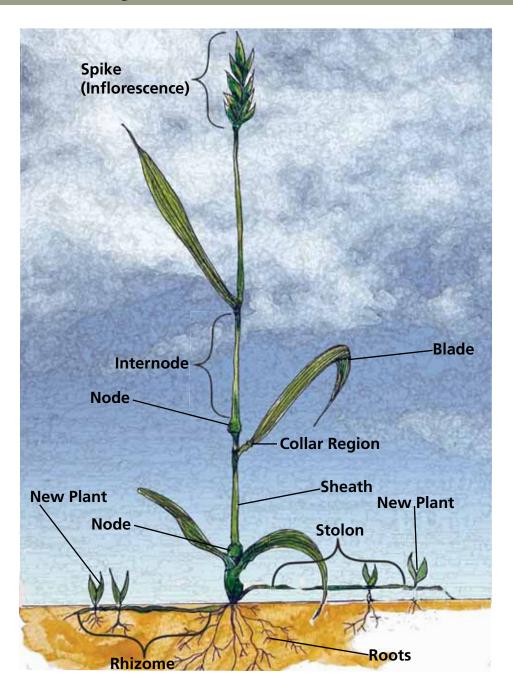
Sampling in a frame that was burned in the 2016 Buffalo Fire. At this location, the sagebrushes and litter were totally consumed by fire. When this picture was taken in June of 2017, there is abundant bare ground, but also abundant forbs and grasses, indicating how this system responds to fire. Photo by NPS/Wacker.

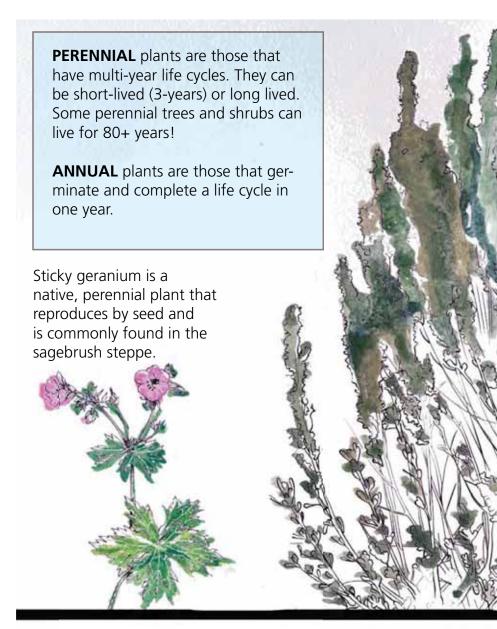
with little leaf cover, but found at nearly every study location. The most infrequent native species are milk vetches, Wyoming big sage, ricegrass, and lava aster, which largely occur on the warmer, drier soil types of the Gardiner basin. The least abundant are bluejoint grass, oval-leaf buckwheat, and scarlet globemallow. Again, these species are more restricted in distribution and not abundant across the study area. The native grasses are widespread in the sage steppe with localized variability in abundance. All the native grasses that we monitor in the understory of the sagebrush steppe are cool season bunch grasses.

Nonnative Plants—The most frequently occurring nonnative species are dandelion, Kentucky bluegrass, timothy, salsify, and desert alyssum; the most abundant are Kentucky bluegrass,

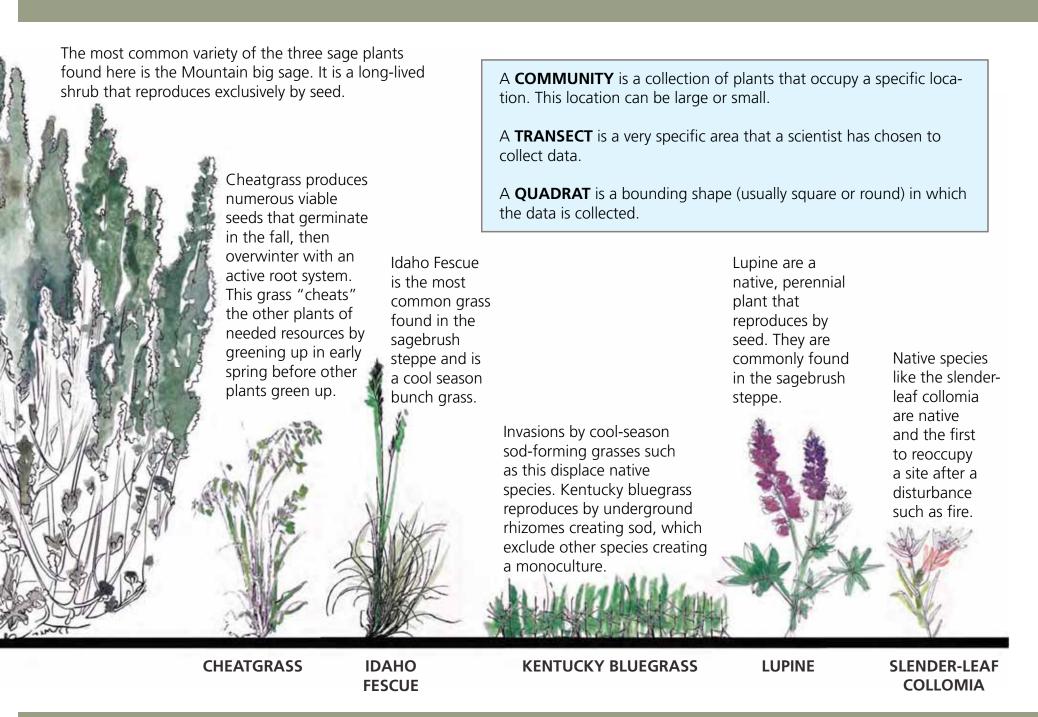
Anatomy of Grass Plants

Yellowstone's Sagebrush Steppe





BIG SAGE





timothy, desert alyssum, dandelion, and cheatgrass. Of these, only desert alyssum and cheatgrass are annual species, the others are perennial. The most infrequent and least abundant nonnative species are houndstongue, Canada thistle, spotted knapweed, and bulbous bluegrass. Houndstongue is a biennial, the others are perennial. Nonnative species can have significant impact on the community regardless of life-span. When all the species we record are aggregated, the most infrequent and least abundant are the nonnatives; simultaneously, the most frequent and abundant are also nonnatives. It is worth noting that some nonnatives are not invasive, and many occur at low frequency or abundance and pose little threat to the native flora.

This monitoring program is focused on the health of the plant community which comprises the sagebrush steppe, emphasizing the presence of invasive species in time and space. This is accomplished in several ways: detection of species unknown to be present in the park, detection and quantification of species that are known to be present but with an unknown spatial extent, quantification of species with unknown abundance, and quantification of the effects of nonnative and invasive species on the native flora. The data collected in this effort are also used to detect changes in the abundance of sagebrush, as well as the other native species that make up this community type.

In the examination of the baseline data, of interest is the frequency and abundance of nonnative, cool season, sod-forming grasses represented by Kentucky bluegrass, timothy, and smooth brome. Sod-forming grasses have strong tillers and can expand the colony by sending up culm (stems) that will develop an inflorescence (flower cluster) from rhizomes (underground stems). Although bunch grasses still have an extensive root system and the ability to send up flowering stems from a root bud, population expansion by this method is much less than in sod-forming grasses. Under conditions of a warming and drying climate, and with continued high-intensity grazing, the nonnative sod-forming grasses could have a competitive advantage over the native bunch grasses. We do not currently have any study plots in areas where extensive patches of sod-forming grasses occur, but the implications to native grasses trigger a need to begin collecting data these areas.

An unquantified benefit to the study is the many observations made while travelling to study sites. Observations include the increased frequency of weeds at trailheads, along trails with high levels of horse use, and on social trails. Of particular interest is the number of Douglas fir trees that have a ring of cheatgrass underneath them in places where it is unexpected. This discovery led to the development of a separate effort to try to detect early season invasives (cheatgrass and desert alyssum) using remote sensing tools such as satellite imagery and aerial photographs. Also of great value is knowing the frequency of occurrence and abundance of the nonnative invasive species that we are not currently aggressively treating. We now have data on species such as desert alyssum and cheatgrass—winter annuals that have the potential to greatly affect habitats in northern Yellowstone. Using distribution data plus our field observations, managers started to treat these species in the fall, when chemical treatment is very effective.

The vegetation resource at Yellowstone is very complex and covers a majority of the park. Because this park is so large, it is logistically impossible to collect all the data we would like. Using a monitoring program stratified by topographic and climatic variables, we can collect data at a reasonable number of representative locations. If the results bring cause for concern, we can establish new plots, increase

the frequency the plots are read, or initiate new management strategies. The critical next step in the monitoring program is to ensure its longevity. The value of this project will only increase with each additional data set, and a commitment to this work will validate the importance of the vast vegetation resources in this unique and irreplaceable landscape.

The grandeur of Yellowstone National Park means different things to different people—some love the wildlife, for others it's about the geysers—for me, the very essence of what is Yellowstone are the huge, awe-inspiring, landscapes stretching for as far as the eye can see. Part of what I love about the views is how different the landscape looks up close, at a middle distance and far, far away. Up close, I can see trees, sagebrush, and flowers. As my focus moves farther, the trees look soft and velvety; the sagebrush all one color, and the flowers, only a yellow hue. When I need to recharge, destress, and focus on the present, I hike out into the park, find a spectacular view to enjoy, and contemplate how incredible it is that the entire system functions so well. The soils sustain the plants that grow under warm sun and cooling rain showers; the wildlife are born under the sagebrush and forage on the grasses. The whole system, so intricate and beautiful, is what makes these places so special and worth protecting for this and future generations.

Literature Cited

See *Literature Cited* section of this issue on page 108.

Stefanie Wacker was the park's Vegetation Ecologist. Her area of interest is terrestrial plant invasions and restoration of disturbed areas. She has undergraduate degrees from the University of Colorado Boulder in Geography and Environmental Science and an Master of Science degree in Biological Science from South Dakota State University.

Author's note: I would like to dedicate this article to my mentor, advisor, teacher, and friend, Dr. Gary E. Larson. Gary was a huge driving force in my love of plants and in my career; I would be a different person without his influence. His legacy is in his students who are working as stewards of this amazing resource all over the nation, many with public land agencies. Rest in peace, Gary, you will be missed.



Big sagebrush (*Artemisia tridentata*): The genus name comes from Queen Artemisia II of Caria (353-351 BCE) who was a botanist, and the specific epithet from the three lobes at the end of the leaf (3 teeth).



A one square meter quadrat is used to delineate the area in which the plants are sampled by species and the area each species covers within the quadrat. NPS Photo/Wacker.

Stefanie recently accepted a position as an ecologist with the National Park Service in the Denver Service Center revegetation program. Nancy Finley, Chief of the Yellowstone Center for Resources notes, "Stef Wacker has been a significant asset to Yellowstone in advancing science and our knowledge of sagebrush communities and their importance in this ecosystem. We are grateful for her thoughtful insights in improving our vegetation program and wish her the best as she looks to new challenges."

Women in Science: Mary Agnes Chase

Charissa Reid

ary Agnes Chase (1869-1963) had a lifelong fascination with the world of plants. Her passion began as a young adult when her brother-in-law encouraged her to study botany after the death of her husband, just one year after their marriage.

After studying the plant life of her childhood home in northern Illinois, Chase became a U.S. Department of Agriculture Division of Forage Plants botanical illustrator in Washington, D.C. The bureau eventually became part of the Smithsonian Institution. Her work led her to a partnership with Albert Spear Hitchcock, a principal scientist with the Smithsonian herbarium.

From 1905 to 1912, Chase explored grasses throughout the United States, which led to the publication of Manual of Grasses of the United States with Hitchcock in 1934. Throughout her life, she authored over 70 publications.

Her focus on grasses led her to Brazil where she documented over 500 new species there. She later conducted "two journeys across South America alone, during which she went by train, boat, donkey, and by foot, became the only woman to stand on top the highest mountain in South America, braved insects that bored into her toes, ran out of food and got hungry..." (Schultz 1949).

Her work at the Smithsonian Herbarium made it a taxonomic resource for botany taxonomy and agricultural scientists whose work resulted in grasses that were higher in nutrition and disease resistant.

Chase was a vocal suffragist, jailed twice for protesting in front of the White House for women's right to vote.

Chase was the eighth Honorary Fellow of the Smithsonian Institution in 1958. She received a Doctor of Science degree at age 89 from University of Illinois and continued to collect plant species throughout the world well into her 90s. She formally retired in 1939, but worked, for no pay, throughout the rest of her life.

Her passion for plants, and grasses in particular, was a lifelong passion. She said, "Grass is what holds the earth together. Grass made it possible for the human race to abandon cave life and follow herds. Civilization was based on grass, everywhere in the world" (Schultz 1949).





Bouteloua megapotamica (Spreng.) Kuntze [Bouteloua megapotamica (Sprengel) Kuntze, Poaceae alt. Gramineae], ink on paper by Mary Agnes Chase (1869– 1963), 29 × 26 cm, for David Griffiths (1867–1935), "The grama grasses: Bouteloua and related genera" in Contributions from the United States National Herbarium (1912, fig. 52), Hitchcock-Chase Collection of Grass Drawings, on indefinite loan from the Smithsonian Institution, HI Art accession no. 6010.0825.



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Who is Inventory & Monitoring? We're over 300 National Park Service staff from across the country and our roles are as varied and diverse as the parks that we serve. We are ecologists, biological science technicians, and data managers; GIS specialists, administrators, physical scientists, and writer-editors. We are all linked by a common love of our national parks, and by our commitment to providing the best science possible as the foundation for managing park natural resources.

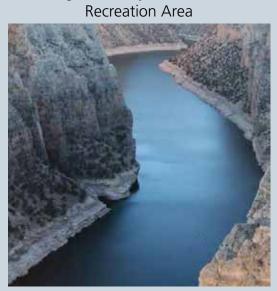
Yellowstone National Park



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Yellowstone Inventory & Monitoring Network in
Yellowstone Science 27(1) The Vital Signs Issue The Vital Signs Issue.

Controlling Invasive Weeds in Yellowstone

Roy Renkin

The earliest efforts in Yellowstone National Park to control an "unwanted" plant were in the 1960s with Dalmatian toadflax. This perennial forb of Mediterranean origin was brought into the United States in 1894 as a garden plant. Park managers found Dalmatian toadflax in 1957; a few years after concessionaires planted it for use as a table ornament in the Mammoth Hotel dining room (Whipple 2001). Plants spread rapidly from the Mammoth Hot Springs area, and resource managers used grubbing, mowing, and chemical herbicide to try to kill it. In the early 1970s, park staff released a nonnative moth to eat the plant, though these efforts were unsuccessful (Story 1985). Dalmatian toadflax eventually spread over a wide area of the sagebrush-steppe community in the upper Yellowstone River valley in and outside the park. Managers thought this weed would displace native sagebrush and grasses, thereby reducing the amount of food for grazing animals.

Weed control efforts in the park continued into the early 1980s, mostly targeting 7 to 10 species considered noxious by surrounding states. Efforts increasingly focused on spotted knapweed, first documented in the park in 1973. This weed spread rapidly through the Pacific Northwest, Montana, and into Yellowstone via roads and developments (Boggs and Story 1987, Allan and Hansen 1999). As the number of nonnative weeds and infested areas in the park increased, managers adopted an Exotic Vegetation Management Plan (NPS 1986) that established four Weed Management Districts in the park. Biologists identified 85 nonnative plant species in the park, but focused control efforts on those most likely to displace native plants.

The number of nonnative plant species in the park increased to more than 185 by 2001. This represents about 15% of the vascular species found in the park despite efforts to coordinate control strategies



Dalmation toad flax



Spotted Knapweed

across the Greater Yellowstone Area (GYA; Free at al. 1990, Mullin 1992, Sheley et al. 1999, Whipple 2001). Managers attempted to prevent weed introductions through early detection and controlling or at least containing infestations. They also increased education and monitoring to better define the extent of weed problems and the effectiveness of control efforts (Olliff et al. 2001). Managers prioritized the treatment of 24 nonnative weeds based on their distribution, likelihood of displacing native vegetation, resistance to control efforts, and cost-effectiveness of treatments (Sheley and Kreuger 1999, Skinner et al. 2000, Olliff et al. 2001, Whipple 2001). They created databases to document areas surveyed and treated to control weeds. Also, they conducted analyses of the likelihood certain weeds occurred in, or could invade, various areas of the park (Allen and Hansen 1999; Pauchard et al 2003; Rew at al. 2005a, b, 2006; Pauchard and Alaback 2006; Lehnhoff et al. 2008). These studies indicated roads, trails, developed areas, and transmission lines created conditions favorable for weed establishment and spread. They also indicated native sagebrush-steppe communities in the Yellowstone, Lamar and Firehole/Madison river valleys, and potentially the more remote and largely intact Hayden and Pelican valleys, were vulnerable to weed invasion.

Park managers completed an Invasive Vegetation Management Plan and Environmental Assessment in 2013 to "preserve, protect, and restore the diversity, ecological integrity, and processes associated with native plant communities in the park." Managers coordinated weed management efforts with other agencies to prevent the entry and establishment of new invasive plants, and to contain, reduce, or eradicate existing infestations. The plan promoted monitoring to describe weed occurrences and distributions and track the effectiveness of control efforts and potential impacts to native plant communities. In addition, the plan encouraged the restoration of native plant communities disrupted or replaced by invasive plants. Lessons learned and information obtained would enable biologists

to adjust management actions over time in response to changing knowledge or conditions.

The introduction and spread of invasive plants is the greatest threat to native plant communities in the park and throughout the GYA (Hanson 2009). There were about 217 nonnative plant species in the park by 2013, an additional 31 from the previous decade. Forty-seven species are on the park's "watch list", while 46 are priorities for control. Management actions are minimal to nonexistent for more than 168 invasive species. Biologists discovered and treated ventenata grass, a new aggressive invader, in two small, but separate, areas of northern Yellowstone in 2018. This plant is increasingly problematic in agricultural and rangeland areas of the intermountain west (Jones et al. 2018) and occurs in Montana counties adjacent to the park. It is likely that increased monitoring will detect other occurrences of ventenata in the park that need quick, aggressive treatment consistent with the established management plan.

It is difficult to map the distribution of nonnative plants in Yellowstone due to the park's large size and varied vegetation communities. As a result, biologists often use satellite imagery and modelling to approximate distributions and predict spread. Each summer, park weed crews, in conjunction with the Northern Rockies Exotic Plant Management Team and the Montana Conservation Corps youth crews, inventory 3,500 to 8,000 acres (1,400 to 3,200 hectares) for about 30 invasive plant species and treat up to 200 acres (80 hectares; NPS 2018). Other efforts to prevent the invasion of new nonnative plants include the annual inspection of about 16 gravel pits outside the park used to obtain materials for park construction projects. Efforts also include the inspection of earth-moving construction equipment to ensure they are free of invasive weed seeds. Managers do not allow hay for packhorses and mules in wilderness areas, and only feed weed-free hay in

other areas. These efforts are coordinated among seven interagency Cooperative Weed Management Areas across the region, including various portions of the park, with similar weed problems that allow for sharing of resources and personnel to address issues (Free et al. 1990). For example, the Hold the Line Initiative-Keeping Leafy Spurge out of Yellowstone National Park in the Henry's Fork Cooperative Weed Management Areas addresses threats to the park while restoring native vegetation in affected areas in Idaho beyond the southwestern boundary of the park. Managers share information from management efforts with the Greater Yellowstone Coordinating Committee's Terrestrial Invasive Subcommittee.

For decades, managers have attempted to restore native vegetation to areas disturbed by construction activities in developed areas or along road corridors (NPS 1997, 2002). However, attempts to restore native vegetation to weed-infested areas are a recent endeavor. Currently, about 75 acres are at varying stages of restoration with native vegetation in the Gardiner Basin area of the park. Managers focused restoration efforts in areas with relatively new infestations of nonnative weeds rather than areas dominated by sod-forming grasses like smooth brome and timothy introduced in the 1900s to provide food for deer, elk, and pronghorn (Houston 1982). In addition, park managers have used chemical herbicide treatments in some areas to reduce the density, or number, of invasive plants (Table 1). Herbicides substantially reduced the densities of houndstongue, Dalmatian toadflax, and yellow toadflax and effectively killed actively growing plants of spotted knapweed and oxeye daisy. However, treatment sometimes stimulates root sprouting or the release of seeds into the soil which has lessened the effectiveness of control efforts with spotted knapweed and oxeye daisy. Biennial to shortlived perennial plants produce many seeds that remain viable in the soil for decades (Davis et al. 1993, Sheley et al. 1999). Thus, control requires persistence.



range) of five weeds in Yellowstone National Park over a 3-year period.

Table 1. The success of herbicide control at reducing the densities (mean and

WEED SPECIES	MEAN % DENSITY REDUCTION	RANGE % DENSITY REDUCTION
houndstongue	-82.6	-67 to -98
dalmation toadflax	-87.4	-48 to -100
yellow toadflax	-97.5	-90 to -100
oxeye daisy	-36	-100 to +92

Managers in Yellowstone need to preserve native plant communities while managing the spread of existing or new invasive plants. This task is difficult given increasing visitation, human disturbance, and a warming climate with conditions often more favorable to invasive plants. People can introduce or spread nonnative plants by dirt or mud on automobiles, over-snow vehicles, and maintenance equipment, as well as through gravel, sand, and topsoil (Whipple 2001). Areas most vulnerable to invasion are those that experience soil disturbance or the removal of vegetation. Weed invasion and establishment along roadsides, trailheads, and established parking areas, as well as along unauthorized trails in increasingly popular wildlife viewing areas, has intensified due to soil compaction and damage to native vegetation. Managers need to address these effects.

Most of the invasive plant species targeted for control in the park are noxious weeds that tend to be biennial or perennial with a lifespan from two to many years. Annual weeds that complete their life cycle in one year have shown the most spread and displacement of native vegetation in the park over the past two decades. These

Cheatgrass

weeds traditionally have not been the focus of large-scale control efforts. Cheatgrass (which managers first documented in the park in 1930), annual wheatgrass, and the nonnative forb desert alyssum have become widespread and dominant, particularly in the lower, drier elevations of the sagebrush steppe communities in northern Yellowstone. All of these winter annuals are capable of germinating in autumn, overwintering in a dormant state, and rapidly depleting soil moisture with early spring growth while native plants are emerging from dormancy. These and other nonnative plant species have replaced native sagebrush and grass communities in portions of the Gardiner basin (Sikkink 2011).

The ecologic and economic impacts and management challenges of cheatgrass in the sagebrush communities in the western United States are well-documented (Mealor et al. 2013). However, managers know little about the biology of desert alyssum or annual wheatgrass, or even their distribution beyond park boundaries. None of these species are designated noxious weeds in surrounding states, although Montana recognizes cheatgrass as a "regulated" plant. Thus, efforts to control them or restore degraded areas are minimal. Both cheatgrass and alyssum can spread over large areas and reduce native plant cover in rangelands of west-central Montana (Pearson et al. 2016). These plants are spreading throughout the park at an alarming rate that will require focused management with new approaches to curb their spread. For example, biologists found desert alyssum in scattered areas along disturbed roadsides in the Hayden Valley in 2016. Biologists initiated herbicide control to prevent the spread and lessen potential impacts to grassland and sagebrush communities

In addition to disturbance, biologists recognize climate as a key factor influencing the spread of nonnative plants and the persistence of native plants (Hellmann et al. 2008). Invasive plants like cheatgrass have tolerances for precipitation and temperature that limit their



Desert alyssum

distribution. Managers expect many of these invasive species to respond to climate warming in ways that negatively affect native sagebrush-steppe communities (Bradley 2009, Prevey and Seastedt 2014, Brummer et al. 2016). Plants like desert alyssum, annual wheatgrass, and ventenata can respond quickly to changes in precipitation and temperature and rapidly spread through openings in native plant communities. Similarly, other invasive plants already broadly established in the sagebrush steppe communities could expand upward in elevation and alter alpine communities under warming climate scenarios. There may currently be climate tolerances that prevent seed germination or seedling establishment of Dalmatian toadflax in the alpine meadows of the park; however, a warming climate could alter these constraints and lead to an increase in the current elevational range of this plant (Pollnac et al. 2014).

Managers will need to adjust strategies over time to protect areas of largely intact native vegetation and minimize human disturbances to the extent possible. In addition, they may modify control tactics to focus on the current margins of invasive weed distributions, target lower-priority "non-noxious" weeds, or invest in more native revegetation efforts. The more immediate and acute problems with invasive weeds contrast with the subtle and long-term effects of a variable and changing climate. Nonetheless, increased vigilance will be required to preserve and protect native vegetation communities in Yellowstone National Park.

Literature Cited

See *Literature Cited* section of this issue on page 108.

Roy Renkin retired as the park vegetation specialist in 2019. He began his career in 1979 in the Division of Forestry & Fire Management in Yellowstone National Park. He worked in the Research Division from 1985-1989. He moved to the Resource Managment Division, which became the Yellowstone Center for Resources in 1992. He spent 41 seasons involved in wildland fire. Roy now lives in Gardiner, Montana and spends lots of time fishing and enjoying his grandkids.

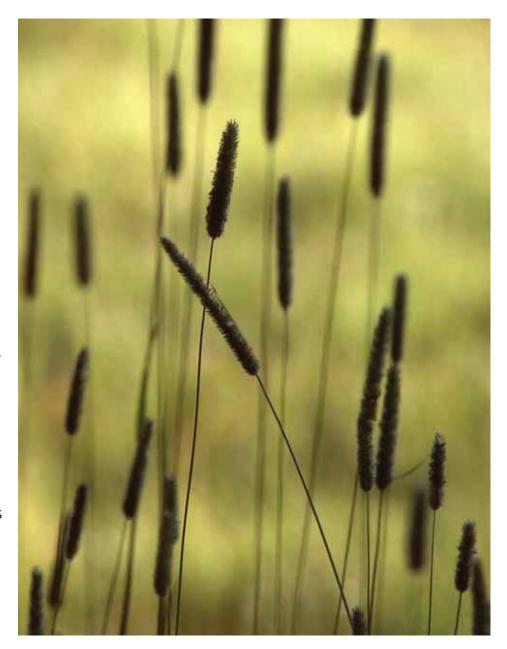


Managing Grassland Communities in Northern Yellowstone

P. J. White, Chris Geremia, & Bill Hamilton

The articles in this edition indicate the overall health of most grassland and sage-steppe communities in the northern portion of Yellowstone National Park (YNP) as generally good. Some riparian and sagebrush communities changed to grasslands during the 1900s due, in large part, to intense browsing by more than 19,000 elk (Hobbs and Cooper 2013). Elk counts have decreased by about 70% since 1994, and aspen and riparian communities are recovering in several areas; though browsing by abundant bison is suppressing recruitment in some areas (Painter et al. 2012, 2015). The compositions of plants in some grassland areas have changed in recent decades, but most of these communities are resilient and productive with healthy soils and energy, nutrient, and water cycles (Geremia and Hamilton 2019). Native plants still comprise a majority of grasslands in areas not historically used for farming, and botanists are restoring native plants in portions of the Gardiner basin that were previously farmed (YCR 2018). The conservation of wildlife has been guite successful, with the continuing recovery of bald and golden eagles, bighorn sheep, bison, cutthroat trout, grizzly bears, peregrine falcons, pronghorn, and wolves. There are about four million visits to the park each year and most people are satisfied with experiencing a wild place and viewing wildlife in their natural habitats (Resource Systems Group 2017).

However, some troublesome trends need further attention. Nonnative plants have infested some areas in recent decades and changed the composition and production of vegetation communities by displacing native plants and altering energy and nutrient dynamics (Renkin et al. 2014). Native bunch grasses in drier areas may not regrow sufficiently after repeated intense grazing, which makes these communities susceptible to reduced productivity and invasion by nonnative plants (Fuhlendorf et al. 2012). Continuing trends towards warmer drier summers with more frequent drought could



worsen this spread and threaten some native grass communities, which in turn, could influence the numbers and feeding patterns of ungulates (Wilmers et al. 2013). Thus, managers need a long-term strategy to monitor and manage grasslands in coordination with ungulate management.

Traditional Monitoring Approach

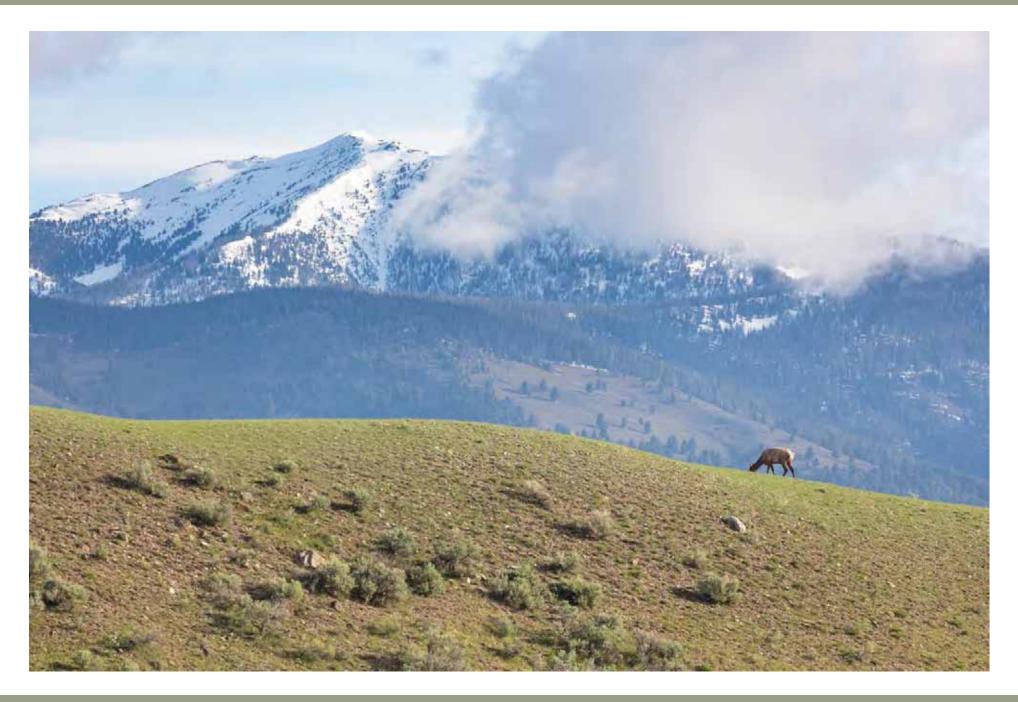
Rangeland scientists have indicated the desired conditions for grassland and sage-steppe communities in northern YNP should be the stable (climax) plant communities that existed historically with low levels of grazing (Hunter et al. 2018). The Natural Resource Conservation Service (NRCS) developed descriptions of these historic vegetation communities based on climate, terrain, soil characteristics, land use, and other factors (U.S. Department of Agriculture 2003). Managers use these ecological site descriptions to evaluate rangeland health by comparing them to existing conditions using indicators such as plant composition, production, and water, nutrient, and energy flow, with differences often attributed to disturbances such as climate change, fire suppression, or overgrazing by large ungulates (NRC 2013).

There are difficulties with applying this approach in YNP and other areas where managers are supposed to conserve wilderness and wild animals with minimal disturbances by people. The NRCS did not develop ecological site descriptions for northern YNP and nearby areas of Montana (Marlow et al. 2019). In addition, plant communities do not always progress towards a single long-standing condition. There are usually different conditions communities could reach depending on trends in climate and disturbances such as cultivation, fire, flooding, grazing, and invasions of nonnative plants. Comparing differences between existing conditions and a desired state has limited value because this approach does not identify the actual causes of such differences (NRC 2013). It also would be difficult to maintain a vegetation community in some agreed-upon

long-standing condition, and such a practice likely would decrease the variety of animals and plants across the landscape (Fuhlendorf et al. 2012).

It would be impossible to recreate natural pre-settlement plant and animal communities in YNP. Colonists slaughtered large wild animals, excluded indigenous people, and conducted farming, ranching, and development that degraded and fragmented historic plant communities. In addition, the climate has warmed substantially over the past 150 years and nonnative plants invaded many areas (White et al. 2013, Whittlesey et al. 2018). The public does not favor allowing numbers of large grazing animals such as bison, deer, or elk to increase unmanaged to the point where disease outbreaks or mass starvation occur (NRC 2013). Thus, managers often limit numbers of ungulates through harvests and captures, which tends to keep animals reproducing at higher rates and, in turn, continues the need for removals.

Defining the appropriate condition for grass and shrub communities influenced by thousands of wild, minimally managed, wide-ranging ungulates is difficult. Grazed vegetation communities will not look the same as ungrazed communities, but generally still maintain productive soils, clean waters, and forage for animals (Fuhlendorf et al. 2012). In addition, managers often make decisions regarding desired levels of grazing and the sharing of forage among various ungulates based on social and political values, not scientific evidence (NRC 2013, Beever et al. 2018). The quantity and quality of plants eaten by ungulates also vary widely across the landscape and among seasons and years due to variations in precipitation, temperature, and grazing intensities (Frank et al. 2013). It is difficult to determine the amount of forage available for eating at any given time and quickly limit numbers of ungulates and grazing to these levels (NRC 2013).



A New Approach

Given similar issues, the National Research Council (2013) recommended a somewhat different approach for managing rangelands grazed by wild, free-ranging horses and burros in the western United States. This approach does not depend on vegetation communities remaining in a long-standing condition over time. It focuses more on landscape patterns and natural processes that are better suited for managing wilderness areas with an assortment of vegetation communities across vast landscapes and disturbances such as wild fires and variable levels of grazing (Fuhlendorf et al. 2012, NRC 2013). This approach provides more flexibility to respond to changing conditions, such as climate warming, and political and social uncertainty (NRC 2013, Beever et al. 2018).

Under this approach, the desired condition for grass and shrub communities in northern YNP would be to maintain a variety of functional plant groups, including bunchgrasses, annual grasses, rhizomatous grasses with root-like underground stems, forbs, and shrubs, supported by healthy soils and functioning water, energy, and nutrient cycles (Geremia and Hamilton 2019). Plant communities will vary widely in their appearance and composition depending on differences in soil and weather conditions, land use and management histories, and historic and current grazing intensities. Many communities will include widespread nonnative plants due to their previous spread. Ungulates will graze some areas intensely and others lightly, thereby providing a mosaic of conditions across the landscape to support a variety of plants and animals (Fuhlendorf et al. 2012). However, each community should still maintain plant productivity, soil organic matter, and functioning energy, nutrient, and water cycles.

Geremia and Hamilton (2019) conducted detailed vegetation composition surveys of grasslands in YNP during 2017-2018 and identified four ecological communities based on soil types and variations in weather. They considered factors that influence plant composition and growth such as temperature, precipitation, soil inorganic nitrogen, soil organic matter, percent sand, pH, and elevation in defining these different communities. These factors vary widely within and among areas; as a result, there was some overlap in soil and weather conditions among the four community types. However, the categorizations are useful for identifying areas that could support similar sets of vegetation communities.

The first type of ecological community consists of perennial graminoids (grasses, sedges and rushes) and forbs, with some rhizomatous grasses, in cool wet areas with nitrogen-rich, clay-loam soils. This type of community occurs in wet areas in the Hayden and Pelican valleys and higher elevations surrounding the Lamar Valley, including Specimen Ridge and the Mirror Plateau. Common vegetation includes tufted hairgrass, silver sage, and timothy grass. Current grazing intensities in this community type are naturally altering plant compositions in some areas, but without adverse effects on production and soil organic matter.

The second ecological community type consists of annual grasses and forbs in warm, dry areas with nitrogen-poor, loam soils. This type of community occurs in previously cultivated areas of the Gardiner basin. Annual grasses such as cheatgrass and wheatgrass, as well as desert alyssum, comprise more than 70% of the plants in some areas, which adversely reduces productivity compared to other community types. Climate rather than grazing appears to be driving the development of these annual plant communities.

The third type of ecological community consists of rhizomatous grasses and shrubs, with some perennial grasses and forbs, in cool dry areas with sandy-loam soils and sufficient soil nitrogen. This type of community occurs in dry, upslope areas across northern YNP, including the Blacktail Deer Plateau, Little America, and the slopes of the Lamar Valley. Common vegetation includes Idaho fescue, junegrass, needlegrass, and big sage. Current grazing intensities

in this ecological community influence plant compositions, but do not adversely affect productivity or soil organic matter. However, a continued warming and drying climate could lead to annual plants dominating more of these communities and negatively affecting productivity and water, energy, and nutrient cycles.

The fourth ecological community type consists of rhizomatous grasses and numerous forbs in cool wet areas with clay-loam soils and sufficient nitrogen. This type of community occurs in wet areas across northern YNP, including the floor of the Lamar Valley where cultivation occurred during the early 1900s. Common vegetation includes Kentucky bluegrass, clover, timothy grass, smooth brome, and dandelion. Cultivated plants spread and caused other ecological community types in the valley to convert to this type. The cultivated plants thrive under intense grazing, with high productivity, healthy soils, and functioning water, energy, and nutrient cycles.

Geremia and Hamilton (2019) recommended monitoring for changes in the composition of functional groups (rather than individual native and nonnative plants), productivity, and soil organic matter at several sites in the various types of ecological communities. If future monitoring detects substantial differences among sites belonging to the same type of ecological community, this evidence may indicate that some type of disturbance, such as invasive plants or overgrazing, is causing one or more sites to transition to a different state (Geremia and Hamilton 2019). Changes in ecological communities from one type to another, such as to a community dominated by annual plants, could be indicative of an undesired condition with reduced ecosystem functions. If undesired changes occur, and managers decide intervention is necessary to restore ecological functions, then they could initiate restoration actions. Managers should implement restoration projects using a flexible, adaptive approach whereby methods are adjusted based on experience and learning to progress towards desired conditions. Restoration projects should use native seeds, cuttings, and transplants when possible (NPS 2006).



Management Zones

Biologists need to develop realistic expectations (desired conditions) and strategies for managing vegetation communities in various areas with different historic land uses and existing conditions. Each strategy should include implementing best management practices to prevent, or at least slow down, the introduction and spread of new nonnative plants. The Gardiner basin could be designated a Cultural Management Zone due to its historic farming, ranching, and wildlife management activities. This basin has had sparse vegetation since at least the 1870s due to active mud flows, low annual precipitation, high winds, and heavy use by livestock and native ungulates during the late 1800s and 1900s (Secretary of War 1871, Whittlesey 1995). Much of this area was homesteaded, farmed, and ranched. During the 1920s and 1930s, the Game Preservation Company purchased much of this area northwest of Gardiner, Montana, and began operating the Game Ranch. Agricultural fields in the Stephens Creek area were irrigated using water from springs and creeks to grow hay to feed elk and pronghorn (Whittlesey 1995). The Game Ranch was added to YNP in 1932 "to improve and extend the winter feed facilities of the elk, antelope [pronghorn], and other game animals of Yellowstone National Park and the adjacent land, and for other purposes ..." The Stephens Creek area was subsequently used for a nursery, horse corral operations, bison capture facility, and native revegetation. Today, nonnative plants such as crested wheatgrass, mustard, Kochia, Russian thistle, cheatgrass, and Canadian thistle infest large areas of the Gardiner basin. These infestations have resulted in a decrease in functional plant groups, productivity, and soil organic matter (Renkin et al. 2014). Given this context, management could focus on continuing historic uses and using agricultural practices to remove nonnative plant infestations and reestablish functional vegetation communities with nutritious forage for wildlife.

The Lamar Valley could be designated an Ecological Research and Education Zone due to efforts to recover bison and wolves and evaluate the effects of these actions on vegetation communities and other wildlife. During 1902-1909, managers introduced bison from northwestern Montana and Texas to northern YNP. These bison were herded during summer, and fenced and fed during winter at the Buffalo Ranch in the Lamar Valley (Meagher 1973). A substantial portion of the valley was cleared of native vegetation and planted with nonnative grasses to produce hay between 1904 and 1952 (Goodacre 1933). Grasses from the abandoned hayfields continued to grow and spread thereafter; as a result, bison continue to congregate and intensely graze these areas each summer (Geremia et al. 2019). In addition, 14 wolves from Canada were brought to YNP in 1995 and placed in or near the Lamar Valley to establish the first known packs in the park since the 1920s (Bangs and Fritts 1996). Wolves spread through the region over the next decade, which led to an incredible burst of scientific investigations and education about predators, ungulates, and effects to vegetation communities that continues today (Smith et al. 2016). Given this context, management could focus on research and education to convey information about the effects of bison and wolf restoration. Recent studies indicate the number of functional plant groups, productivity, and soil organic matter are high and similar to measurements in the 1980s and 1990s (Geremia and Hamilton 2019). Biologists are monitoring the abandoned hayfields to determine how bison grazing maintains high quality diets by improving plant growth and productivity (Geremia et al. 2019).

The vast landscape between the Gardiner basin and the Lamar Valley could be designated a Natural Vegetation and Wildlife Migration Zone. Most of the grassland and sage-steppe communities in this area were not farmed, and livestock have not grazed there since the 1920s (Whittlesey 1994). As a result, nonnative plants have not infested large areas, though they are scattered through the native



communities. This area provides movement corridors and seasonal ranges for ungulates and other wildlife. Thousands of ungulates travel along the Yellowstone River and over Mount Everts between their winter and summer ranges, including bighorn sheep, bison, elk, mule deer, and pronghorn. Protection of this area is important because disturbances by people could reduce the survival of wildlife that depends on this corridor for seasonal movements. Protection would also support a 2018 order (No. 3362) by the Secretary of the Interior to enhance and improve the quality of ungulate winter ranges

and movement corridors in the western United States. Given this context, management could focus on preserving mostly native plant communities, preventing infestations of nonnative plants, and limiting disturbances by people to wildlife movements.

Adaptive Management

The conservation of vegetation and wildlife communities in YNP should be undertaken using a flexible management approach that incorporates monitoring and research to identify undesired changes that are occurring, and decide on necessary management

actions. Using this approach biologists evaluate current conditions, identify undesired trends, implement management actions, monitor progress towards desired conditions, and adjust actions to improve progress (Williams et al. 2007). Condition assessments need to occur in numerous places because vegetation changes across the landscape and, as a result, wildlife use portions of the landscape differently (Becker et al. 2013). Assessments of vegetation condition should include plant composition (functional groups) and indicators of energy, nutrient, and water transfer such as plant production and soil organic matter. Assessments over time should evaluate if differences within or among areas are driven primarily by weather (precipitation, temperature), components of soils, the circulation of water (hydrology), or grazing intensity. Biologists should also assess the variety of wildlife (biodiversity) using each site to determine if variations in grazing intensity contribute to local differences (Geremia and Hamilton 2019).

Biologists should assess changes in conditions due to grazing, climate warming, and other effects using an experimental framework that includes pairs of grazed and ungrazed plots sampled through summer and across years. In addition, biologists should use remote sensing indices to describe variations and estimate plant production across the vast landscape. We recommend biologists input this information into models of the system designed to predict trends. Models could incorporate seasonal ungulate distributions to estimate forage use and overlay this information onto forage production estimates to predict forage consumption across the landscape (Geremia and Hamilton 2019). Biologists could incorporate new information as it becomes available and revise forecasts based on the outcomes of management actions.

Moving Forward

The Yellowstone Center for Resources is conducting an exercise to develop management and monitoring goals for grassland and

sage-steppe communities in northern YNP. This planning process will identify priority resources for conservation and management concerns. Biologists will assess historic land uses, existing conditions, and trends in vegetation and wildlife communities and, as necessary, develop management actions to progress towards desired conditions (NPS 2017). Thereafter, biologists will implement work plans, monitor their effectiveness, and adjust management activities as necessary. Important resources and values for the park include preserving the existing variety of native animals and plants, inspiring scenery, geothermal wonders such as geysers and hotpots, an intact wilderness with minimal disturbances from people, and its cultural heritage to enhance visitor education and enjoyment (NPS 2014). Management concerns include a warming climate, development outside the park, invasive plants and animals, impacts from increasing visitation, and the spread of nonnative diseases. Park staff are using scenario planning and other tools to identify possible future situations, their implications, and potential management responses (U.S. Fish & Wildlife Service 2018). They also are working to identify and monitor key indicators of whether ecological communities are transitioning to an undesired state. The information presented in this issue will inform these efforts.

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Literature Cited

See Literature Cited section of this issue on page 108.

P.J. White (see page 11).

Interview: Dr. Douglas A. Frank

r. Douglas A. Frank is a professor of biology at Syracuse University. His research focuses on the effects of climate and grazing mammals on energy and nutrient processes in grasslands. Since 1986, Doug has pioneered work on the ecology of Yellowstone's grazing ecosystem. He demonstrated grazing by ungulates increased plant production, like on the Serengeti in Africa. Yellowstone was the first temperate system where that's been shown.

NOTE: This interview was conducted by Charissa Reid, science communications specialist, on July 2nd, 2019 at the Yellowstone Center for Resources, Mammoth Hot Springs, Yellowstone National Park.

Charissa Reid (CR): How it is that you came to Yellowstone and began your research here?

Doug Frank (DF): I started work here in 1986. I became interested in Yellowstone while a field technician at Olympic National Park. The project there was how the introduced population of mountain goats was affecting sub-alpine plant populations.

I was working with a woman by the name of Robin Reid, who's now a professor at Colorado State University. Robin had been reading some papers by Sam McNaughton at Syracuse University. He was studying grazing in the Serengeti Ecosystem of east Africa. I started reading his papers and found every article shed new light on some exciting way that herbivores were affecting Serengeti grasslands.

The classic view of large herbivores, both domestic and wild, was that they negatively impacted plant production, the grasses that they fed on. Sam was discovering that they were actually stimulating plant growth in the Serengeti ecosystem. And that was new! Some thought that he was a heretic at first because it was so different than how we viewed grass/large herbivore interactions. The results were very solid though, so I began wondering if those kinds of dynamics were happening elsewhere in other systems that wild herbivores grazed grasslands. And an obvious temperate system, a North American system, that you could test that notion was Yellowstone.

CR: Where are you originally from?

DF: Originally from the Chicago area but after graduating from college at University of Illinois I took seasonal jobs and traveled around out west.

CR: What did you study in college?

DF: Biology, with a focus in ecology. After graduating I first volunteered with the Student Conservation Association as an interpreter at Mount Rainier National Park. I continued working seasonally at Mount Rainier for a few more years as a backcountry and front country ranger while getting a Master's at the University of Washington studying plant succession on Mount Rainier. After that is when I started working at Olympic National Park.

CR: How did you get from your work in Olympic to conducting fieldwork in Yellowstone?

DF: That's a great question. I worked for Francis Singer for a year. Francis was a staff biologist that had just arrived in the park, and he hired me for a summer. That was the summer of 1986. I had by that time been communicating with Sam [McNaughton] and had asked him if he was interested in taking on a graduate student working in Yellowstone. Sam was sometimes brief with his responses, and he just said, "If you get accepted to graduate school, I guess I'll take you on as a student." I was accepted and after my summer working in the park with Francis I started my graduate program in the fall of 1986 working with Sam.

CR: What was the focus of your early work here in the park?

DF: The earliest work was a dissertation study focused on how Yellowstone's large herbivores affected grassland aboveground production. As I mentioned, Sam had discovered that grazers in the Serengeti stimulated their own forage production and I was curious if the same phenomenon could happen in a temperate system like Yellowstone.

CR: That was a pretty exciting time in Yellowstone history. We were ramping up for wolf reintroduction. Was your work tied to some of that?

DF: I think there were nice discussions about wolf reintroduction at the time. But the big issue relevant to my work was that I started working in the park right after Austin Chase published his book [Playing God in Yellowstone] about Yellowstone.

There was a pretty large uproar about how the park's wildlife management policy was affecting the park's grasslands. A lot of folks felt that was the park was overgrazed.. There was interest by the park in funding research. Congress actually provided some money for Yellowstone to investigate this issue. Sam and I were awarded a grant and I received some other support from other sources to conduct the study. The study was a nice convergence of a funding opportunity to pursue my own intellectual interests about how grazing affects grasslands and seeing if the ungulate-grassland dynamics in the Serengeti were also going on in a temperate system.

CR: What was the study design?

DF: It was a test of how herbivores influenced production, and for that we needed a non-grazed treatment. So, you're comparing production between a non-grazed grassland within an exclosure, and a grazed grassland. We did that at various sites around the park.

CR: Are they the ones that are visible from the road when you drive

towards northeast entrance?

DF: My own exclosures are down. The ones that you see are the really old exclosures the park set up in 1958 and 1962. Mine were smaller - they were about 15 meters on a side and replicated per grassland location.

CR: What were your methods? How did you quantify things?

DF: When you're studying plant growth in a system with abundant herbivores, the plants are simultaneously growing and being grazed, so you cannot just measure the accumulation of shoot biomass. The method we used was similar to the one that Sam devised for measuring shoot production in the Serengeti. The idea is that you sample frequently in a grazed grassland and you have a set of temporary exclosures that are used to measure the incremental growth over a short period of time inside the exclosures that is protected from being grazed. You don't want to leave those exclosures up too long because if the animals are having a feedback effect on plant growth, if they're reducing the plant growth or they're increasing plant growth, then you're reducing that effect if you keep the exclosures up. You move the exclosures to a new location in the grazed grassland and then you measure the incremental growth in the exclosures at the new location. This is done repeatedly over the growing season. Then to determine annual shoot production, you just sum the growth that occurred during the sampling periods.

Using this method, you can determine the amount of aboveground production of plant growth in the grazed grassland. Inside the fences you sample at the same frequency, but you do not need to have the moveable fences inside the permanent fence because animals aren't removing any [plant] tissue.

CR: I've talked to Chris (Geremia) quite a bit about the work they're doing now with weighing and grinding the grasses and having the

species analyzed. There's probably a lot of new technology that's changed how this work is done over the years. Back then how did you make those measurements?

DF: Well, to measure plant biomass we used an indirect method, a calibrated nondestructive method. If you pass a narrow pin through the vegetation at a fixed angle, the number of contacts that the pin makes with the vegetation correlates well with the amount of biomass, standing biomass, in the plot.

CR: Sounds very intricate and as though it would be extremely tedious.

DF: It's a sadistic kind of a torture for the people who are doing it because you're standing over a plot for half an hour, an hour, just passing the pin at the right-angle, counting contacts with different plant species and recording them.

CR: I wondered how the grazing model, the agricultural model, was framing the conversation. How did you try to shift that conversation with your work?

DF: My motivation was an intellectual one. Scientific questions and trying to understand how the Yellowstone grassland was operating, functioning.

CR: As opposed to politics?

DF: Yes!

CR: How did politics influence your efforts?

DF: [Compared to an agricultural grazing model] I took a different view of looking at the vitality, the health, the performance of grassland. My interests are to try and understand the pathways by which animals feed back on plant growth. There's a lot of different really interesting pathways. The framework is how they're influencing energy and nutrient flows. And so, although we're measuring, and do account for, species identity, we're interested [in

the pathways]. It's like when I talk to students, I tell them, when you go to the doctor, the doctor's not interested in how much gray hair you have or what you look like. What they're interested in is your blood chemistry and your physiology/physiological measurements. That's what we're trying to do studying Yellowstone grasslands. We're interested in the energy dynamics and how Yellowstone grazers are affecting those dynamics. In other words, how much energy is being acquired by the system through the plants, through photosynthesis, and how do the animals affect that energy acquisition.

We can measure that by determining how they affect plant productivity. Then at the same time we also can measure how the animals influence resources like soil nutrients and water that plants need to regrow after being grazed to gain a greater understanding of how herbivores affect plant production? Grazers can have some obvious effects on soil nutrients by defecating and urinating that provide additional nutrients for plants.

However, there are other mechanisms in which herbivory can increase essential nutrients that are less obvious. For example, grazing stimulates soil microbial populations that turn over nutrients, and other microbes like mycorrhizal fungi, that help the plants absorb those nutrients. There are all sorts of really fascinating indirect effects that the animals have on plants besides defoliating them and defecating and urinating.

Range scientists classically look at species composition to determine how much disturbance is going on in the grassland and whether or not that disturbance is too much. Whether that's appropriate for a grassland [in] a national park is something I think is debatable. They are taking their model for cattle grazed systems and applying it to parks. I think this is a mistake and leaves us to try and manage like we are raising cattle! We don't want to turn national parks into cattle managed grasslands. They are something more. There's something different and special about these parks.

CR: A very fundamental understanding that most people have these days is that if there's a really big increase in an animal population, plants played a role in controlling the population because of available energy and food. Are you also looking at how the plants are affecting the animal populations or are you more just focused on the plants?

DF: Actually, we measure the plants and we're trying to understand how grazing and an increase in grazing intensity is affecting plant growth. That's a plant focused study and, thus far, as you know, things have changed. A fascinating aspect about working in this system is that it's extremely dynamic, it's always changing. For example, about 25 years ago Richard Inouye, a colleague at Idaho State University, and I compared actual evaporation among different ecosystems around the world. Actual evapotranspiration is a climate variable that takes into account temperature and precipitation to estimate the moisture available to plants in a system. Yellowstone turned out to have one of the greatest levels of between-year variation in actual evapotranspiration among the sites we examined around the world.

CR: Wow, that's amazing.

DF: Yes. With climate being a major driver of ecosystem processes, you'd expect a lot of variability in plant growth and other things. We're really kind of plant focused. We've looked at the nutrition of plants and how nutritious the plants are for herbivores. We've been [looking] at how herbivores are increasing their own forage quantity, but they also increase their forage quality. They increase the nutrient content of their forage. Very important. Nutrient content. Nutrients themselves are elevated when we measure them in grazed grasses compared to ungrazed grasses.

CR: That's pretty cool that they're actually improving their own habitat. How has the makeup of grassy places like Lamar Valley changed over time? Have you seen exotic [plants] affect the system?



DF: There are exotic, or we like to say invasive plants in the park. When I started my work in the late 1980s, there were a lot of invasive plant species in the Lamar Valley. They were some of the dominants there.

Chris Geremia and I have compared my species composition data from the 1980s with current species abundances that he has measured at the same grassland sites in recent years. Native species that grew at the sites that I sampled are still there, but the balance, the abundances of species have changed. It's hard to know what the cause of that is because there is variation that you can expect to occur on an annual basis. There is a lot of temporal climatic variation. There's also been an increase in atmospheric CO2 [carbon dioxide] concentrations, which is a substrate for photosynthesis. It's been shown when you increase CO2 concentration, plant growth increases. That tends to especially stimulate plants that are fast growers like weeds, like invasives, compared than others.

CR: What does the word mesic mean?

DF: Relatively wet. The Lamar Valley or the swales where you see more productive plant growth.

CR: Versus somewhere more dry, like the middle of Hayden Valley?

CR: The middle of Hayden Valley is pretty mesic. However, there is a lot of spatial variation there. You can have a site that's truly mesic, you know, like a swale in the middle of Hayden Valley the size of this room that has a totally different set of species growing than an adjacent drier slope.

CR: Has your research mostly focused on those mesic communities?

DF: We've studied all of them. Our interest has been to try to understand where the animals are feeding and how much they feed at those various sites from mesic grassland at the bottom of slopes to the mid-slope sites to hilltops.

CR: Was tracking the animals, was that a part of it too? How did you observe where they were grazing?

DF: We don't track animals. We don't know who's grazing the sites, we just know that a certain amount has been removed. We just measure consumption. In the more recent work, I've been collaborating some with Rick Wallen and Chris Geremia and they're tracking very closely with camera traps who is at their various sites, so they have more information than we ever had about who's grazing the sites. During the earlier studies, we just knew that the plants were being grazed. That they were being consumed. But we didn't know by whom.

CR: What changes have you seen in grasslands and grassland patterns as elk numbers have decreased and bison numbers have increased?

DF: When I started, it was all about elk. Elk was the dominant ungulate species. There were 20 or more thousand elk that were counted on the northern winter range back then, and there were fewer bison using the northern range. Elk were everywhere, I mean, it was very exciting, and the fall ruts were incredible. You'd see elk everywhere. There were no wolves at the time, so they weren't hiding in the trees. In the fall, you'd walk out at night and be surrounded by bugling elk. Those are very cool memories of being in the park back then. It is interesting now, of course, but it was very, very different in the late-80s and early-90s compared to today.

Differences in grazing patterns, you know, bison being very large herbivores, prefer to graze mesic, productive sites and they've elevated the [grazing] intensities in some productive areas like the Lamar and below the Lamar Valley. Those are areas that you see a lot of bison through the course of the summer. You didn't see ungulates, bison or elk, stay throughout the summer in those areas back when I started, because both elk and bison migrated up the elevation gradient. They left the valleys, the Lamar and Yellowstone



valleys, starting in late April usually, and were gone for the most part, by mid-May. They were following the green wave.

The green wave was a band of very nutritious vegetation that swept up the elevation gradient through the growing season. The animals moved with this wave of nutritious forage through the spring and summer months. And they didn't return for the most part until the first winter storms that usually occurred by the end of October or sometimes in November. After those storms is when you would see them in the Lamar Valley, maybe further down from there.

The grazing patterns of bison have been very different since after the wolves were reintroduced. Wolves were released and their primary prey was elk. As everybody knows, the elk population then declined sharply. We were measuring, back in the late eighties at the height of elk densities, grazing intensities of around 40%. It varied from site to site, but on average, around 40-45% of the aboveground tissue was removed. And now measurements of consumption rates for mesic sites like the Lamar Valley are quite a bit higher. These are areas where bison tend to camp out and re-graze through the growing season, which is very different.

CR: In the 60s, we never saw bison in Yellowstone unless you drove down to Lake or maybe Old Faithful in the winter. A couple of weeks ago there was a calf born in front of YCR [Yellowstone Center for Resources building]. So very different. It's one of the things that is so much fun about working here. You wait long enough, and sometimes you don't have to wait very long, and something changes. I remember doing an interview with John Good. He was a ranger here in the sixties when they were shooting elk. And he said that every time I saw an elk, he always saw the perfect kill shot. Unheard of today. You've obviously been here for an important shift. What are the main factors driving grass production in Yellowstone?

DF: This is a big question. There are a lot of factors that make it really complex to understand which of them are having a greater influence.

CR: Which ones do you think are most important?

DF: Well they're different and all important to a different degree. Ecologists usually think about what we call bottom-up factors that influence the resources like nutrients and water that plants need to grow. And so those include climate and its variability that is a hugely important factor influencing plant production. Climate not only affects water availability, it also affects nutrients and nutrient turnover by governing the activity of microbes that provide nutrients for plants. The major resources that control and limit plant growth in a system like Yellowstone are water and nitrogen. So those are two major factors that impact plant growth in Yellowstone- water and nitrogen, both of which are impacted by climate..

A second bottom-up factor affecting grassland production is soil condition. Anybody who has walked around the grasslands of Yellowstone has likely noticed a lot of spatial heterogeneity, a lot of patchiness, in the types of species that grow and the plant biomass that is supported in different patches. A lot of this spatial variability is due to topographic gradients in the landscape and their effects on soils. Grasslands at the base of slopes are wetter and support a lot of plant biomass. It's going to be much more productive at the base of slopes than elsewhere where it's drier. Those are bottom-up effects. The topographic effect is a bottom-up effect because it influences the properties of soils that can retain moisture and increase the availability of important nutrients like nitrogen for plant uptake. In addition, there's an important effect we call in ecology a topdown effect. An effect that herbivores have on production. In some systems, you know, that effect can be negative, it can inhibit plant growth. But in Yellowstone we've shown that it can increase plant production, but that effect can vary spatially depending on where on the landscape you are. The largest positive effects you have are in mesic grassland that are both relatively wet and nitrogen-rich, where plants have the resources to regrow after being grazed.

CR: The affluent communities?

DF: Yeah, that's right. The 1%! There's a number of factors - these climatic factors and topographic factors, and top-down factors, such as herbivory.

CR: Are you familiar with this video that's been circulating called Wolves Create Rivers? It's a video that's been done about trophic cascades. Doug Smith and I have talked a lot about it because it's very popular and we actually get a lot of questions about it in the science office here. Wolves are changing everything, but it's such a simplification of what's happening. With your study, I would see that that would also be the danger - I would almost think that that kind of simplification would be really seductive for the public.

DF: Right? Yeah. It's complex when you have a lot of important factors influencing something as important as grassland production. It's such an important process because that's a measure of the energy that is being acquired by the system! You know, it's like your budget, your home budget. The size of your budget allows you to buy food, shelter, everything. It's the energy the plants are acquiring that support everything else in the system. All the other animals, including elk and bison.

CR: What nagging questions are still out there that you haven't yet addressed?

DF: Well, there's a couple of burning questions I have right now. There's a lot of little ones, but there's two burning questions. One is to understand what the properties of a grassland system like Yellowstone and those that you find in the Serengeti, that sustains them. How are these systems sustainable in the face of such chronic high levels of herbivory?

For decades people have studied properties of grasses allowing them to regrow after being defoliated, their physiological properties. Some grasses seem to be adapted to being grazed. When they're grazed,

they create more stems and they regrow very quickly for various reasons. These are plants that are adapted to grazing.

However, when considering how herbivory affects plant production within the context of a grassland, it's not just a function of the isolated physiological response of a plant to being grazed. It's a function of how those plants are interacting with their neighbors and the different communities of soil microbes that determine the availability of nutrients for those plants.

We found that grasses and soil microbes interact in ways that increase the availability of nutrients after grasses are grazed in Yellowstone.

DF: Plants and soil microbes have a very intimate, close interaction that benefits them both. Soil microbes rely on plants to provide them carbon in the form of dead leaves and roots or exudates out of the tips of their roots and plants rely on their microbes growing in close association with their roots to provide them with nutrients that are a byproduct when microbes decompose the organic residues provided by plants. Grazing increases the rate that plants exude carbon compounds that can be used by soil microbes, which in turn increases the activity of those microbes and the rate at which they make nutrients, such as nitrogen, available to the grazed plant.

One of the burning questions is how at an ecosystem level, and by ecosystem level I mean the plant-soil system, how are both plants and the soil microbial community partnering to allow plants to recover or grow or respond positively when they are grazed. It's the ecosystem response, not just the plant response. How are these responses, these plant-microbe interactions choreographed after a grazing event? That's really one of the things that I'm really fascinated about.

CR: How would you study that?

DF: It so happens that several colleagues and I have just submitted a grant proposal to study it. There are two ways. One is a greenhouse experiment during which we grow plants collected from inside and outside the long-term, two-hectare exclosures in Yellowstone. Inside those exclosures, the plants haven't been grazed for over 50 years. I have previously grown plants collected inside and outside the exclosures in a greenhouse at Syracuse University and they look different. They're genetically different. They look different and respond to clipping differently. The ones outside are adapted to grazing, and the ones inside, tend to not respond well to grazing, to clipping with scissors. They have differentiated into grazing-adapted plants and ungrazed, non-grazing adapted plants. So, during the proposed experiment we will grow plants collected from inside and outside the exclosures in pots with soils from inside and outside the exclosures with and without different communities of soil microbes. Some of the pots have no microbes -they are the controls- other pots have only mycorrhizae fungi, or only the free-living bacteria and fungi, or the unmanipulated full soil community. When we clip the control plants without soil microbes, their response includes only their plant physiological response to defoliation. The response of clipped plants in pots with only soil mycorrhizae includes interactions between plants and mycorrhizae that may alter how plants respond to clipping. In a similar fashion clipped plants growing with only the free-living bacteria and fungi or the full complement of soil microbes may have different responses to clipping based on the interactions with the different communities of soil microbes they are growing with.

That's how we can differentiate the relative roles that these different microbial communities play in the plant response to defoliation. And then in the field, we can also examine the genomic function of the soil communities.

CR: What's genomic function?

DF: The presence of genes, the abundance of genes in the soil microbial community that we would expect to benefit plants. There are genes that regulate nitrogen and phosphorus transport from the mycorrhizae fungus to the plant. Those have been identified in mycorrhizae. There's likewise in the free-living bacteria population genes that are associated with the mineralization of nitrogen or phosphorous or hormone production, that benefit plants, that increase plant production.

This is work that I can't perform, but a colleague, Lluvia Flores-Renteria at San Diego State University, will do. She will look at the abundance of these genes in soil collected inside and outside exclosures in the field. That is the baseline information for a field manipulation experiment. In grasslands outside the exclosures that have been grazed for a long time, we will put up fences to eliminate grazing and track how the microbial communities and the genes they express change when animals are excluded and plants are no longer grazed.

How does gene abundance and the traits of the soil microbial communities and plants change over a few years? Do they trend towards plant and soil attributes that we see in the exclosures? And in parallel, inside the exclosures, we will clip plots and monitor the soil microbial attributes over time. Do those plant and soil traits trend towards what we see in the grazed grassland? They probably won't get entirely there after a couple, three years of the study, but are they heading in that direction? That is how we've proposed to study it.

CR: That was one of your burning questions, but you said you have two.

DF: The second one is that one of the reasons why grazers are increasing plant production based on a number of studies we've conducted in the park, is that they're increasing the availability of soil nitrogen for plant uptake. Earlier I was saying how nitrogen is

a limiting factor, resource, for plant growth. When animals urinate, they add nitrogen and the plants in those patches turn greener and grow taller. They are greener because there's more photosynthetic machinery, chemistry to allow plants to photosynthesize and grow more. So the animals reduce the extent to which plants are limited by nitrogen.

Water is the other major limiting factor of plant growth in Yellowstone grassland. If grazers are reducing the limitation of one of two limiting factors, nitrogen, they may make the grasslands more sensitive to the other, water or the vagaries of climate, precipitation. The other burning question that I have is to what extent do grazers increase the sensitivity of Yellowstone grasslands to variation in precipitation and do they make the system more responsive to climate change as a consequence. I would like to be able to investigate that. I think that has important ramifications for park management and how predicting the degree to which Yellowstone grassland production and the capacity for the system to support large herbivore herds may shift with climate change. It would be a compelling conservation argument for sure with everything going on. So, if you have any sources of funding ... (laughter).

CR: I have no funds! A few weeks ago, I was a Lowe's in Bozeman and they had this display set up and it was a robot like the ones you can buy to sweep the floors in your house, but it was for your grass. I took a picture of it and I sent it to [Chris] and said, I found a robotic bison. Still funny, but I see that it's not that simple because you know, there's no comparison between the two other than the cutting. You have answered my questions which is how you consider what the animals do to the plants. Not only by walking on it, but also defecating and urinating as well. It is quite a puzzle. It's hard to disentangle those different effects because they have influences. For that robot to be a bison it would need to defecate, urinate, trample. What is the most significant change in Yellowstone's grassland since you started your studies? You want to pick just one?

DF: Chris Geremia and Rick Wallen have recently resampled sites that I first examined in the 1980s. We found that although the species composition shifted, the same species occurred at the sites compared to what grew there before. So the system has been pretty doggone resistant, as far as the presence of native species is concerned. However, there probably has been a growing abundance of invasive species that may have changed the properties of Yellowstone grasslands and the grazing patterns of herbivores in ways that we don't know.

There's also been an enrichment in atmospheric CO2 that affects plant growth in some species more than others. And, of course, the regional climate is shifting, becoming warmer and including more extreme drought and rainfall events. All these things are happening simultaneously - talk about complexity. Consequently, one would expect some changes in species composition. What's causing those changes? Probably all of them, but which play a dominant role? It's tough to know without experimentation. I think the overriding conclusion for me is resistance of Yellowstone grassland to change in the sense that productivity is more or less the same at sites today as we measured back in the late eighties. Even with all these changes in climate, atmospheric CO2, the threat of invasive species, at least among the grasslands we resampled, the dominant, uncommon, and rare native species occurring at sites several decades ago are still there today in roughly in the same abundances. That is not to say that the grasslands have not changed at all and there are real threats to their integrity. I think there probably have been some shifts in composition and function.

CR: I was talking to another biologist once who was a fan of The Big Lebowski, and he was saying I think the most striking thing for him after all these years of research is that Yellowstone abides. It's funny, but it is what you're saying - even though there's been all this drastic change you're still seeing all the species.

DF: Yes. Yellowstone abides. For sure.

CR: So, in answer to the question, what has been the most significant change in Yellowstone's grassland since you started your studies, your answer might be that it hasn't really changed?

DF: A striking thing for me has not been the change, but the resistance of the system to major change. Species lists for sites seem to be the same between when I started working in Yellowstone and today. Also we have found that grassland production is sustained even under some of the higher grazing pressures that bison are exerting today. So, yes, some important properties of Yellowstone grassland seem to resist change.

CR: What is the most pressing issue or conservation challenge facing grasslands in Yellowstone?

DF: Good question. Because that's the crux. The current controversy that's occurring in Yellowstone and elsewhere around the world's refuges is what are we trying to conserve? You know, back when I started working here it was all about the Leopold Report and we were trying to preserve these vignettes of the past which made a huge amount of sense and it was a target that we could aim for. Even though the how to do it was difficult, we at least had a goal. Today it's more difficult. This is not my original idea, there are a lot of people thinking about this, but we must re-envision what the target is and what we're trying to conserve.

We have all of these factors, a global influence of CO2 enrichment, global warming, invasive species expansion. Not only in national parks, but everywhere around the world. In addition, 40 years ago, the national parks tended to be in the middle of relatively low populated areas. And now for a lot of parks, development is encroaching upon their boundaries. The increasing development outside of Yellowstone's boundaries is causing a rift with the local communities.

Getting back to the question, so what do we do? The pre-European vignettes are out of reach. We cannot stop the tide of global and regional effects on parks. You know, it's like standing with your arms up trying to stop a tsunamis. You just can't do it. So, what we need to do, and this is my opinion, and there are people who will disagree, but we need to try and preserve the dominant, important natural processes; hopefully the major processes for which the park was set aside in the first place.

In Yellowstone, in my opinion, we need to preserve those important grassland - large herbivore interactions, dynamics.

CR: Yellowstone is the only place that I'm aware of where there is a considerable effort trying to understand, to measure grazer effects on these important processes like production, nutrient cycling. There's very extensive program monitoring to make sure that we're not passing the threshold in which these animals are degrading the system. I don't envy park managers trying to come up with policy. It's a difficult [question]; what processes should we be considering?

DF: Where do you draw the line? Where do you decide that we've gone too far this direction or the other direction, we need to step in and do some manipulation of the park? Those are difficult questions. You know, I'm a person who can provide some hopefully useful ecological information about how the system is functioning. I'm not able or really should I make those policy decisions.

CR: When I first started working with the Park Service, we were really trying to communicate with people about prey and predation and the importance of predation - helping them understand that like if they saw a grizzly bear take an elk calf that was an exciting, positive experience. Right? I watched the same thing happen during the fires of 1988 where there was this whole understanding developed with the public about the fact that fire was not necessarily just destructive. It was also a positive for some plant communities.

I've been telling Chris Geremia that you guys need a public relations firm. I don't think people understand the importance of subtle relationships between grazers and plants or even the importance of plants to the system. We've worked so hard in the Park Service to try to help people understand that we're not just here to preserve an individual bison but rather a bison population. Maybe we haven't really done a great job of communicating the value of ecological processes beyond the very specific examples I just gave you.

DF: I agree with you. They're really complicated. They require a certain basic understanding of how grasslands work, what plants need to grow, the cycles of nutrients and how energy is acquired and dispensed.

CR: I like to think people are willing to listen and learn a little bit. Why did you choose to spend a large part of your professional career in Yellowstone?

DF: I have always really enjoyed being in wilderness and so was naturally drawn to places like Yellowstone. I'm inherently interested in complexity, the complexity of terrestrial food webs and the energy and nutrient dynamics that sustain them.

This isn't answering your question. The real reason is, I want to learn in-depth how the Yellowstone ecosystem functions, how ungulates influence productivity and how the system with so much herbivory is sustainable over time. Those are the fundamental questions that have driven my research.

Science operates slowly and addressing and answering these questions takes time. So you write a grant and you get some funding if you're lucky, fortunate enough, and it takes years to, you know, perform that study and write up your findings... then you realize you have another set of questions beyond that.

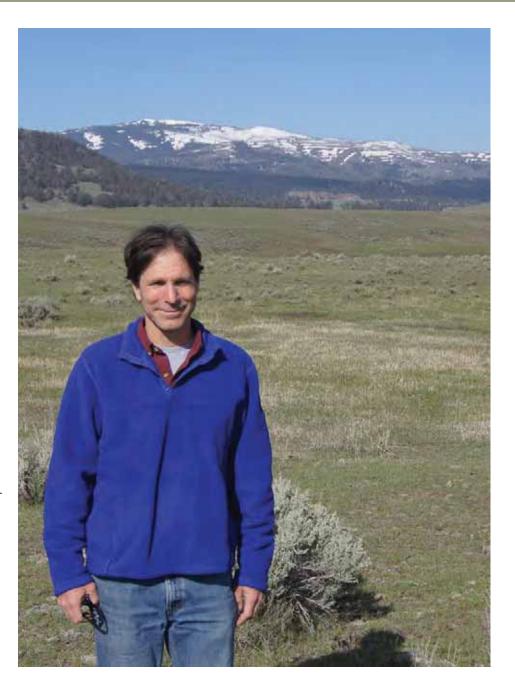
CR: Then you write your paper and then all the young biologists that just started their career say, oh, no, no, no, that's not right. Isn't that how it works?

DF: One should be skeptical when there are new and unusual discoveries, but hopefully your science is solid. So over time other investigators corroborate your findings. And that's, you know, that's what we have found here in Yellowstone. When Sam [McNaughton] and I found that animals were increasing plant production in Yellowstone, like they were in the Serengeti, it was the first temperate system where the phenomenon was reported. And people were skeptical. But we have repeatedly found it to occur in subsequent studies in Yellowstone and [Chris] Geremia is seeing the same thing in his current work. It's been shown in other temperate systems too.

CR: Well, it sounds like Yellowstone's not going to run out of questions for you to ask any time soon.

DF: No!

CR: Well we're lucky to have you in Yellowstone. I feel very fortunate to speak with you. P.J. White is very complimentary of you. He and [Chris] Geremia both said, if we're going to talk about this subject, we have have to talk to Doug. We're happy that you contributed. Thank you.



Wildlife in Yellowstone: What Are We Trying to Preserve?

P.J. White (adapted from White 2016)

Tellowstone National Park was established, in part, to "provide" against the wanton destruction of the fish and game found within" for their "preservation in their natural condition ... for the benefit and enjoyment of people" (Park Protective Act of 1894). The park protects a diversity of aquatic, microbial, and terrestrial life in about 2.2 million acres of one of the largest temperate ecosystems in the world. Superintendents are tasked with conserving "the wild life [sic] therein ... by such means as will leave them unimpaired for the enjoyment of future generations" (Organic Act of 1916). As a result, about 99% of the park is currently managed as wilderness or undeveloped land where human disturbance is minimized compared to outlying areas and animals live in a relatively undisturbed setting. However, preserving natural conditions with minimal human impacts is challenging in modern society where rapid, widespread changes to habitats are occurring due to a warming climate, proliferating invasive species, and extensive development. Likewise, preserving wild animals unaffected by human intrusion becomes more difficult as visitation to the park increases and interactions and conflicts between people and wildlife increase.

Wildlife has been defined as animals living in a natural, undomesticated environment. The current management principles and wilderness ideals of the National Park Service strongly equate minimizing human intrusion with maintaining wildlife and wildness. However, it is well documented that native peoples significantly modified their environment for thousands of years through fires, harvests, and other activities. Also, the implementation of Yellowstone's mandate about preserving wildlife has changed over time based on the prevailing attitudes, desires, and values of society at the time. Early in the park's history, many animals were harvested for food because there were few services for visitors. Hunting was prohibited in 1894, but angling continues to this day—though a

catch-and-release philosophy now prevails. Until the 1960s, nature and wildlife were viewed as needing assistance or improvement from people. As a result, favorable nonnative fishes were introduced, predators and wildfires were suppressed, ungulates were fed during some winters, hatchery-raised fish were stocked in lakes and rivers, and black and grizzly bears could beg along roads and feed at dumps.

This management paradigm was reversed during the 1970s and 1980s to reduce human intervention and allow natural ecological processes to prevail. This approach led to a wilderness ethic where humans were viewed as visitors rather than curators, and attempts were made to "re-wild" grizzly bears and other animals by removing human influences such as feeding. During subsequent decades, efforts were made to restore native species and the ecological processes that sustain them, including the recovery of bald eagles, gray wolves, grizzly bears, and peregrine falcons, the suppression of nonnative fish and the reintroduction of native cutthroat trout and Arctic grayling, and the recovery of a viable population of plains bison.

Today, visitors to Yellowstone have a wide variety of expectations regarding wildlife, with some wanting to see free roaming, but approachable, animals that don't threaten their safety and others wanting unconstrained, uninhibited behavior by animals free of human influences. This contrast is reflected and reinforced by current management and messaging in the park. At entrance stations, visitors are warned wildlife are unpredictable and dangerous. Soon thereafter, however, they encounter large mammals near developed areas and along roadsides that are used to the daily presence of non-threatening people and, as a result, seem tame and safe to approach for viewing and photography. In these areas, rangers initially attempt to manage the behavior of people rather than wildlife to maintain

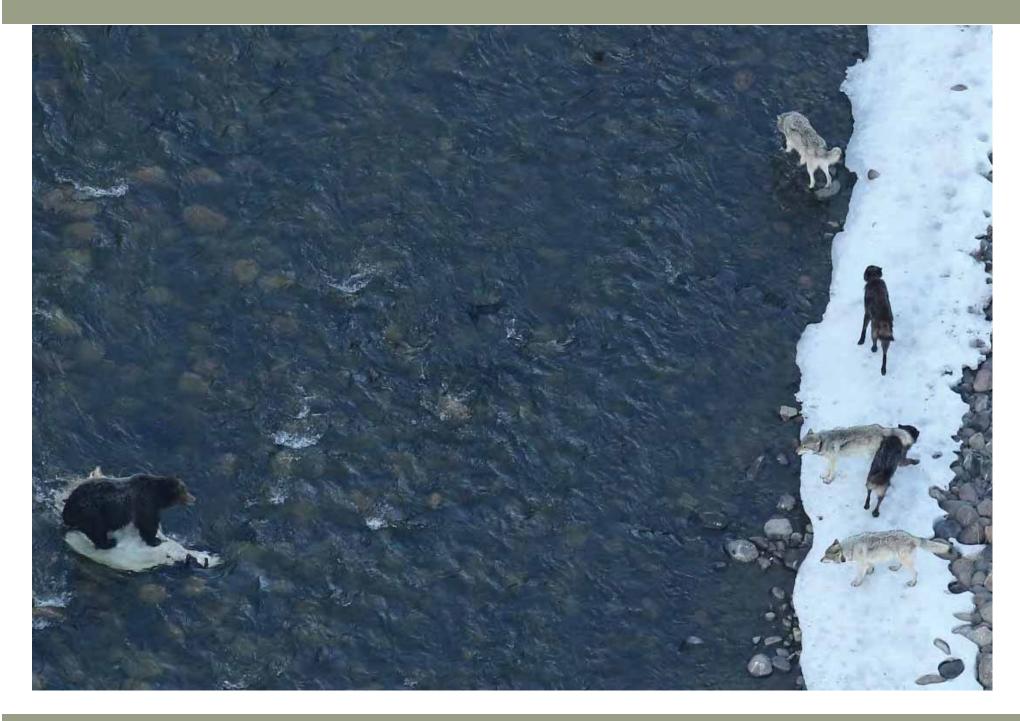
separation and safety. However, animals are at times hazed from areas to alleviate traffic congestion and unsafe congregations of people venturing too close. For the relatively small portion of visitors that hike away from developed areas and roads, there are signs at trail heads to reinforce warnings about the unpredictable nature of wildlife and recommend safety measures. Also, there are required training videos in backcountry permit offices for visitors that venture overnight into wilderness areas. Wildlife are less accustomed to encountering people in these areas and, as a result, are generally less approachable and may react aggressively if surprised during unexpected close encounters.

This wide range of historic and current perceptions and management approaches makes it difficult to discern precisely what managers in Yellowstone are trying to preserve with regards to wildlife. Clarity regarding what constitutes wildlife preserved unharmed in relatively natural conditions is important for evaluating whether the park's preservation mandate is being achieved, and for deciding what intensity and types of management actions are appropriate in the park. Not too long ago, some colleagues and I proposed "a wild bison population can be defined as one that roams freely within a defined conservation area that is large and heterogeneous enough to sustain ecological processes such as migration and dispersal, has sufficient animals to mitigate the loss of existing genetic variation, and is subject to the forces of natural selection" (White et al. 2015). In hindsight, this technical description of an ecologically and genetically viable population did not highlight a key component we are trying to maintain in animals—wildness, or untamed behavior.

While thinking about this oversight, I recalled some of the unrestrained behaviors and unspoiled conditions that evoked awe, fear, and wonder during my journeys in the park. I remember the warning "humph" of a grizzly bear after I had walked unaware to within 25 yards of him lying on a patch of snow in a narrow strip

of trees on a high-elevation ridge—and breathlessly thanking him after he got up and walked away instead of attacking. I remember watching a very pregnant pronghorn doe pursue a fleeing coyote for more than one-half of a mile to protect a fawn or two that had yet to be born. I remember a peregrine falcon hurtling from the sky and chasing an aerobatic teal turn-for-turn until the duck eventually crashed into rocks along the riverbank. I remember a grizzly bear almost effortlessly flipping a massive bison carcass over with one push, and a group of bison inexplicably banding together to defend a wounded elk from a pack of wolves for hours. And I remember finding an old female elk lying at the base of a tree during winter—having died in her sleep after living for about 20 years and likely





producing many calves in an environment filled with predators and other dangers until her worn teeth failed her. These are a few of the memories that, to me, are the real expressions of wildness in Yellowstone.

Attempting to coalesce the essence of these recollections into a definition of "wildlife" is frustrating, however, and led me to recall conversations about Supreme Court Justice Potter Stewart who, in 1964, when asked to define obscenity indicated he couldn't define it, but he knew it when he saw it. So, how do we combine the technical and the intuitive to define a realistic benchmark of what we are trying to preserve in Yellowstone with regards to wildlife? I propose the following: wildlife are untamed, free-roaming animals that live in an environment not dominated by humans and whose behaviors, movements, survival, and reproductive success are predominantly affected by their own daily decisions and natural selection. Mechanisms that contribute to natural selection include how wild animals compete for food, mates, and space; how they protect themselves and respond to encounters with predators; who they choose to associate and mate with; and how they move about the landscape and endure variable environmental conditions. Animals with traits that make them better adapted to the environment will tend to survive, reproduce, and transmit their genetic characteristics to succeeding generations more than other animals. Through this process, natural selection shapes wild behaviors and characteristics.

The word "untamed" in the definition incorporates the concept of wildness and uninhibited behavior but is somewhat problematic because its meaning is subjective based on the perceptions of the observer and, as a result, could be difficult for managers to evaluate. Some people contend untamed animals should be wary of humans and avoid interactions with them, while others perceive untamed animals as free-roaming and unconfined, with their avoidance or indifference towards humans having little bearing on whether they

are wild. I favor the latter classification because I don't equate a fear of humans with being wild. All animals develop their responses to humans based on experience. If these experiences are non-threatening, the animal learns there is no need to respond. If the experiences are threatening or unpleasant in some way, the animals learn to flee and avoid areas frequented by people. As a colleague that conducts research in Antarctica pointed out, penguins on the continent aren't afraid of people and often approach with apparent curiosity, yet they are about as wild an animal as one could find.

Under my proposed definition for wildlife, actions such as feeding or husbandry that shield animals from forces of natural selection or attempt to mimic natural conditions in a zoo-like atmosphere should be avoided. Likewise, sustained or intensive human interventions such as repeated captures, handling, and culling should be avoided, if possible, because they could alter natural selection in unforeseen and unintended ways. While perhaps not optimal, animals habituated to human presence would still be considered wild if they maintained their independence from supplemental food and security provided by humans—despite close and frequent interactions.

At a time when wilderness appears to be less accessible to our increasingly urban society, we should not underestimate the value of Yellowstone and the ease of access to its viewable geysers, scenery, and iconic wildlife for even the most urbanized citizens of the world. Many visitors fondly remember their experiences at the park for the rest of their lives; even if some of the animals they observed were habituated to humans and the conditions that contributed to their inspiration may not have been pristine. Park managers should continue to promote an environment where wildlife remain uncontrolled, and visitors can be impressed and inspired by their uninhibited behaviors. As park historian Paul Schullery emphasized, the greatest value of Yellowstone may be the "authenticity of its wildness—the opportunity for us to be awed and learn from nature making its own decisions."

In Memoriam: John Maxwell Good

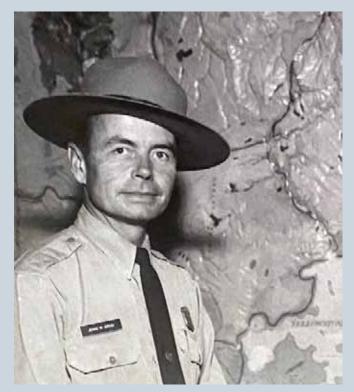
ormer National Park Service superintendent and longtime
Jackson resident John M. Good died Dec. 5, 2019 at home in
Meridian, Idaho. He was 95.

Born March 15, 1924, in St. Louis, Good began his National Park Service career in 1951 as a cave guide at Carlsbad Caverns National Park in New Mexico and retired as superintendent of Everglades National Park in Florida in 1981.

Born and raised in St. Louis, Good learned his lifelong love of the outdoors spending summers at his aunt and uncle's farm in the Ozark Mountains of southern Missouri. After serving in the Navy during World War II he attended Washington University in St. Louis for both his bachelor's and master's degrees in geology. While on vacation he visited several parks and became interested in working for the National Park Service. He joined the agency in 1951, dedicating his working life to national parks and their mission of preserving natural and cultural resources for public use and enjoyment.

He worked at seven parks during his career, including serving as chief naturalist of Yellowstone National Park (1960-68), superintendent of Acadia National Park in Maine (1968-71), deputy superintendent of Yosemite National Park in California (1971-76) and superintendent of Everglades National Park, Florida (1976-81).

Highlights of his NPS career include a series of land exchanges in Acadia that solidified park boundaries and serving on the initial board of trustees during the establishment of the College of the Atlantic in Bar Harbor, Maine; working with Yosemite Superintendent Lynn Thompson and Chief Ranger Jack Morehead as the National Park Service faced challenges of a rapidly changing society and visitor demographics in the wake of the Yosemite riot; and protecting Florida Bay by eliminating commercial fishing and initiating the legal efforts that required the state of Florida to acknowledge perpetual water rights for Everglades National Park.





The Florida Bay work earned him an "attaboy" from Boston Red Sox slugger and avid Florida fly fisherman Ted Williams, who had told him he didn't think ending commercial fishing could be done.

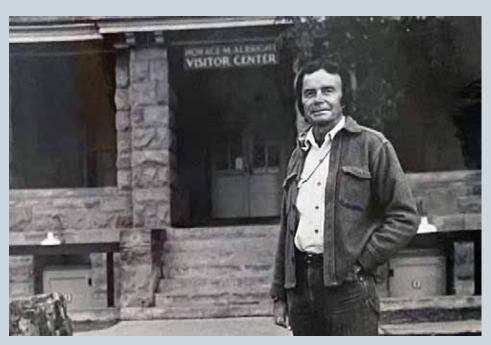
When asked what perspective he could offer wildlife managers of today, John Good, offered these words of advice: "We were so sure. Remember that wonderful line of Charlie Brown's. 'Now how can we lose this ball game when we're so darned sincere?'... If you could have gone back and sat in on a ranger conference in 1961, you would have found the same attitude that remains today. That we know what we're doing. Most people—most reasonable people will accept that we do. We said that in 1961, we're saying it now in 1999. I don't know whether what we're doing is exactly right. All I remember is that to the Greeks, the ancient Greeks, a cardinal sin was hubris. And hubris was pride. And certainty. And so, I wave my finger from the ancient past and say, beware hubris, beware certainty."

After retirement Good finished his field work and wrote "Interpreting the Landscape: Recent and Ongoing Geology of Grand Teton and Yellowstone National Parks" with his good friend, U.S. Geological Survey geologist Dr. Ken Pierce. He worked as a volunteer for years for the Yellowstone wolf reintroduction project with Rick McIntyre. The success of the reintroduction made him quite happy because he knew the key role they play in restoring the Yellowstone country.

John continued to spend as much time as possible outdoors fly fishing, cross-country skiing, hiking, camping, paddling and bird watching for as long as he could in many areas of the country and around the world.

Good is survived by his wife of 45 years, Edna; her son, Randy Carroll; daughter Katherine Good-Smith; son Lou Good; and grandson John Beck.

The family asks that, in his memory, everyone fights hard to preserve our public lands and public access to them as John.





Species in this Issue

Compiled by Karin Bergum

Animals

Allillia				
	Common Name	Scientific Name	Family	
Bacteria	Brucellosis	Brucella abortus	Brucellaceae	
Birds	Bald eagle	Haliaeetus leucocephalus	Accipitridae	
	Golden eagle	Aquila chrysaetos	Accipitridae	
	Peregrine falcon	Falco peregrinus	Falconidae	
Fish	Cutthroat trout	Oncorhynchus clarkii	Salmonidae	
-	Lake trout	Salvelinus namaycush	Salmonidae	
Insects	Toadflax brocade moth	Calophasia lunula	Noctuidae	
Mammals	Bison (buffalo)	Bison bison	Bovidae	
	Black bear	Ursus americanus	Ursidae	
	Cattle (domestic)	Bos taurus	Bovidae	
	Cougar (mountain lion)	Puma concolor	Felidae	
	Coyote	Canis latrans	Canidae	
	Deer	" Odocoileus hemionus (mule deer) and O. virginianus (white- tailed deer)"	Cervidae	
	Elk	Cervus canadensis	Cervidae	
	Grizzly bear	Ursus arctos	Carnivora	
	Horse (domestic)	Equus caballus	Equidae	
	Moose	Alces alces	Cervidae	

(中央工業の数人性の人)	3			
	Common Name	Scientific Name	Family	
- 40	Mountain lion (cougar)	Puma concolor	Felidae	
	Mule deer	Odocoileus hemionus	Cervidae	
	Pronghorn	Antilocapra americana	Antilocapridae	
	Sheep (domestic)	Ovis aries	Bovidae	
	Thomson's gazelle	Eudorcas thomsonii	Bovidae	
	White-tailed deer	Odocoileus virginianus	Cervidae	
	Wildebeest	Connochaetes spp.	Bovidae	
	Wolf (gray)	Canis lupus	Canidae	



Plants

Common Name	Scientific Name	Family	Growth Habit	Life Cycle	Status	Growth Form
Alfalfa	Medicago sativa	Fabaceae	Forb	Perennial	Introduced	
Annual wheatgrass	Eremopyrum triticeum	Poaceae	Graminoid	Annual	Introduced	tufted
Aspen	Populus tremuloides	Salicaceae	Tree	Perennial	Native	
Basin big sage	Artemisia tridentata ssp. tridentata	Asteraceae	Shrub	Perennial	Native	
Big sagebrush	Artemisia tridentata	Asteraceae	Shrub	Perennial	Native	
Bluebunch wheatgrass	Pseudoroegneria spicata	Poaceae	Graminoid	Perennial	Native	tufted
Bluegrass	Poa spp.	Poaceae	Graminoid	Perennial	-	
Bluejoint reedgrass	Calamagrostis canadensis	Poaceae	Graminoid	Perennial	Native	rhizomatous
Bulbous bluegrass	Poa bulbosa	Poaceae	Graminoid	Perennial	Introduced	tufted
Canada thistle	Cirsium arvense	Asteraceae	Forb	Perennial	Introduced - Noxious Weed	
Cheatgrass	Bromus tectorum	Poaceae	Graminoid	Winter Annual	Introduced- Invasive	single culmed
Clover	Trifolium spp.	Fabaceae	Forb	Perennial	Introduced	
Columbia needle grass	Achnatherum nelsonii	Poaceae	Graminoid	Perennial	Native	tufted
Crested wheatgrass	Agropyron cristatum	Poaceae	Graminoid	Perennial	Introduced	tufted
Dalmation toadflax	Linaria dalmatica	Plantaginaceae	Forb	Perennial	Introduced - Noxious Weed	MAN IS
Dandelion	Taraxacum spp.	Asteraceae	Forb	Perennial	Introduced	200
Desert alyssum	Alyssum desertorum	Brassicaceae	Forb	Annual	Introduced	\$10 M
Douglas-fir	Pseudotsuga menziesii	Pinaceae	Tree	Perennial	Native	200
Draba	Draba spp.	Brassicaceae	Forb	Annual	Native	TO SECOND
Field chickweed	Cerastium arvense	Caryophyllaceae	Forb	Perennial	Native	20
Fringed sage	Artemisia frigida	Asteraceae	Shrub	Perennial	Native	
Geranium	Geranium spp.	Geraniaceae	Forb	Perennial	Native	
Greasewood	Sarcobatus vermiculatus	Sarcobataceae	Shrub	Perennial	Native	

Common Name	Scientific Name	Family	Growth Habit	Life Cycle	Status	Growth Form
Green rabbitbrush	Chrysothamnus viscidiflorus	Asteraceae	Shrub	Perennial	Native	
Houndstongue	Cynoglossum officinale	Boraginaceae	Forb	Biennial	Introduced - Noxious Weed	
Idaho fescue	Festuca idahoensis	Poaceae	Graminoid	Perennial	Native	tufted
Juneberry (Serviceberry)	Amelanchier ainifolia	Rosaceae	Shrub	Perennial	Native	
Junegrass	Koeleria macrantha	Poaceae	Graminoid	Perennial	Native	tufted
Juniper	Juniperus spp.	Cupressaceae	Conifer	Perennial	Native	
Kentucky bluegrass	Poa pratensis	Poaceae	Graminoid	Perennial	Introduced	rhizomatous
Kochia	Bassia scoparia	Amaranthaceae	Forb	Annual	Introduced- Invasive	
Lava aster	Ionactis alpina	Asteraceae	Forb	Perennial	Native	Kar 188
Lodgepole pine	Pinus contorta	Pinaceae	Conifer	Perennial	Native	
Lupine	Lupinus spp.	Fabaceae	Forb	Perennial	Native	PA DATES
Milkvetch	Astragalus spp.	Fabaceae	Forb	Perennial	Native	
Mountain big sage	Artemisia tridentata ssp. vaseyana	Asteraceae	Shrub	Perennial	Native	
Mountain mahogany	Cercocarpus Kunth	Rosaceae	Tree	Perennial	Native	4
Needle-and-thread	Hesperostipa comata	Poaceae	Graminoid	Perennial	Native	tufted
Oatgrass	Danthonia spp.	Poaceae	Graminoid	Perennial	Native	tufted
Oats	Avena sativa	Poaceae	Graminoid	Annual	Introduced	
Oregon grape	Mahonia repens	Berberidaceae	Shrub	Perennial	Native	
Oval-leaf buckwheat (Cushion buckwheat)	Eriogonum ovalifolium	Polygonaceae	Forb	Perennial	Native	
Oxeye daisy	Leucanthemum vulgare	Asteraceae	Forb	Perennial	Introduced - Noxious Weed	
Phlox	Phlox spp.	Polemoniaceae	Forb	Perennial	Native	
Pussytoes	Antennaria spp.	Asteraceae	Forb	Perennial	Native	
Reed grass	Calamagrostis spp.	Poaceae	Graminoid	Perennial	Native	rhizomatous
Rice grass	Achnatherum spp.	Poaceae	Graminoid	Perennial	Native	tufted
Rockcress	Arabis spp.	Brassicaceae	Forb	Perennial	Native	
Wild rose (Woods' rose)	Rosa woodsii	Rosaceae	Shrub	Perennial	Native	
Rubber rabbitbrush	Ericameria nauseosa	Asteraceae	Shrub	Perennial	Native	
Russian thistle	Salsola spp.	Chenopodiaceae	Forb	Annual	Introduced	

Common Name	Scientific Name	Family	Growth Habit	Life Cycle	Status	Growth Form
Sagebrush	Artemisia spp.	Asteraceae	Shrub	Perennial	Native	
Salsify	Tragopogon dubius	Asteraceae	Forb	Biennial	Introduced	
Sandberg's bluegrass	Poa secunda	Poaceae	Graminoid	Perennial	Native	tufted
Scarlet globemallow	Sphaeralcea coccinea	Malvaceae	Forb	Perennial	Native	
Sedge	Carex spp.	Cyperaceae	Graminoid	Perennial	Native	
Shrubby cinquefoil	Dasiphora fruiticosa	Rosaceae	Shrub	Perennial	Native	
Silver sage	Artemisia cana	Asteraceae	Shrub	Perennial	Native	
Slender-leaf collomia	Collomia linearis	Polemoniaceae	Forb	Annual	Native	
Slender wheatgrass	Elymus trachycaulus	Poaceae	Graminoid	Perennial	Native	tufted
Smooth brome	Bromus inermis	Poaceae	Graminoid	Perennial	Introduced	rhizomatous
Spotted knapweed	Centaurea stoebe	Asteraceae	Forb	Biennial	Introduced - Noxious Weed	
Sticky geranium	Geranium viscosissimum	Geraniaceae	Forb	Perennial	Native	
Timothy	Phleum pratense	Poaceae	Graminoid	Perennial	Introduced	tufted
Tufted hairgrass	Deschampsia cespitosa	Poaceae	Graminoid	Perennial	Native	tufted
Ventenata grass	Ventenata dubia	Poaceae	Graminoid	Winter Annual	Introduced - Noxious Weed	tufted
Western yarrow	Achillea millefolium	Asteraceae	Forb	Perennial	Native	
Whitebark pine	Pinus albicaulis	Pinaceae	Conifer	Perennial	Native	
White coralberry (Snowberry)	Symphoricarpos spp.	Caprifoliaceae	Shrub	Perennial	Native	
Willow	Salix spp.	Salicaceae	Shrub	Perennial	Native	
Winterfat	Krascheninnikovia lanata	Amaranthaceae	Forb	Perennial	Native	
Wyoming big sage	Artemisia tridentata ssp. wyomingensis	Asteraceae	Shrub	Perennial	Native	
Yellow toadflax	Linaria vulgaris	Plantaginaceae	Forb	Perennial	Introduced - Noxious Weed	

Karin Bergum is a contract technical editor for Yellowstone Science. Her interest in genetics and plants led her to pursue an undergraduate degree in Agronomy and Seed Science from Iowa State University, and later a Master of Science in Rangeland Ecology from the University of Wyoming. She and her husband Dan spend any free moment outdoors on adventures with their sons Colter and Teddy.



Being an Effective Leader

P.J. White (adapted from White, 2016)

I was probably one of the worst second lieutenants in the history of the United States Marine Corps. Though painful to admit, it was sadly true; as many senior officers pointed out at the time. To this day, I marvel at some of the stupid decisions I made. Fortunately, I was a quick study and improved substantially, eventually grasping the lesson that successful leadership is essentially about two things which are equally important: accomplishing the mission and taking care of your people. I have maintained this philosophy through many years in wildlife biology and it has served me well. If you work hard to consistently fulfill these two tenets, you will eventually earn the respect and trust of your co-workers; regardless of what position you occupy in the chain-of-command.

To accomplish the mission, the leader of a particular group or project needs to define the problem or task for their coworkers, answer questions and consider ideas, refine a plan based on this input, and then supervise the successful completion of the project. Everyone at every level should work at becoming a better leader by participating in the planning of their daily activities, being prepared to accomplish their assigned tasks, focusing and paying attention to detail during these activities and, as necessary, being creative to solve problems. In addition, everyone needs to take responsibility for their actions. We all make mistakes—acknowledge them and learn from them. Furthermore, try to live your life with honor (do what's right), courage (do what's right even when it's hard), and integrity (be true to yourself and others). It's not easy and I've failed to live up to these ideals many a time, but it's important to strive to attain them.

Successful leadership comes through ideas, planning, supervision, and hard work. The rarest commodity in wildlife biology is an original idea. Wildlife management is often about solving problems and ideas to reach solutions come from being curious and thoughtful about the world around you. Planning involves setting realistic objectives and timeframes and preparing for the inevitable contingencies.

Detailed planning is essential because, as the Cheshire Cat explained to Alice in Wonderland, any road will get you there if you don't know where you're going. In other words, if you don't define clear objectives and a precise process to attain them, you'll fail to advance toward the desired outcome. Supervision involves choosing good people, training them, providing guidance on what you expect, and letting them use their abilities and ingenuity to get the job done; all the while monitoring their progress to ensure successful completion.

To take care of their people, leaders need to make sure their coworkers have the proper training and equipment for the task, as well as a strong commitment to safety. When conducting the daily activities, everyone needs to focus on their tasks, be alert to their surroundings and changing conditions, and pay attention to detail. Everyone needs to be prepared to implement contingency actions if things do not go as planned. If anyone observes an unsafe situation, either rectify it or distance yourself and your coworkers from it and then bring it to the attention of your supervisor. If a situation doesn't feel right, back away and assess why. Trust your instincts. If others are exhibiting unsafe behavior, let them know about it and correct it. Don't remain quiet and watch someone get hurt.

Some accidents will happen despite every precaution. The goal is to keep them minor and rare. If someone is injured, make sure they receive treatment and are taken care of. If you are injured, let people know as soon as possible. No one should be punished or ridiculed for reporting an injury, no matter how minor it may appear initially. You should encourage the reporting of close calls or near-misses that highlight a safety concern that needs to be corrected and shared with others to prevent future injuries. Safety needs to be a creed and a culture in your group; people must believe in it and live it to be successful. For example, the United States military has a creed, never leave anyone behind, that is not always possible or attainable, but essential nevertheless because everyone believes their buddies will do everything in their power to live up to it. There is no doubt about this

commitment; it is absolute and, therefore, reassuring. Obviously, the day-to-day risks taken by wildlife biologists should be far less than our brothers and sisters facing combat in defense of our country and ideals. However, a similar creed is still applicable—everyone should come home safe to their families and friends each day.

Last but not least, I appropriated the following bits of advice and ideas regarding leadership from a wide variety of wise people, ranging from my father, Bert White, to the author of the book Don Quixote, Miguel de Cervantes, to the former Chief of the Yellowstone Center for Resources, John Varley, to famous football coach, Vince Lombardi, to the extremely successful businessman, Bill Gates, to the legendary Marine, Chesty Puller.

These teachings have been very helpful to me throughout my career, and I hope they will be helpful to you during your journey. Remember, no one will help you if you don't first help yourself by putting forth maximum effort.

Know and Be Yourself (strengths, weaknesses, and tendencies)

Establish Your Team's Identity (mission, objectives, and values)

Establish a Chain of Command (effective flow of information)

Set High Standards with Clear Expectations (motivate and excel)

Be Bold and Decisive (be confident and take calculated risks)

Be Prepared (acquire and use the best available information)

Plan Ahead and Get Feedback (encourage candor/different viewpoints)

Strive for Success, Not Perfection (develop simple, flexible plans; adapt)

Communicate and Delegate (empower ingenuity and decision making)

Supervise (instruct, provide guidance, monitor progress, and debrief)

Accept Responsibility (don't make excuses, make corrections)

Educate and Train (focus on inexperienced leaders; cross train)

Praise in Public, Punish in Private (reward excellence and initiative)

Develop a Culture of Safety (believe in it and live it)

Don't Waste Time (focus on the things you can change)

Be Respectful and Listen (consider alternatives before deciding)

Be Careful with Fraternization (treat everyone fairly; don't discriminate)

Become Adept at Negotiation (change behaviors to attain results)

Just Do It (debate ends when the boss makes a final decision)

Take Things in Stride (life's not fair; deal with unexpected problems)

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Sneak Peek

Douglas W. Smith

Pellowstone is a land of large mammals and geology. Geology was first - geysers – and this is why Yellowstone was made into a national park. The animals came later, and they came with a flourish: bears, bison, elk, and later wolves to name the most famous ones. Of course, sweeping mountain vistas and world class scenery wasn't bad either. Fish got their share of attention, especially after lake trout infested Yellowstone Lake and precious cutthroat were threatened. Other fish stocks were cherished and nurtured. But what about the birds? They've been around too.

This is what the next issue of Yellowstone Science is all about - this late discovery of bird riches. Although riches may overstate the situation a little, there is a vast array of birds in the world's first national park. Songbirds thrive in the grasslands and streamside vegetation, but do struggle in the vast lodgepole forests stretching across the park's interior. Raptors are another story – 19 species of hawks, falcons, owls, and eagles nest in Yellowstone. More pass through on annual migrations. Water birds are resplendent: common loons, trumpeter swans, American white pelicans, and double-crested cormorants are somewhat unique and all occupy the park. The anchor for loons and swans in the entire region is the park.

All discovered late and competing for attention with the bubbling springs and megafauna in the world's most famous park. Read what we have learned. An entire issue!





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