YELLOWSTONE BISON

conserving an AMERICAN ICON in modern society

EXECUTIVE SUMMARY

EDITED BY

P.J. White, Rick L. Wallen, and David E. Hallac

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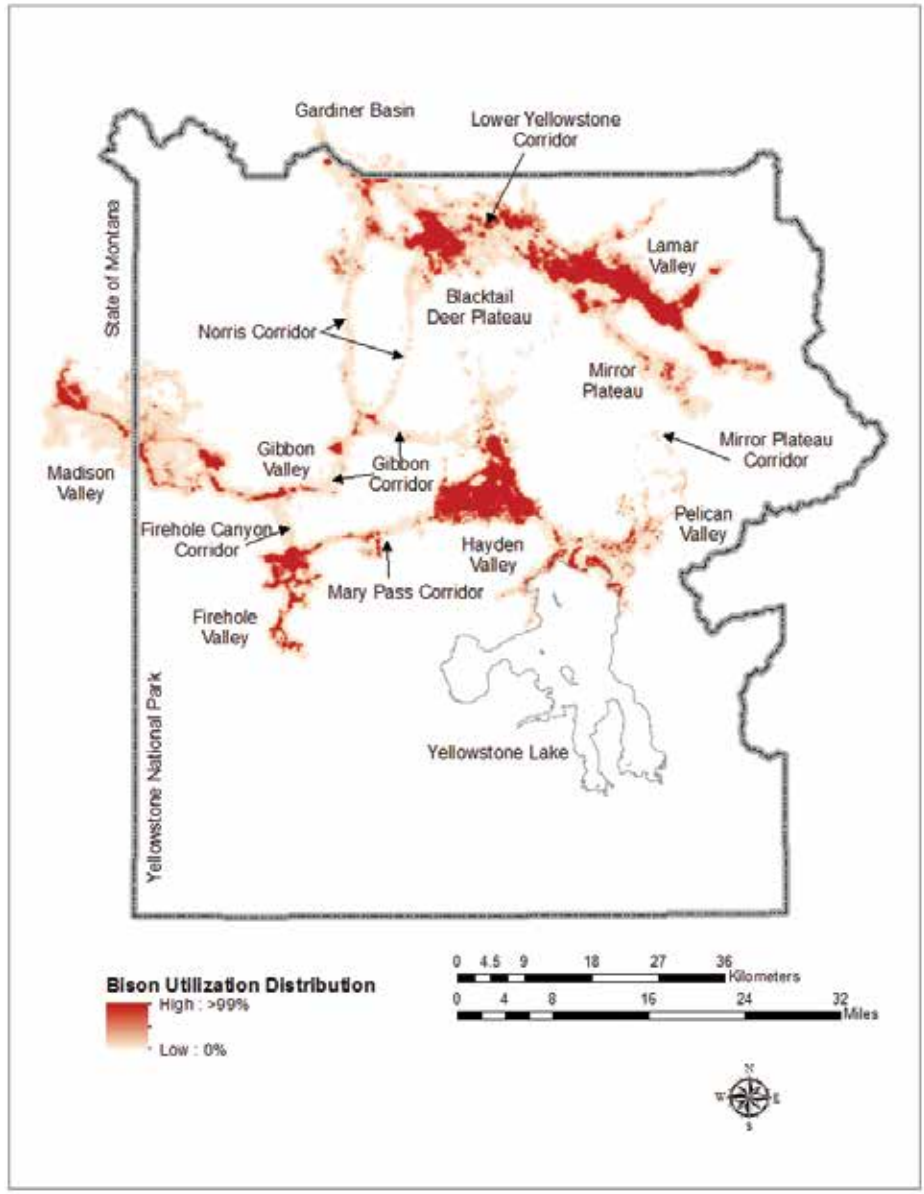

Names of various places and areas used by bison in and near Yellowstone National Park. Darker shading indicates areas used more frequently by 66 adult female bison fit with radio collars during 2004 through 2012.

Bull bison in the Pelican Valley of Yellowstone National Park.

Introduction

P.J. White, Rick L. Wallen, and David E. Hallac

The plains bison (*Bison bison* or *Bos bison*), also commonly known as buffalo, once numbered in the tens of millions and ranged across much of North America, from arid grasslands in northern Mexico, through the Great Plains and Rocky Mountains into southern Canada, and eastward to the western Appalachian Mountains. Plains bison are symbolic of the American experience because they are an inherent part of the cultural heritage of many American Indian tribes and were central to national expansion and development. Only a few hundred plains bison survived commercial hunting and slaughter during the middle to late 1800s, with the newly established (1872) Yellowstone National Park providing refuge to the only relict, wild, and free-ranging herd of less than 25 animals. This predicament led to one of the first movements to save a species in peril and develop a national conservation ethic by a few visionary individuals, American Indian tribes, the American Bison Society, the Bronx Zoo, and federal and state governments. Bison numbers increased rapidly after protection from poaching, reintroduction of bison to various locations, and husbandry.

Today, more than 400,000 plains bison live in conservation and commercial herds across North America. Despite this success, several scientists recently concluded that plains bison are ecologically extinct because less than 4 percent (20,000) are in herds managed for conservation and less than 2 percent (7,500) have no evidence of genes from inter-breeding with cattle. Most bison are raised for meat production, mixed with cattle genes, protected from predators, and fenced in pastures. As a result, wild bison no longer influence the landscape on the vast scale of historical times by enhancing nutrient cycling, competing with other ungulates, creating wallows and small wetlands, converting grass to animal matter, and providing sustenance for predators, scavengers, and decomposers.

Yellowstone bison comprise the largest conservation population of plains bison and are one of only a few populations to have continuously occupied portions of their current distribution. Perhaps more importantly, Yellowstone bison are managed as wildlife in multiple large herds that currently move across extensive portions of the landscape within and near Yellowstone National Park. Bison exist on this landscape with a full suite of native ungulates and predators, while being exposed to natural selection factors such as competition for food and mates, predation, and survival in challenging environmental conditions. As a result, Yellowstone bison have likely retained adaptive capabilities that may be diminished in other bison herds across North America that are managed like domesticated livestock in fenced pastures with human-induced seasonal movements among pastures, no predators, selective culling of older bulls to facilitate easier management, and selection for the retention of rare alleles—the function and importance of which have not been identified. Yellowstone bison also provide meat for predators, scavengers, and decomposers, and allow visitors to observe this symbol of the American frontier in a wild, unfenced setting.

A lone bison roams the wide-open spaces of Yellowstone National Park.

Clouds and bison across Hayden Valley, Yellowstone National Park.

The Population

Douglas W. Blanton, P.J. White, Rick L. Wallen,
Katrina L. Auttelet, Angela J. Stewart, and Amanda M. Bramblett

Attributes

Plains bison are massive animals, with males having larger maximum weights (900 kilograms or 1,985 pounds) than females (500 kilograms or 1,100 pounds). Males are full-grown by 5 to 6 years of age, while females mature near 3 years of age. Adult bison are generally dark chocolate-brown in color, while calves of the year are born reddish tan and begin turning brown at about 2.5 months. Both sexes have relatively short horns that curve upward and are retained for their lifespan, as well as protruding shoulder humps of large muscles that allow them to swing their heads from side-to-side to clear snow from feeding patches. Bison are strong swimmers, can run 55 kilometers (35 miles) per hour, can jump over objects about 1.8 meters (6 feet) high, and have excellent hearing, vision, and sense of smell. Bison are social animals that often form herds. Mature males fight to determine individual dominance, with the winners proceeding to copulate with receptive females. Following courtship, mature males separate and spend the rest of the year alone or in small groups. The rest of the bison disperse into groups dominated by adult females.

Distribution and Habitat

Historically, bison occupied about 20,000 square kilometers (7,720 square miles) near the sources of the Yellowstone and Madison rivers. Today, this range is restricted to Yellowstone National Park and some adjacent areas of Montana characterized by high-elevation shrub steppe, with meadows, grasslands, and well-defined riparian corridors surrounded by moderately steep slopes of mountain ranges and plateaus. Bison in northern Yellowstone congregate in the Lamar Valley and on adjacent plateaus for the breeding season (rut) from mid-July through

mid-August. During the remainder of the year, these bison mostly use habitats along the Yellowstone River drainage. Bison in central Yellowstone occupy the central plateau of the park, extending from the Pelican and Hayden valleys in the east to the lower elevation and geothermally influenced Madison headwaters area in the west. Bison in central Yellowstone congregate in the Hayden Valley for breeding. Most of these bison move between the Madison, Firehole, Hayden, and Pelican valleys during the rest of the year. However, some bison travel to northern Yellowstone before returning to the Hayden Valley for the subsequent breeding season.

Feeding

Yellowstone bison feed primarily on grasses, sedges, and other grass-like plants. Bison are ruminants with a multiple-chambered stomach containing microorganisms, such as bacteria and protozoa, that facilitate the break-down of plant material. They alternate between consuming plants and ruminating, which is regurgitating partially digested food and chewing it again to further break down plant material. Bison gain and lose weight seasonally, with gains during the spring and summer and losses during autumn and winter. They move from higher-elevation summer ranges to lower elevations during autumn through winter. As snow depths increase, the available foraging areas for bison are reduced to increasingly limited areas at lower elevations and on geothermally warmed ground. Also, snow melts earlier at lower elevations so there are earlier vegetation green-up and energy-efficient foraging opportunities while summer ranges at higher elevations are still covered with snow. Their return migration to higher elevations corresponds with new vegetation growth.

Population Dynamics

Summer counts of bison in central and northern Yellowstone have varied widely since 2000, from about 2,400 to 5,000. Further expansion of the population is currently constrained by the availability of low-elevation winter habitat where forage is relatively accessible. Much of Yellowstone

National Park is mountainous, with deep snow pack that limits access to forage and increases energy expenditures during winter. Also, large portions of the original range for bison are no longer available outside the park due to agricultural and residential development. Furthermore, there are political and social concerns about allowing bison outside the park, including human safety and property damage, competition with livestock for grass, diseases such as brucellosis that can be transmitted between bison and cattle, depredation of agricultural crops, and a shortage of funds for state management. The lack of tolerance for bison in most areas outside Yellowstone National Park is the primary factor limiting restoration across their historic range in the Greater Yellowstone Area.

NPS Photo

Preparing blood samples for brucellosis testing procedures.

Brucellosis

P.J. White, David E. Hallac, Rick L. Wallen, and Jesse R. White

WILD BISON AND elk in the Greater Yellowstone Area were infected with *Brucella abortus* bacteria by domestic European cattle before the 1930s. This disease decreases the birthing rates of Yellowstone bison and has indirectly influenced survival rates due to the culling of exposed animals by humans. Moreover, this disease has been an overriding factor influencing the distribution and management of Yellowstone bison due to concerns about transmission of the bacteria back to cattle and economic losses to producers. Thus, brucellosis directly limits the potential for further recovery of bison in the Greater Yellowstone Area. In contrast, elk in the Greater Yellowstone Area are managed and treated much differently, even though brucellosis is also endemic in their populations and has been repeatedly transmitted from them to cattle over the last decade.

Many disease regulators believed brucellosis would not persist in elk in the Greater Yellowstone Area without frequent transmission from Yellowstone bison or elk dispersing from places in Wyoming where aggregations of elk are fed by humans during winter. However, surveillance during the past decade indicates brucellosis prevalence has increased substantially in several elk populations in the other portions of the Greater Yellowstone Area. These increases are coincident with increasing elk numbers and/or aggregations of elk on lower-elevation winter ranges, including a greater proportion of private land than 20 years ago. These elk populations appear to support the disease independently of Yellowstone bison or feed-ground elk. Also, in recent years the distribution of elk testing positive for brucellosis exposure has expanded beyond the periphery of the Greater Yellowstone Area and now encompasses more than 20 million acres (8 million hectares).

The estimated risk of brucellosis exposure to cattle from Yellowstone bison is insignificant (less than 1 percent) compared to elk (more than 99 percent of total risk) because elk have a larger overlap with cattle and

are more tolerated by state managers and livestock producers. Many of the approximately 450,000 cattle in the Greater Yellowstone Area are fed on private land holdings during winter and released on public grazing allotments during summer—but throughout the year they are allowed to mingle with wild elk. Management to suppress brucellosis in bison will not substantially reduce the far greater transmission risk from elk. Therefore, numerous independent evaluations have recommended management actions for brucellosis focus on maintaining separation between bison and cattle, while attempting to decrease elk density and group sizes in areas where mingling with cattle occurs.

The eradication or even a substantial reduction of brucellosis in wild bison and elk is not attainable at this time given available technologies. An effective brucellosis control program for wildlife in the Greater Yellowstone Area would require the development of highly effective vaccines for both elk and bison, a delivery system that can cost-effectively provide the vaccine to thousands of female bison and tens of thousands of female elk, and diagnostics that would allow biologists to discriminate between previously infected and infectious animals to gauge vaccination efficacy. The development of separate vaccines for bison and elk would likely be necessary due to their different physiologies and protective immune responses. However, there has been little progress in vaccine development, delivery systems, and diagnostics due to a lack of market incentives and restrictions on research due to the classification of *Brucella abortus* as a select agent that could be packaged as a biological weapon by terrorists and used to threaten public health or national security.

Given the myriad of problems to overcome to substantially reduce brucellosis infection in wild bison and elk distributed across a vast region, we suggest an alternate approach to protect domestic livestock: developing an infection-blocking vaccine for cattle. This alternative would have a much higher likelihood of effectively reducing brucellosis transmission risk in a shorter period of time because of a better understanding of cattle as a model in the veterinary sciences, the substantially larger number of facilities available for research on cattle, the better

nutritional condition of cattle that may increase vaccination success, and the ability to efficiently capture and vaccinate all cattle. Current cattle vaccines are only 65 to 70 percent effective against abortion and 10 to 15 percent effective against infection. Thus, there is substantial room for improvement. Although significant resources have been expended to develop and test vaccines in the past, there have been several advances in recent years (e.g., DNA vaccines, nanoparticles) that suggest breakthroughs may still be possible. We realize the development of a perfect vaccine that prevents brucellosis infection in cattle will be challenging, but it seems logical to fully explore this prospect before embarking on the much more complex and difficult task of developing and delivering multiple vaccines for wildlife across a vast geographic scale.

NPS Photo

Bison at the Buffalo Ranch in the Lamar Valley of Yellowstone National Park, circa 1930.

Historical Perspective

Rick L. Wallen, P.J. White, and Chris Geremia

A RESTORATION PROGRAM for Yellowstone bison was initiated in 1902 when park managers began to increase bison numbers and perpetuate the species. Husbandry (e.g., reintroduction, fencing, herding, feeding) was used to restore and propagate a new herd in northern Yellowstone, and some of these bison were then relocated to central Yellowstone to augment the remaining bison from the indigenous herd. After bison numbers increased to 500 to 1,000 animals in each region of the park, they were culled to limit numbers below the perceived capacity of the habitat to support them and to try and eliminate the disease brucellosis. After several decades, traditional livestock management practices such as husbandry and selective culling were discontinued, and bison were allowed to re-establish their ecological role in ecosystem processes. Bison numbers increased under this new management paradigm, and during winters in the 1970s and 1980s, hundreds of animals from the central and northern regions began to migrate and expand their ranges towards the park boundary and into Montana. The State and the National Park Service agreed to control bison near the park boundary and about 3,100 bison were culled during 1985 through 2000. These migrations and culls generated intense controversy among environmentalists, stock growers, and management agencies regarding issues of bison conservation and disease containment. As a result, the federal government and the State of Montana negotiated a court-mediated settlement in 2000 that established guidelines for cooperatively managing the risk of brucellosis transmission from bison to cattle, while maintaining about 3,000 bison and allowing some to occupy winter ranges on public lands in Montana.

The Interagency Bison Management Plan uses risk management procedures to maintain spatial and temporal separation between bison and cattle in Montana. For bison to transmit brucellosis directly to cattle, infected bison must leave the park, enter areas where cattle graze, shed infectious

tissues via abortions or live births, and have cattle contact these tissues before they are removed from the environment or the *Brucella* bacteria die. The plan was designed to progress through a series of management steps that initially tolerated only bison testing negative for exposure to *Brucella* bacteria on winter ranges outside Yellowstone National Park. Over time, the plan would allow limited numbers of untested bison on key winter ranges adjacent to the park when cattle were not present. Management tools include hazing by humans to prevent bison movements into non-tolerance areas, capturing bison near the park boundary and testing them for brucellosis exposure, sending some bison to research or meat processing facilities, vaccinating bison and cattle, allowing some bison to use habitat adjacent to the park during winter, and conducting research on bison, brucellosis suppression, and quarantine. The plan was adjusted in 2005 and 2006 to include bison hunting as a management action outside Yellowstone National Park and increase tolerance for bull bison in Montana because there is virtually no risk of them transmitting brucellosis to cattle. These adjustments allowed bison not tested for brucellosis exposure to migrate to winter ranges outside the park and provide hunting opportunities for state-licensed hunters and American Indians with rights, reserved through treaties with the U.S. government, to hunt on certain federal lands. Hunting in Yellowstone National Park is not authorized by Congress and longstanding policy prohibits hunting in units of the National Park Service system unless specifically authorized. The Montana-licensed and tribal subsistence hunts have resulted in variable harvests each year (the maximum was 322 animals in 2013-2014) depending on how many bison moved outside the park in response to snow depths in the higher mountains.

In 2008, several other adaptive management adjustments were approved to: (1) further describe the circumstances for bison occupying habitats outside the park, (2) establish a precedent for minimizing the shipment of bison to meat processing facilities, (3) re-affirm the commitment to vaccinating bison, (4) develop a method for sharing decision documents with the public, and (5) develop metrics for annual monitoring and reporting on management actions. In addition, a 30-year livestock grazing restriction

and bison access agreement was signed with a private landowner to remove livestock from lands located just north of the park boundary. This agreement led to adjustments to the Interagency Bison Management Plan in 2011 and 2012 to increase tolerance for untested bison north and west of the park boundary. During 2011 through 2014, 200 to 1,100 bison migrated to habitat in the Hebgen and Gardiner basins of Montana during winter. In addition, the Animal and Plant Health Inspection Service implemented a rule in 2010 that allows detections of brucellosis in domestic livestock to be dealt with on a case-by-case basis. This rule removed the provision for automatic reclassification of any class-free state or area to a lower status if two or more herds are found to have brucellosis within a 2-year period or if a single brucellosis-affected herd is not depopulated within 60 days. This reclassification often had adverse economic consequences on producers state-wide because a "brucellosis-free" classification allowed them to export cattle to other states or nations without testing. Today, as long as outbreaks are investigated and contained by removing all livestock testing positive for exposure, corrective regulations are not imposed on the rest of the cattle producers in the state. In fact, brucellosis transmitted by wild elk was detected in several domestic bison and cattle herds in Idaho, Montana, and Wyoming during 2009 to 2014, without any state-wide corrective actions implemented.

Bison moving in single file through unbroken snow near Tower Junction in the northern region of Yellowstone National Park.

Seasonal Distributions & Movements

Chris Geremia, P.J. White, Rick L. Wallen and Douglas W. Blanton

Yellowstone bison are highly mobile and can traverse large expanses of land in relatively brief intervals of time. They are considered migratory because most animals move back and forth between seasonal ranges at various times of year to better access resources. Most bison return to the same seasonal ranges each year, which are large in size (more than 50 square kilometers [19 square miles]). The primary factors influencing bison movements are: seasonal vegetation changes that affect food quality, the breeding season, the distribution, size, and quality of foraging sites, snow onset and accumulation that affects energy expenditures and access to food, and bison density in an area. Many of these factors are largely beyond the control of managers, and as a result, large migrations of bison onto low-elevation winter ranges in Montana will occur when the right alignment of weather and bison numbers occur.

During summer, bison in northern Yellowstone are concentrated in an approximately 40-kilometer (25-mile) long region along the Lamar River from Cache Creek in the east towards the confluence of the Yellowstone River in the west. Some bison make prolonged forays to the high-elevation Specimen Ridge and Mirror Plateau, with occasional trips to the Pelican and Hayden valleys. Bison in central Yellowstone return to the Hayden Valley from wintering areas in western and northern Yellowstone, with nearly all animals in the Hayden Valley during July and August. In late summer, many bison travel back and forth between the Hayden Valley, northern shore of Yellowstone Lake, and the Pelican Valley. In early autumn, bison make brief trips from summer ranges to most winter ranges, with nearly all animals subsequently returning to the summer range. These exploratory trips may enable bison to assess

food availability across winter ranges or access remaining high-quality food prior to vegetation dying.

As winter progresses, bison in northern Yellowstone move downslope to the lower Yellowstone River drainage (Tower, Slough Creek, Hellroaring) and Blacktail Deer Plateau. From there, bison may move further northwest to the lower-elevation Gardiner basin where snow pack is lower and new vegetation growth begins earlier in spring. These movements are made along several pathways that follow the Yellowstone and Gardner rivers. Bison from central Yellowstone leave the summer range and move to western Yellowstone following a historic migration route (Mary Mountain pass) that connects the Hayden Valley and Firehole River drainage. From the Firehole River drainage, bison move downslope to access several meadows along the Firehole, Gibbon, and Madison rivers. Movements are relatively fluid between these meadows, with short stays in any given meadow. Bison from central Yellowstone may also move to northern Yellowstone using the river and roadway corridor that connects the Gibbon Canyon with Mammoth Hot Springs. Some of these bison gradually move upslope to the Blacktail Deer Plateau and lower Yellowstone River drainage, before moving to lower-elevation areas in the Gardiner basin.

Movement patterns are reversed in spring (April-June) as snow melts and bison follow new vegetation growth from lower to higher elevations. The onset of new vegetation growth typically begins three weeks earlier in northern Yellowstone than in central Yellowstone. Thus, return movements occur earlier in northern Yellowstone and coincide with the time when many bison from central Yellowstone are just reaching low-elevation wintering areas along the Madison River and eastern portion of Hebgen Lake outside the western boundary of the park in Montana. Emergence of new vegetation in the Hebgen Lake basin coincides with the calving period for bison, and several hundred bison from central Yellowstone move to this winter range at this time. These animals tend to remain in this area during calving, before returning to higher-elevation summer ranges inside Yellowstone National Park.

Large year-to-year differences in the timing, extent, and hardness of snow pack, as well as the emergence of snow-free areas in spring, occur in northern Yellowstone. Consequently, bison are less likely to track changes in food resources at broad scales because they cannot depend on being able to access food in specific seasonal ranges during similar times each year. Higher-elevation areas with more available forage (due to high summer plant growth) and some snow cover may provide increased access to food compared to lower-elevation areas with less snow but less available forage (due to lower summer plant growth). However, in years with high snow cover, foraging efficiency in higher-elevation areas decreases and bison must move to lower-elevation areas. Bison learn to respond to these changes in foraging efficiency, and as a result, there are large annual variations in numbers of bison on specific winter ranges. Conversely, bison in central Yellowstone exhibit regular seasonal distributions because the timing and extent of snow conditions are similar between years. Annual variations occur, but overall, conditions are similar enough among years to decrease foraging efficiency in a predictable manner across various seasonal ranges. As a result, bison learn to move to specific ranges at specific times of year to exploit differences in food availability.

Male and female bison in the Lamar Valley of Yellowstone National Park during the midsummer rut.

Reproduction & Survival

Chris Geremia, P.J. White, Rick L. Wallen, and Douglas W. Blanton

Reproduction

Female bison typically reach sexual maturity and conceive their first calf at 2 or 3 years of age. Males are capable of breeding at this age, but generally do not until they are 5 or 6 years old because older, larger, and more experienced males monopolize opportunities. The gestation period lasts about 285 days (9½ months) and the majority of births in Yellowstone bison occur during April and May. Calving dates in northern Yellowstone precede those in central Yellowstone by about 14 days, which likely reflects the earlier onset of snow melt and new plant growth on lower-elevation grasslands in northern Yellowstone. Calving often overlaps with spring migrations from winter to summer ranges, and calving locations likely depend on when these migrations commence—which could be delayed due to prolonged snow pack or late emergence of new vegetation at higher elevations. Bison give birth to a single calf that weighs between 15 and 30 kilograms (33 to 66 pounds).

In recent decades, reproductive rates appeared to differ between bison in central and northern Yellowstone. The probability of a bison in northern Yellowstone giving birth was 78% (95 percent credible interval = 0.72 to 0.84), compared to 63% (0.56 to 0.69) in central Yellowstone. The probability of giving birth was lowest at 3 years of age and increased with age. Birth rates were lower during years with deep or hard snow pack, but no drought-related effects were detected. The probability of Yellowstone bison giving birth prior to infection with brucellosis was 80% (0.73 to 0.86), but decreased to 48% (0.27 to 0.70) during the first pregnancy after infection. The probability of giving birth to a live calf remained suppressed at 64% (0.57 to 0.70) during years subsequent to initial exposure to *Brucella* bacteria.

Survival

Bison are long-lived, with some females living 20 or more years. Males have lower survival and rarely live past 12 years of age in the Yellowstone population, which is probably due to the increased mortality risk associated with the intense sparring for mates during the breeding season. Newborn bison have an increased risk of mortality from predation, disease, and harsh weather. In recent decades, survival during the first 2 months of life was about 75%, and about 87% during the rest of the first year. These calf survival rates are remarkably high compared to other ungulates such as elk (less than 30%) in the Yellowstone ecosystem following the recovery of black and grizzly bears, mountain lions (cougars), and wolves.

The probability of an adult female bison in northern Yellowstone surviving one year was 96% (0.94 to 0.98) during recent decades. Adult females in central Yellowstone had somewhat lower annual survival rates of 91% (0.88 to 0.94). Survival probabilities increased early in life and peaked at 3 years of age, which coincided with the age of first reproduction for most females. Survival remained consistently high for 3- to 9-year-old females in northern Yellowstone. There was some indication of lower survival rates for females in northern Yellowstone as they aged past 10 years, but additional data are needed to better define this relationship. In contrast, females from central Yellowstone had high survival through 7 years of age, followed by a pronounced decrease in survival beginning at a surprisingly young age compared to their possible life span of more than 20 years. Bison invest substantial energy and other resources into reproduction, which may induce decreases in survival at an earlier age. Also, as bison age, tooth wear reduces their ability to chew plant material into small enough particles to facilitate efficient digestion by microbes in their rumen. This wear may be worsened by the abrasive action of silica in rhyolite soils, some of which may be retained on plants eaten by bison using thermally influenced areas in central Yellowstone.

Survival rates have remained relatively unchanged through substantial variations in bison abundance and drought conditions, but decreased

during years with deep snow pack. Since 1985, more than 6,000 bison have been removed from the population by humans, primarily through capture and shipment of bison to meat processing facilities and secondarily through hunting. Overwhelmingly, these human removals to reduce the risk of brucellosis transmission from bison to cattle in Montana and limit population growth have been the primary cause of bison mortality. By controlling bison numbers during winters with large migrations into Montana, humans have indirectly regulated bison survival. Winter-kill (starvation) continues to be a substantial cause of bison mortality during winters with severe snow pack. However, predation is becoming a larger factor following wolf restoration and grizzly bear recovery. Wolves kill more bison in late winter as snow pack increases and its effects reduce bison condition and increase their susceptibility to attack. Wolves also kill more bison as bison numbers increase relative to elk and there are more bison calves in the population. The average age of adult bison killed by wolves in Yellowstone was 10 years. Wolves can exist almost entirely on bison, as observed in Wood Buffalo National Park in Canada. At this time, however, wolves in Yellowstone still prefer elk and only tend to kill significant numbers of bison during winters with deep and prolonged snow pack that make malnourished animals more abundant and susceptible.

Bison feeding near Swan Lake in Yellowstone National Park.

Nutritional Ecology

John J. Treanor, Jessica M. Richards, and Dylan R. Schneider

Yellowstone is a dynamic landscape and changing environmental conditions have a strong influence on key life events for bison, including survival early in life, growth needed to reach reproductive maturity, and successful breeding during adulthood. The preferred forage of Yellowstone bison is grasses and sedges, with forbs and shrubs making up less than 6 percent of their diets. The high-elevation ranges in Yellowstone National Park are dominated by cool season grasses that tend to be high in nutrients in the spring, but decrease as the growing season progresses. Younger plants contain more soluble carbohydrates and less fiber, which makes them more digestible than older plants. However, grasses mature quickly and become fibrous, which greatly reduces their digestibility. Bison have a four-chambered stomach that can process bulky amounts of fairly indigestible plant components. The fore stomach, or rumen, serves as a fermentation chamber where millions of bacteria, protozoa, and fungi convert cellulose into energy-yielding fatty acids that are digestible by bison. The protein content in forage provides rumen microbes with essential amino acids for the synthesis of microbial proteins, which are then absorbed as they pass through the rumen.

Yellowstone bison meet their nutritional demands for growth and reproduction during summer, when plants are growing and high in nutritional value. Forage intake during summer affects fecundity, the development of calves, and the replenishment of body reserves needed to survive winter. Conversely, bison are nutritionally deprived and consume low protein diets during late autumn and winter when plants are senescent. As a result, they minimize energy costs and rely on body reserves when nutritional intake is inadequate for maintenance. Yellowstone bison have responded to seasonal changes in forage availability and quality by overlapping the most nutritionally demanding phases of their life cycle with the availability of high-quality forage. About 80 percent

of their calving occurs during April 25 through May 25, which coincides with the emergence of growing forage on low-elevation winter ranges. Thus, lactation commences when forage high in protein and digestible energy becomes available. Lactation influences the rate of growth in young animals, and their body size entering winter reflects the food available to their mothers for milk production. Over-winter mortality is typically lower for larger juveniles due to their better body condition.

In addition, Yellowstone bison adjust their nutritional intake through habitat selection and migratory movements as the availability and quality of forage changes seasonally across the landscape. They move from summer ranges at relatively high elevations to lower elevations during autumn through winter, and then return to the summer ranges in June. Vegetation quality has little influence on the selection of foraging areas used by bison during winter because plant tissues have senesced and are of low nutritional value. Instead, factors that influence the availability of forage such as snow pack and bison density become more important. As a result, most bison move to foraging areas at lower elevations and areas with thermally warmed ground as snow depths increase at higher elevations. During spring, there are more energy-efficient foraging opportunities for bison at lower elevations because snow melt and vegetation growth commence earlier. Thus, most calving occurs in these areas. The return migration of bison to higher-elevation summer ranges coincides with patterns of new vegetation growth on the landscape. Highly digestible plants eventually become widely distributed, and as a result, energy intake by bison increases. As the growing season advances and grasses mature, however, there is a decrease in the proportion of higher-quality leaves to lower-quality stems. As a result, bison become more selective and consume the upper portions of grasses which are higher in crude protein and digestible energy.

In summary, Yellowstone bison have developed a set of strategies to meet their nutritional needs throughout the year. The availability of high-quality forage during spring and summer promotes successful reproduction and the accumulation of body reserves for winter survival, while winter forage helps reduce the rate at which these reserves are

mobilized. As winter progresses, fat reserves may be needed for energy, especially for pregnant females during late gestation. Calving is synchronized with the emergence of spring forage, which allows bison to meet the high nutritional demands of lactation. The growth and survival of calves is positively affected by the nutritional quality of summer forage. Therefore, bison increase forage intake during the growing season, which enhances assimilation of nutrients. During the dormant season, food intake is reduced and bison conserve body reserves by reducing activity and metabolic rates. Lower-elevation winter ranges provide bison with access to forage and reduce the energy expenditure of moving through the deep snow found at higher elevations. Yellowstone bison are adapted to seasonal changes in forage nutrition and winter conditions with digestive, physiologic, and behavioral strategies that allow them to survive and reproduce in a dynamic environment.

NPS Photo

Bison and cowbirds during the spring green-up in Yellowstone National Park.

Ecological Role

Rick L. Wallen, P.J. White, and Chris Geremia

Large grazers like bison are important species in ecosystems because they have strong influences on plant and animal communities. For example, grazing can increase the availability and distribution of nitrogen to plants, which in turn, can increase plant production. Also, bison provide food for many predators, scavengers, and decomposers, and their carcasses deposit nutrients into the soil that create fertile patches for plant growth. In addition, grazing and wallowing can create specific environments that result in greater plant diversity across the landscape by holding water in depressions, enabling colonization by pioneering plant species, and increasing the diversity and use of areas by other animals.

Bison inadvertently act as "ecosystem engineers" by creating and responding to heterogeneity within their range of distribution. Their heavy bodies and sharp hooves combine to till the soil and disturb roots of grasses and grass-like plants. This prevents grassland succession to shrubs or trees and provides grasses with greater access to sunlight, which is important for growth. Large groups of bison contribute to natural disturbances that influence plant species composition and distribution across large portions of grasslands and shrub steppe, similar to fire, windthrow, and mass soil erosion events. Moderate grazing by bison induces the production of new grass tissue and increases plant community production to the limits determined by water and nitrogen availability. In addition, the combined effects of grazing and fire—called pyric herbivory—can result in greater plant diversity and habitat heterogeneity than either process alone.

Bison can enhance plant growth by making nitrogen and organic matter (e.g., urine, feces, and carcasses) more abundant and accessible to soil microbes, and distributing nutrients across the landscape. During the 1980s and 1990s, the grazing of grasses and deposition of organic

matter by migratory ungulates (primarily elk) in northern Yellowstone approximately doubled the rate of nitrogen mineralization and production of leaves, roots, and stems by grasses. However, rates of ungulate grazing and nitrogen cycling decreased by up to one-half during the late 1990s as the numbers of elk decreased substantially due to hunter harvest, predation, and winter-kill. Also, energy and nutrient dynamics were rearranged across the landscape, with grazing decreasing more in areas with higher productivity. Since that time, the number of bison in northern Yellowstone has more than tripled, which could reestablish the stimulating effects of grazing on nitrogen cycling and plant production. However, large groups of bison that repeatedly graze areas and remove plant tissue through the summer growing season could have quite different effects on grasslands than herds of elk that graze areas for relatively short periods during their migration to higher-elevation summer ranges. Scientists are currently studying the effects of this recent change.

Ungulate grazing and nutrient deposition generally increases grass production from low to moderate grazing intensities, but decreases production at higher grazing intensities because too much leaf tissue is removed. During 1998 to 2000, less than 50 percent of the herbaceous, non-woody vegetation in the Hayden Valley of central Yellowstone was consumed by herbivores during the growing season, which approximates a moderate grazing rate. In some areas, however, bison removed more than 30 percent of new growth in spring and 70 percent of the remaining plants during winter. Higher consumption could decrease plant production if bison numbers continue to increase and bison regraze the same plants during a single season or consecutive seasons. As a result, the prevalence of grasses could decrease while forbs and grazing-tolerant plants increase—though the outcome will depend on the density of bison relative to the food-limited capacity of the environment to support them.

If current trends continue with increasing bison numbers and decreasing elk numbers, then bison will become more available as prey for wolves and other predators (e.g., bears), with potential indirect effects to elk and other ungulates. Predation on a particular species can be

strongly influenced by the presence of other prey species that maintain predators at higher densities—a process known as apparent competition. For example, an increase in the abundance of one prey species can result in a decrease in the abundance of another prey species due to an increase in the number or distribution of predators. This situation was observed in the Canadian Rocky Mountains where wolves primarily fed on moose, but also killed woodland caribou as alternate prey. An increase in moose numbers resulted in higher wolf numbers that contributed to a range-wide decrease in numbers of less abundant caribou. Thus, increased predation on abundant bison by wolves in Yellowstone could enable wolves to sustain higher numbers and kill more of their primary prey, elk, than would otherwise be likely based on lower elk numbers.

NPS Photo

NPS Photo

Bison moving snow with its head to feed.

Adaptive Capabilities & Genetics

Rick L. Wallen and P.J. White

Yellowstone bison went through a population bottleneck (i.e., a drastic reduction in numbers) in the late 1800s that was caused by human exploitation. There were less than 25 indigenous bison in central Yellowstone by 1902 and they persisted at relatively low numbers (less than 500 bison) for many generations. Populations that begin with, or are reduced to, a small number of animals contain less genetic variation than populations with a larger number. Thereafter, chance losses of genetic variation may continue due to inadequate gene flow with other populations, and over time, reduce the abilities of animals to adapt to new environmental challenges. However, Yellowstone bison do not show the effects of inbreeding and have retained significant amounts of genetic variation. The high genetic diversity observed in Yellowstone bison despite their being nearly extirpated may be explained, at least in part, by the human creation of a bison herd in northern Yellowstone during 1902 from unrelated bison with somewhat different genetic make-ups that eventually interbred with the indigenous herd in central Yellowstone.

Bison from the central and northern regions of Yellowstone are genetically distinguishable, which likely reflects, in part, the population bottleneck caused by nearly extirpating Yellowstone bison in the late 19th century, the creation of another breeding herd in northern Yellowstone from bison of unrelated breeding ancestry, and human stewardship thereafter. These genetic differences were maintained over much of the last century by strong female philopatry (i.e., fidelity) to breeding areas, with most females returning to the same area each year. As a result, there was little gene flow between bison from the central and

northern regions of the park. However, observations of radio-collared female bison indicate that in the most recent generation female groups are emigrating between central and northern Yellowstone and contributing to gene flow that could decrease genetic differences between bison in these regions.

Some scientists have argued that the National Park Service should actively manage to preserve the genetic distinctiveness of bison in central and northern Yellowstone. The conservation of genetic diversity is extremely important, but it is arguable whether the preservation of a population or genetic substructure that was created and facilitated in large part by humans should be the goal. Alternatively, ecological processes such as natural selection, migration, and dispersal could be allowed to prevail and influence how the population and genetic substructure is maintained into the future. Bison from central Yellowstone began dispersing to northern Yellowstone in the 1980s and these dispersal movements have continued to increase with bison abundance. Gene flow between breeding herds could lessen some potential effects of population substructure and non-random culling on the loss of genetic diversity. Thus, current management actions attempt to preserve bison migration to essential winter range areas within and adjacent to Yellowstone National Park and bison dispersal between central and northern Yellowstone. The current population distribution and genetic substructure may or may not be sustained over time through ecological and evolutionary processes. The bison will determine that.

To preserve genetic variation over decades and centuries, the bison conservation initiative by the U.S. Department of the Interior and the North American conservation strategy for bison by the International Union for the Conservation of Nature recommended that population (or breeding herd) sizes should be at least 1,000 bison, with approximately equal sex ratios to enable competition between breeding bulls. Furthermore, a wild bison population was defined as one with sufficient numbers to prevent the loss of genetic variation, low levels of cattle hybridization, and exposure to some forces of natural selection, including competition for breeding opportunities. Currently, Yellowstone

bison comprise the only population of plains bison that has achieved these goals, with more than 1,000 bison in both central and northern Yellowstone, moderate to high variation in male reproductive success, and no evidence of hybridization with cattle.

Intensive management actions near the boundary of Yellowstone National Park to reduce the risk of brucellosis transmission to cattle outside the park could potentially result in a substantial loss of genetic diversity and affect population substructure. Sporadic culls of more than 1,000 bison in some winters to maintain separation between bison and cattle has removed a disproportionately large number of females and reduced population growth. Therefore, in 2008 managers made several adjustments to the Interagency Bison Management Plan to minimize future large-scale culls of bison, evaluate how the genetic integrity of bison may be affected by management removals, and assess the genetic diversity necessary to maintain a robust, wild, wide-ranging population that is able to adapt to future conditions. Given the importance of male reproductive success and population size on the loss of genetic variation, we recommend managing for at least 3,000 to 3,500 total bison over decades, while minimizing selective culling and preserving opportunities for bison migration and dispersal.

Lakota Sioux spiritual leaders conduct a ceremony in the northern region of Yellowstone National Park to honor bison.

Cultural Importance

Rick L. Wallen, P.J. White, and Tobin W. Roop

Portions of the Great Plains and Rocky Mountains in the Yellowstone area were part of the natural range of bison from prehistoric times and also served as the homeland of various native peoples who hunted bison herds as they moved across the landscape. At least 10 American Indian tribes lived and hunted in the Greater Yellowstone Area during both historic and prehistoric times, and an additional 16 tribes claim association with the Yellowstone region. Bison traditionally provided food, clothing, fuel, tools, shelter, and spiritual value to many tribes, and were central to the culture of tribes who traveled to the region to hunt bison. However, the slaughter of bison herds by colonizing Euro-Americans altered the interrelated world of native people and bison and resulted in decimated, localized populations of both. Yellowstone bison have a special significance to many tribes because they are the last living link to the indigenous herds of bison that once roamed across North America. These tribes view Yellowstone bison as inextricably linked to their existence and survival, and as a result, feel obligated to serve as their guardians. Some American Indians believe Yellowstone bison have been treated unjustly, similar to native peoples during the westward expansion of this country. They accurately point out Yellowstone bison are managed differently (i.e., hazed, captured, culled) because some individuals have brucellosis, while elk also infected are not subject to similar actions. As a result, tribal representatives have informed managers at Yellowstone about many issues important to them concerning the management of bison, including: (1) respectful treatment, (2), allowing bison to roam freely without fencing or hazing, (3) transferring brucellosis-free bison to the tribes after they have completed an approved quarantine protocol, and (4) distributing meat, skulls, and hides of bison that are killed to the tribes.

Bison also define the Euro-American experience because they were central to national expansion and development. Bison occupied the landscape of the Great Plains in large numbers (25 to 30 million by some accounts) and provided food, fuel, and travel routes for early pioneers and passersby. Bison hides became a valuable resource for making clothes and blankets to sleep under during long, cold winters. As Euro-American colonists learned that many American Indian cultures depended on bison for their subsistence, the government used this information to exploit and conquer tribal cultures. Bison became a marketable commodity, and by 1820, commercial hunting operations were harvesting bison in large quantities and trading or selling hides for export to the eastern United States and Europe. Following the annihilation of plains bison, public sentiment to prevent the extinction of bison was widespread and the American Bison Society, Bronx Zoo, New York Zoological Society, and others initiated programs to propagate and recolonize preserves specifically to increase bison numbers. These efforts contributed to the development of our national conservation ethic based on public ownership of wildlife, as well as our national park system.

Though domesticated bison are now accepted as an agricultural commodity, restoring wild bison to public lands is still an appalling thought to many cattle ranchers because they perceive bison as a threat to their way of life and a detriment to their economy. Bison are considered direct competitors with livestock producers for real estate on large flat valley bottoms and the grass that grows there. However, in recent decades, many rural areas in the Greater Yellowstone Area have become more demographically and economically diverse, with recreation, tourism, and amenity living competing with agriculture and natural resource extraction economies. As a result, more residents in these communities now consider the environment and wildlife viewing to be primary economic assets. Furthermore, Yellowstone National Park plays a large economic role in the region, with visitors providing substantial economic activity to surrounding gateway communities. Approximately 3.5 million visitors during 2012 spent more than $400 million in local communities, which

supported about 5,600 jobs and generated $473 million in combined visitor and workforce sales, $165 million in labor income, and $272 million in related income, profits, and taxes. About 50 percent of surveyed visitors, including residents and non-residents, indicated seeing bison was a reason for their trip.

Despite their biological and cultural importance, bison are the only wild North American ungulate that has not been recovered across significant portions of their historic range. Unlike bighorn sheep, caribou, deer, elk, moose, mountain goats, and pronghorn, bison receive little tolerance on private or public lands outside of national parks and similar protected areas. Thus, they have failed to gain legitimate status as wide-ranging wildlife and their conservation is constrained by real and perceived conflicts. As the United States progresses further into the third century of its existence, acknowledgement of the historical conditions that challenged native peoples and Euro-American pioneers will be an important cultural value to society. Also, preservation of one of the last unfenced, wide-ranging bison populations subject to nearly all the evolutionary pressures from which their ancestors evolved would be a tremendous achievement that could invigorate the restoration of the ecological role of plains bison as a species in western North America.

Staff on horseback hazing bison near Undine Falls in the northern region of Yellowstone National Park.

Current Management

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The Interagency Bison Management Plan between the National Park Service and State of Montana includes three general categories of actions: (1) conserving a viable population of wild bison, (2) managing brucellosis transmission risk, and (3) reducing the prevalence of brucellosis in bison. Managers attempt to maintain Yellowstone bison numbers near an end-of-winter guideline of 3,000. During June and July, biologists conduct counts and age and gender classifications of bison in central and northern Yellowstone. Biologists then use long-term weather forecasts and population and migration models to predict bison abundance and composition at the end of the upcoming winter, as well as the numbers of bison likely to migrate to the park boundary. Predictions are used to establish annual removal objectives for bison based on abundance, brucellosis suppression, distribution, and demographic (age, breeding herd, sex) goals. Other members involved with the Interagency Bison Management Plan include the Animal and Plant Health Inspection Service, Confederated Salish and Kootenai Tribes of the Flathead Nation, InterTribal Buffalo Council, Montana Department of Livestock, Montana Fish, Wildlife & Parks, Nez Perce Tribe, and the U.S. Forest Service.

Bison are currently allowed to migrate onto National Forest System and other lands north of the boundary of Yellowstone National Park and south of Yankee Jim Canyon each winter and spring. Bison are not allowed north of the mountain ridge-tops between Dome Mountain/Paradise Valley and the Gardiner basin on the east side of the Yellowstone River and Tom Miner basin and the Gardiner basin on the west side of the Yellowstone River. Bison are allowed to roam freely into the Absaroka-Beartooth Wilderness north of the park where there are no cattle. West of the park, bison are allowed to migrate onto and occupy the Horse Butte peninsula at the east end of Hebgen Lake and other nearby areas. Hazing of bison is conducted by staff to prevent mingling with cattle, ensure human safety, prevent property damage,

and prevent the movement of bison outside of agreed-upon tolerance zones or onto private property where landowners do not want bison. Most bison that do not naturally return to the park on their own are hazed back to park lands on or near May 1st (north) or May 15th (west). Bison are allowed to occupy the Eagle Creek/Bear Creek area, Cabin Creek Recreation and Wildlife Management Area, and the Monument Mountain Unit of the Lee Metcalf Wilderness year-round.

Several management tools are used to reduce bison numbers as necessary, including: (1) public and treaty harvests in Montana, (2) culling (shipment to meat processing facilities) at the park boundary capture facility, (3) culling (shooting; shipment to meat processing facilities) in Montana to prevent bison mingling with livestock or threats to human safety or property, and (4) transfer of bison to research facilities. Hunting is used to manage the abundance and distribution of bison in Montana, while providing harvest opportunities and cultural and spiritual engagement. Bison are sometimes captured (1) for brucellosis testing and vaccination, (2) to cull bison infected with brucellosis, (3) to reduce bison numbers, (4) because they have repeatedly resisted hazing to keep them within agreed-upon tolerance zones, and (5) because there are already large numbers of bison in the tolerance zones and additional bison could induce movements into no-tolerance areas or cause human safety and property-damage issues. Bison testing positive for brucellosis exposure may be sent to meat processing facilities, while test-negative bison may be vaccinated in an attempt to reduce the prevalence of brucellosis infection. The National Park Service has agreements with some American Indian tribes and a tribal organization to periodically provide them with bison for shipment to meat processing facilities and the subsequent distribution of meat, hides, horns, and other bison parts to their members for nutritional and cultural purposes. In addition, the Montana Department of Livestock and the Animal and Plant Health Inspection Service use existing regulations and incentives to make sure that all cattle in the Yellowstone area are vaccinated.

The conservation of Yellowstone bison has been successful under the Interagency Bison Management Plan, with overall abundance ranging between 2,400 and 5,000 since 2000. Bison move across an extensive landscape and

are subject to a full suite of grazing competitors and predators, other natural selection factors, and substantial environmental variability. The population is prolific and has recovered rapidly from decreases in abundance due to culling or natural mortality. The bison have high genetic variation that should be maintained with a population that averages at least 3,000 to 3,500 bison. Also, adjustments to the plan increased tolerance for bison in Montana by expanding the northern and western conservation areas and allowing more bison to occupy these areas during winter and spring. There have been no known transmissions of brucellosis from bison to cattle. However, the prevalence of brucellosis within the population has not been reduced and several key assumptions within the plan were faulty or problematic to implement. For example, expected advances in vaccine, diagnostics, and delivery technology did not occur, and as a result, the plan overestimated the feasibility and effectiveness of vaccination. Also, some aspects of the plan such as test-and-slaughter at capture facilities were never completely or consistently implemented for various reasons. In addition, the plan underestimated bison reproduction and survival rates. As a result, more bison must be removed to regulate the population towards 3,000. This has contributed to a continued reliance on capture and shipment of bison to meat processing facilities, which is extremely controversial. These successes and failures highlight the difficulties associated with managing for competing objectives—conserving bison and suppressing brucellosis—that are implemented and have effects across different time scales.

Watching wild bison in Yellowstone's Lamar Valley.

The Future

P.J. White, Rick L. Wallen, Chris Geremia,
John J. Treanor, and David E. Hallac

The debate about how to conserve and manage Yellowstone bison involves a variety of issues, including abundance and distribution, brucellosis infection (including in elk), genetic integrity, habitat, property damage and human safety, wildness and intensity of management, cultural and economic values, and hunting. Incorporated in these overarching issues is a broad spectrum of beliefs, concerns, and values held by a diverse range of stakeholders, including advocates, local community members, regulators, and scientists, American Indian tribes, and the national and international public. There are several key points pertinent to this debate and future management.

Key Points

Yellowstone Bison Are Migratory Wildlife, Not Livestock—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 forces of natural selection. Yellowstone bison are exceptional at meeting these criteria. The mission of the National Park Service is to preserve native species and the processes that sustain them. Wildlife species in Yellowstone National Park are not managed like domestic stock on a ranch and are generally allowed to move freely. While the park provides a large amount of habitat for bison and other ungulates, it does not encompass many of the lower-elevation winter ranges used by these animals when deep snow limits access to forage at higher elevations. As a result, some tolerance is necessary outside the park for wild bison to access resources for their survival, similar to the acceptance

already provided to bears, bighorn sheep, deer, elk, moose, pronghorn, wolves, and other wildlife.

Brucellosis Will Remain in the Greater Yellowstone Area for the Foreseeable Future—Eradication of brucellosis in wild bison and elk is not feasible at this time due to: (1) the absence of an easily distributed and highly effective vaccine, (2) limitations of current diagnostic and vaccine delivery technologies, (3) potential adverse consequences (e.g., injuries, changes in behavior) from intrusive suppression activities, (4) effects of nutrition, condition, and pregnancy/lactation during winter that lessen protective immune responses from vaccination, and (5) chronic and increasing infection in elk which are widely distributed and could re-infect bison. Even a modest decrease in brucellosis prevalence would be difficult in the coming decades given current technology and existing conditions. Vaccination was envisioned as a primary method to reduce brucellosis in Yellowstone bison, but the best available evidence suggests vaccination at this time would not substantially suppress brucellosis and could have unintended adverse effects to the bison population and reduce wildlife viewing opportunities for residents and visitors.

Intensive Management of Yellowstone Bison Is Necessary at Times—Yellowstone bison will continue to move into Montana during winter, with more bison migrating as their numbers and winter severity increase. Due to existing agricultural and residential development, however, there is not sufficient low-elevation habitat in areas where bison are currently tolerated that could sustain many hundreds or thousands of animals for extended lengths of time. Thus, bison attempt to migrate further during some winters, including into areas occupied by hundreds of cattle. Also, bison will eventually attempt to pioneer new areas as their abundance increases, similar to the range expansion that occurred in the past. When bison cross the park boundary into Montana their management is the prerogative of the state, including coordinated management with the Gallatin National Forest on National Forest System lands. Montana has allowed several hundred bison to migrate outside

Yellowstone National Park and occupy suitable winter range in the state, and tolerance on additional range may occur in the future. However, mass migrations of bison have, at times, upset state and local governments and many private landowners and cattle operators. If bison were allowed to disperse unimpeded into cattle-occupied areas of Montana, it is likely those bison would be lethally removed by state employees or during regulated hunts. Also, the State might retract some tolerance for bison. Thus, management practices such as hunting, hazing, capture, and culling are necessary at times to limit the abundance and distribution of bison, while incrementally building acceptance for them in modern society.

Yellowstone Bison Can Support Conservation and Cultural Practices Elsewhere —Yellowstone bison have high reproductive and survival rates for a wild population exposed to numerous predators and substantial environmental variability. Thus, bison abundance increases rapidly when environmental conditions are suitable, which could quickly fill available habitat and out-pace acceptance for them in Montana. As a result, harvesting and culling bison is currently necessary at times to keep the limited tolerance for them in Montana from being rescinded. Public and treaty harvests and the provision of meat from culled bison to tribes and food banks could improve cultural, economic, nutritional, and social well-being. Also, the use of quarantine to restore brucellosis-free Yellowstone bison to tribal and public lands would enhance the conservation of the species in North America.

A Path Forward

The conservation of wild, wide-ranging bison in modern society is a great challenge facing natural resource managers because it requires increasing habitat availability and social tolerance outside protected areas. Biologists at Yellowstone National Park have developed management plans for bison that include demographic, ecological, and genetic objectives such as:

- Maintain 2,500 to 4,500 bison and average at least 3,000 to 4,000 over decades to preserve genetic diversity;
- Minimize the effects of selective culling on bison and allow numbers in the central and northern regions of the park to vary depending on dispersal rates and natural selection;
- Maintain similar proportions of males and females and an age structure of about 70 percent adults and 30 percent juveniles to facilitate competition for mates;
- Sustain ecological processes such as predation, migration, dispersal, and competition for mates and food in the park and other agreed-upon conservation areas; and
- Restore the contributions of bison to herbivore-grassland dynamics, the predator-prey-scavenger association, and many other relationships in the ecosystem.

Brucellosis Containment

Given current technology and existing conditions, intrusive human actions such as vaccination or fertility control are unlikely to substantially decrease brucellosis infection in wild bison and elk. If disease regulators want to suppress brucellosis in wildlife across the Greater Yellowstone Area, then they need to initiate a dialogue with all the stakeholders regarding what should be done based on various mandates, values, and view points, and what can be done based on existing conditions and technologies, as well as biological feasibility and economic costs. In the meantime, the best alternative for suppressing brucellosis transmission is to maintain separation between bison, elk, and cattle during the transmission period from February to June.

Tolerance

A measured increase in tolerance for bison on available habitat in the Greater Yellowstone Area is necessary and attainable for long-term conservation success. Allowing bison to occupy public lands outside Yellowstone National Park until most bison calving is completed (early June) will not significantly increase the risk of brucellosis transmission

from bison to cattle because: (1) bison parturition is typically completed weeks before cattle occupy nearby ranges, (2) female bison quickly consume most birthing tissues, (3) ultraviolet light and heat degrade *Brucella* on tissues, vegetation, and soil, (4) scavengers remove fetuses and remaining birth tissues, and (5) management maintains separation between bison and cattle on nearby ranges. Allowing bison to occupy public lands outside the park through their calving season will help conserve bison migratory behavior and reduce stress on pregnant or lactating females and newborn calves, while still minimizing the risk of brucellosis transmission to cattle. It will also reduce the cost, duration, extent, and intensity of hazing necessary to encourage bison to return to the park or other year-round tolerance areas outside the park during early summer.

A vexing problem for managing Yellowstone bison is the lack of lower-elevation valley habitat available in the Gardiner basin and southern Paradise Valley north of Yellowstone National Park. Most of the valley bottoms in this area, which have higher plant availability and more moderate snow conditions than surrounding mountains, are already used for agriculture and residential development. As a result, up to 800 bison have been held in the Stephens Creek capture facility and other confinement pastures in and near Yellowstone National Park and fed hay for months during some winters to prevent their mass migration north of the park. These animals were released during spring, but confinement and feeding obviously conflicts with the management of bison as wildlife subject to natural selection factors and could have unintended consequences such as food-conditioning, disease transmission during confinement, and disruption of traditional migratory patterns. Consequently, there is a continuing need to refine management practices and increase tolerance to better protect migratory bison and avoid unnaturally concentrating them during late winter and calving periods.

Hunting

Harvests in Montana by state and treaty hunters could play a more significant role in limiting bison numbers and distribution outside the

park to further lessen brucellosis transmission risk and the frequency of large shipments of bison to meat processing facilities. Increasing the harvest of bison in future years will require increased tolerance for bison in Montana, better access for hunters, creative harvest strategies with non-traditional seasons, and commitments by hunters to adjust harvest methods in response to bison habitat use patterns. Bison managers need to implement strategies that avoid aggregations of hunters along the park boundary and allow bison to migrate into areas away from roads where they can be hunted in a fair-chase manner. Also, bison managers from the various American Indian tribes with treaty hunting rights in Montana and federal and state agencies need to better coordinate to collectively manage the overall harvest of bison by age, breeding herd, and sex, and avoid exceeding the social tolerance for bison hunting and associated gut piles near residential areas or the park boundary. Seasonal or year-round tolerance for wild bison should be attainable in some portions of the Greater Yellowstone Area where brucellosis transmission risk to cattle is low. Managers could use actions such as fencing, hazing, delaying cattle turn-on dates, and conservation easements or incentives to increase tolerance for bison, while maintaining separation with cattle and resolving conflicts with human safety and private property.

Capture & Culling

In some winters, several hundred bison may need to be captured and culled from the population at boundary facilities to reach removal objectives for that year. If managers are culling bison primarily to limit their abundance, then they should cull animals in a non-selective manner to avoid potential adverse demographic and genetic consequences that could compromise population viability. Culling bison in proportion to their availability in the population may: (1) mimic aboriginal harvests or natural mortality events, (2) help maintain an age structure that is close to historical distributions, and (3) avoid artificially allowing brucellosis or other factors to act as key selective forces.

If feasible, managers should implement smaller removals (25 to 50 bison) near the park boundary consistently through the migration season and in proportion to age and sex availability in the population. This stepwise approach would: (1) limit bison held within capture facilities and minimize effects on hunting opportunities, (2) reduce logistical constraints of transporting large numbers of bison to meat processing facilities over brief periods, (3) avoid transporting females late in pregnancy to meat processing facilities, and (4) lower the chances of out-of-park abundance surpassing levels that exacerbate conflict. When necessary, large removals of 500 or more bison could be implemented during severe winters and/or at high bison densities when large numbers of bison naturally migrate to lower elevations.

Quarantine Facilities & Terminal Pastures

The ecological and adaptive value of Yellowstone bison merits efforts to relocate some animals testing negative for brucellosis exposure to quarantine facilities for further testing and eventual release elsewhere. Quarantine facilities could be paired with terminal pastures so that any animals that test positive for brucellosis could be killed for food. These paired facilities would reduce the frequency of large shipments of bison to meat processing facilities when females are late in pregnancy, while enhancing bison conservation and the cultural heritage and nutrition of American Indian tribes. If necessary, pregnant bison could be held in terminal pastures through calving, with test-positive animals eventually killed and test-negative calves and other animals sent to quarantine. There is significant interest by federal and state agencies, Native American tribes, non-governmental organizations, and private entities in receiving brucellosis-free Yellowstone bison and/or constructing and operating a quarantine facility on their lands. Also, the Department of the Interior recently identified 20 locations on federal lands within the historic range of plains bison that may be suitable for receiving Yellowstone bison completing quarantine.

Public Engagement

Most stakeholders are not satisfied with the level of involvement provided by the partners of the Interagency Bison Management Plan, which primarily amounts to comment periods at public meetings. Rather, stakeholders want substantive input into the decision-making process to influence management strategies before they are adopted and implemented. As a result, managers should consider alternate forms of public involvement such as stakeholder workshops with presentations and discussion that allow information and ideas to be transferred and deliberated between managers, scientists, and the public. Management committees comprised of all interested stakeholders could be formed and sustained to develop ideas and recommendations similar to the Citizens Working Group on Yellowstone Bison and the model used for managing the Book Cliffs and Henry Mountains populations in Utah. Furthermore, human dimensions have a large influence on policy change when it comes to tolerance for large wildlife such as bison outside national parks and refuges. Additional information is needed on political and socioeconomic factors such as: (1) comparative costs and public preferences for various management alternatives, (2) non-market values of wild bison, (3) the demand for bison that are removed from the population, (4) traditional knowledge from American Indians and local communities, and (5) public attitudes, behaviors, and knowledge of bison, brucellosis, and management.

Conclusions

The overriding issue regarding the conservation of Yellowstone bison and plains bison elsewhere in North America is whether the public will support wild bison living outside preserves. Arguments against tolerance for Yellowstone bison, or their restoration elsewhere, are generally presented in terms of disease, protection of property, and human safety concerns—even though elk have similar effects yet are tolerated without intrusive management because they are economically valuable for hunting. However, there are also underlying issues about grass (i.e., competition with cattle), political control (i.e., state versus

federal rights), and the continuing transition of communities from traditional rural occupations and lifestyles such as ranching to tourism and the enjoyment of natural amenities (i.e., locals versus outsiders). While these characterizations may be overly simplistic, disease regulators and livestock interests have certainly perpetuated misperceptions regarding the risks posed by bison for decades. These misperceptions have strongly influenced the management of bison and severely limited their conservation and distribution across the landscape.

The reluctance to allow Yellowstone bison onto more public lands in the Greater Yellowstone Area can no longer be justified solely based on brucellosis risk to the cattle industry. There is recognition by disease regulators and wildlife managers that the risk of brucellosis transmission from bison to cattle is minute compared to elk which are generally free to roam. Also, the economic consequences of occasional brucellosis outbreaks in cattle are greatly reduced since the Animal and Plant Health Inspection Service changed its regulations in 2010 to deal with outbreaks on a case-by-case (rather than state-wide) basis, and designated surveillance areas for brucellosis were established. Despite several detected transmissions of brucellosis from elk to cattle, the gross annual income from cattle sales in Montana surpassed $1 billion six times during 2005 to 2013, with record-high cattle prices since 2010. Furthermore, studies in Wyoming have clearly demonstrated that the costs of measures to prevent brucellosis transmission from elk to cattle are exorbitant compared to the costs of an occasional outbreak.

Current conditions in the Greater Yellowstone Area present an opportunity to manage bison similar to other wildlife in some areas outside national parks and refuges. Tourism and recreational activities have a large and growing influence on the economy, and the vast majority of visitors and hunters to the area enjoy seeing bison move across the greater landscape in large numbers. In fact, the Yellowstone area provides a unique attraction—the opportunity to see bighorn sheep, bison, deer, elk, pronghorn, and large predators such as bears and wolves in close proximity on the landscape and within view from paved roadways. Furthermore, American Indian tribes have become more engaged

with the management of bison in the area, sharing their traditional knowledge, restoring bison to tribal lands, and renewing subsistence hunts to improve their cultural, nutritional, and social well-being. As a result, efforts to respect the presence of bison as wildlife on the larger landscape will be welcomed by native peoples and the majority of the local, national, and international public. This vision is attainable because decades of management have shown that there are relatively few conflicts between bison, residents, and the millions of visitors each year in Grand Teton and Yellowstone national parks. Acceptance of bison as wildlife in some areas outside parks and refuges will enhance bison restoration, enrich visitor experience, improve public and treaty hunting opportunities, and boost local and state economies. The time is right to recover bison, the iconic symbol of the power and strength in our nation, as wildlife in appropriate locations of the Greater Yellowstone Area and elsewhere.

NPS Photo

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The iconic bison deserves our best efforts to assure its place on the American landscape. I am grateful to the authors for clearly articulating the issues we face as we collectively determine the future of these animals. The authors have given us a chance to advance our discussions based on a common understanding of the science, culture, and politics surrounding bison.

— Daniel N. Wenk, Superintendent of Yellowstone National Park

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