Status of the Yellowstone Bison Population

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Report YCR-2023-03, Yellowstone Center for Resources

November 3, 2023

Bison running in the Lamar Valley of Yellowstone National Park.
Photograph by Neal Herbert, National Park Service, 2018.

This report is dedicated to Dr. Mary Meagher, a pioneer in wildlife biology, who immeasurably increased our knowledge of Yellowstone bison and changes occurring in the park over time.

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Citation: White, P. J. 2023. The status of Yellowstone bison. Report YCR-2023-03, Yellowstone Center for Resources, Yellowstone National Park, Mammoth, Wyoming.

Abbreviations and Acronyms

Abbreviation	Full Term/Description
APHIS	Animal and Plant Health Inspection Service
BCTP	Bison Conservation Transfer Program (quarantine)
DNA	deoxyribonucleic acid
et al.	and others
et seq.	and what follows
°F	degrees Fahrenheit
GYE	Greater Yellowstone Ecosystem
IBMP	Interagency Bison Management Plan
ITBC	InterTribal Buffalo Council
IUCN	International Union for the Conservation of Nature and Natural Resources
MCA	Montana Code Annotated
MDOL	Montana Department of Livestock
MFWP	Montana Fish, Wildlife and Parks
NPS	National Park Service
U.S.	United States
USC	United States Code
USDA	U.S. Department of Agriculture
USDI	U.S. Department of the Interior
USFS	U.S. Forest Service
USFWS	U.S. Fish and Wildlife Service
YNP	Yellowstone National Park

Introduction

Bison standing near Soda Butte Creek in Yellowstone National Park.
Photograph by Jim Peaco, National Park Service, 2005.

Congress established Yellowstone National Park (Yellowstone, YNP, or the park) in 1872 to "provide for the preservation ... of all timber, mineral deposits, natural curiosities, or wonders within said park, and their retention in their natural condition" … "for the benefit and enjoyment of the people." Congress placed the park "under the exclusive control of the Secretary of the Interior" and declared the Secretary "shall provide against the wanton destruction of the fish and game found within said park, and against their capture or destruction for the purposes of merchandise or profit" (16 United States Code [USC 21] *et seq*., 17 Stat. 32). Yellowstone is significant because it was the world's first national park and it preserves geothermal and scenic wonders, abundant and diverse wildlife, and an 11,000-year continuum of human history. As a result, the park provides visitors with a wide range of opportunities to experience wildness, be inspired by its wonders, and learn from its history.

Yellowstone was established, in part, to protect a remnant herd of bison that survived the massive slaughter of wildlife in the region during the 1870s and 1880s. Over the next 150 years, park managers worked to restore a viable population of wild, free-ranging bison, with 4,940 counted in summer 2023. However, the restoration of bison to portions of the ecosystem outside the park was precluded by concerns about the transmission of the disease brucellosis from bison to cattle. Cattle infected bison and elk in the park with brucellosis early in the 1900s. Brucellosis can induce abortions in ungulates (hoofed mammals) and be transmitted among bison, cattle, and elk if they contact infectious birthing tissues or a newborn calf. Transmissions to cattle can have economic consequences on the ability of producers to export cattle to other states or nations.

During 2014, 2015, and 2018, the United States (U.S.) Fish and Wildlife Service (USFWS) received three petitions requesting Yellowstone bison be listed as threatened or endangered under the Endangered Species Act of 1973, as amended (16 USC 1531 *et. seq*.). All the petitions identified Yellowstone bison as a distinct population segment of plains bison, while two of them identified the central and northern breeding herds of Yellowstone bison as distinct segments. A distinct population segment is a discrete and significant population segment of a species that can be analyzed as if it were a species under the Endangered Species Act. In 2022, the USFWS found the petitioners presented credible information the substantial reduction in historic range and lack of access to existing winter range due to culling, hunting, hazing, and quarantine may potentially threaten Yellowstone bison.[1] The petitioners also presented information suggesting overutilization, disease, and loss of genetic diversity due to culling may be threats. The USFWS decided to complete a finding on the petitions to list Yellowstone bison by the end of 2026.

The USFWS conducts species status assessments to provide biological information, analyses, and predictions to support decisions pursuant to the Endangered Species Act. An assessment begins with the compilation of information on the species in the wild, including natural history and ecological needs, and then describes the current condition of the species, including its current abundance and distribution, demographics and conditions of habitats, and genetic diversity. The assessment addresses the conservation biology principles of resiliency, redundancy, and representation, and forecasts the viability of the species over time given various scenarios of future environmental conditions and conservation efforts. This report provides information relevant to the status review of Yellowstone bison by the USFWS, including whether these bison constitute a distinct population segment, factors used to evaluate whether a species is threatened or endangered, conservation biology principles of resiliency, redundancy, and representation, and other overarching principles for the conservation and retention of genetic diversity in bison.

Chapter 1 provides general information on the behavior and traits of North American bison, while Chapter 2 outlines the management history and population trends of Yellowstone bison. Chapters 3 through 5 provide information on the demography (reproduction, survival), seasonal movements, and nutritional condition of Yellowstone bison. Chapter 6 focuses on predation and the potential for competition among bison and other ungulates for food and habitat. Chapter 7 discusses the adaptive capabilities, ecological role, and genetics of Yellowstone bison, while Chapter 8 focuses on their cultural importance. Chapter 9 describes current management, while Chapter 10 addresses risks and threats to the sustainability of the Yellowstone bison population.

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[1] Throughout this document, the word 'cull' refers to bison captured for possible inclusion in quarantine, shipment to slaughter, and shooting on-site. The word 'harvest' refers to bison shot during hunts outside the park by members of tribes pursuant to long-standing treaties with the federal government and public hunters with permits from Montana Fish, Wildlife and Parks. The word 'removals' refers to the combined numbers of harvests and culls.

Chapter 1—Natural History

A bison with cowbirds on its back in Yellowstone National Park.
Photograph by Jim Peaco, National Park Service, 2009.

This chapter provides general information on the taxonomy, distribution, physical traits, behavior, ecology, and life history of bison in North America. Unless otherwise denoted, this information is from a mammalian species report on bison (Meagher 1986) and a chapter in the book *Ecology, Evolution, and Behaviour of Wild Cattle* (Plumb et al. 2014), including the references cited therein. Specific information on Yellowstone bison is provided in the rest of the chapters of this report.

Taxonomy

The scientific name of bison, which are commonly and interchangeably called buffalo, is *Bison bison* (genus, species). Bison belong to the mammalian order *Cetartiodactyla*, which include descendants of an even-toed ungulate ancestor, the suborder *Ruminantia*, which has ruminant digestion, and the family *Bovidae*, which includes the Asian water buffalo (genus *Bubalus*), African buffalo (*Syncerus*), North American bison (*Bison*), and domestic cattle and their wild relatives (*Bos*). The bison and cattle lineages diverged about 2.5 to 3.7 million years ago, with bison reaching North America about 135,000 to 195,000 years ago (Stroupe et al. 2022). Some taxonomists believe bison and cattle should be combined into one genus, *Bos*, since they are genetically similar and can hybridize (Douglas et al. 2011, Stroupe et al. 2022). However, the American Bison Specialist Group of the International Union for the Conservation of Nature and Natural Resources (IUCN) has retained the genus, *Bison*, in its species status and conservation plan (Boyd et al. 2010b).

Most taxonomists recognize two subspecies of North American bison: plains bison (*Bison bison bison*) south of central Canada and wood bison (*Bison bison athabascae*) to the north in Canada and west in Alaska. The subspecies apparently diverged about 5,000 years ago (Boyd et al. 2010b). Biologists originally distinguished these subspecies based on geography and morphological and pelage characteristics, but humans relocated both subspecies to areas within the others historic range; thereby confounding their distributions and resulting in substantial hybridization. Some geneticists maintain populations of plains and wood bison have similar mitochondrial gene sequences and, therefore, are not subspecies (Douglas et al. 2011, Forgacs et al. 2016). However, most taxonomists still recognize these subspecies, as do the American Bison Specialist Group and Canada's National Wood Bison Recovery Team (Boyd et al. 2010b).

Distribution

Tens of millions of bison once ranged across western North America. Historically, plains bison lived from southern Canada to northern Mexico and throughout most of the present-day U.S., except for New England and a few southern and western areas (Potter et al. 2010). However, plains bison were extirpated in the eastern portion of the U.S. by the late 1700s, the midwestern portion by the 1840s, and nearly west of the Mississippi River in the late 1800s. There were only a few hundred plains bison left by the mid-1880s and, today, unfenced, wild plains bison live on less than 1% of their historic range in five states, including Alaska (Wrangell-St. Elias), Arizona (Grand Canyon), Montana (Yellowstone), Utah (Book Cliffs, Henry Mountains), and Wyoming (Grand Teton/National Elk Refuge; Yellowstone); three provinces, including Alberta (Elk Island), British Columbia (Pink Mountain), and Saskatchewan (Prince Albert); and the state of Chihuahua in Mexico (Freese et al. 2007, Sanderson et al. 2008, Gates and Ellison 2010).

Historically, wood bison lived in Alaska, southward through the Yukon and Northwest Territories, and eastward through British Columbia, Alberta, and Saskatchewan. They were not as abundant as plains bison due to more limited habitat, with a rough estimate of about 168,000 bison circa 1800 (Potter et al. 2010). By the late 1800s, numbers of wood bison decreased to about 250 to 300 in the area encompassed by present-day Wood Buffalo National Park in Alberta and the Northwest Territories (Gates and Ellison 2010). The number of wood bison subsequently increased to about 1,500 to 2,000 before managers released about 6,600 plains bison into areas with wood bison during 1922 to 1928 (Douglas et al. 2011). Today, wild wood bison live in six provinces in Canada, including Alberta (Wood Buffalo), British Columbia (Hay-Zama and Etthithun Lake), Manitoba (Chitek Lake), Northwest Territories (Mackenzie, Nahanni, Slave River Lowlands), Saskatchewan (Grasslands), and the Yukon (Aishihik).

Most habitats in the historic range of bison are no longer available because people converted them to agricultural production (farming, ranching) or settlements. In addition, there are concerns about bison moving outside parks and preserves where they could outcompete livestock, eat agricultural crops, transmit diseases such as brucellosis to livestock (see Chapters 2 and 9), and cause human safety and property damage concerns, such as vehicle strikes and broken fences. As a result, the recovery of plains bison is constrained by their inability to access lower-elevation grasslands and the distribution of wood bison is limited by the extent of available wet meadows.

Genetics

Like humans, bison contain genetic material called deoxyribonucleic acid (DNA) that codes for their physical traits and metabolic processes. Each cell in their body contains a single copy of DNA in its nucleus, arranged in paired chromosomes with one from the mother and another from the father. Geneticists use tracts of repetitive DNA (called microsatellites) or variable areas of DNA (called single nucleotide polymorphisms or SNPs [snips]) to determine ancestry and study genetic diversity, which provides the potential for adaptation to changing conditions (Stroupe et al. 2022). In addition, organelles called mitochondria in cells have their own DNA which is passed down through maternal lineages and reflects mutations that allow the tracking of genetic information over long periods of time. Geneticists often study neutral genetic markers, which are variants of gene sequences believed to convey no fitness advantage to the animals (Halbert and Derr 2007, 2008).

During the late 1800s, bison in North America experienced a rapid and severe population 'bottleneck' due to a 99% reduction in abundance from perhaps 30 million to less than 1,000 bison, primarily due to indiscriminate killing for hides (Potter et al. 2010, Stroupe et al. 2022). By 1900, colonists had extirpated wild plains bison from Canada and only a few dozen remained in YNP in the U.S. About 250 to 300 wild wood bison remained in Wood Buffalo National Park (Hedrick 2009, Potter et al. 2010, Douglas et al. 2011). Between 1873 and 1889, livestock ranchers preserved other bison herds by catching wild calves and placing them in private herds, including the McKay and Alloway herd in Saskatchewan, Jones herd in Kansas, Walking Coyote herd in Montana, Goodnight herd in Texas, and Dupree herd in South Dakota. Managers used bison from these private herds to augment the remnant wild populations in Yellowstone and Wood Buffalo national parks (Halbert and Derr 2007, Stroupe et al. 2022).

There are concerns about the genetic integrity of bison due to this bottleneck and the resulting isolated and small remnant populations of wild bison. Reductions in genetic diversity can decrease individual reproductive success, increase mortality, and diminish the potential for animals within a population to adapt to changing conditions over time (Boyd et al. 2010a). Genetic diversity can be reduced through population bottlenecks by founder effects (a small number of individuals from a larger population become isolated), genetic drift (change in the frequency of a gene variant [allele] by chance), and inbreeding (mating of close relatives); all which bison have experienced over the last 150 years (Boyd et al. 2010a). Other genetic concerns with bison include introgression of cattle genes, domestication through husbandry and unnatural selection, and the loss of genetic lineages, including extensive hybridization between plains bison and wood bison (Hedrick 2009, Boyd et al. 2010a; see Chapters 7 and 10).

Today, all plains bison are descendants from less than 100 bison in five private herds and the indigenous bison in YNP that survived near extinction in the late 1800s (Halbert and Derr 2007). Thus, remnant and reconstituted populations were derived from very few animals (founders) from the larger original population (gene pool), which certainly resulted in the loss of genetic information and the potential for genetic drift and inbreeding. In addition, the crossbreeding and transfer of genetic material from cattle to bison (called introgression) occurred on four of the five private ranches during the late 1800s and early 1900s. Bison and cattle do not naturally breed but human-induced crosses of male bison and female cattle in captivity can produce some fertile offspring; though there are negative effects like low fertility in the first generation (Halbert and Derr 2007, Boyd et al. 2010a,b). Further crossing of these hybrids with animals genetically like the parents (called backcrossing) are fertile and look like pure bison (Douglas et al. 2011). The Walking Coyote herd was not cross bred but part of it was sold to Pablo and Allard who purchased bison from other herds with hybridized bison. As a result, recent complete sequencing of all genetic information (called a genome) in nuclear samples from bison and cattle found cattle introgression in all North American populations more than a century after hybridization (Stroupe et al. 2022). In addition, cattle gene introgression into mitochondrial bison genomes is widespread across North America (Ward et al. 1999, Freese et al. 2007, Halbert and Derr 2007).

Despite the severe bottleneck late in the nineteenth century, levels of genetic diversity remain relatively high in bison, perhaps due to the widespread distribution of bison and gene flow among populations before the bottleneck. The remnant herds left after the bottleneck spanned much of the pre-existing bison range across western North America and, as a result, retained much of the genetic diversity (Wilson and Strobeck 1999, Halbert and Derr 2008, Hedrick 2009, Boyd et al. 2010a, Douglas et al. 2011). The bottleneck was relatively short in duration and followed by rapid population growth, which provided a limited time for genetic drift and inbreeding to occur (Boyd et al. 2010a). After managers protected bison from poaching, their numbers doubled between the late 1880s and early 1900s and they were considered safe from extinction by 1909 (Potter et al. 2010). There were about 30,000 plains bison by 1970, with about equal numbers in public and private herds, and about 10,880 wood bison in 11 conservation herds by 2008 (Potter et al. 2010). However, there was substantial mixing of genetic lineages as managers relocated bison to augment remnant populations or establish new populations (Stroupe et al. 2022). As mentioned previously, managers released about 6,600 plains bison into Wood Buffalo National Park during 1925 to 1928, which subsequently hybridized with the native wood bison. Managers then relocated some of these hybrids to Mackenzie Bison Sanctuary and Elk Island National Park during 1963 and 1965 to establish new herds (Hedrick 2009, Boyd et al. 2010a).

Bison from YNP, the National Bison Range, and Fort Niobrara National Wildlife Refuge in Nebraska have genetically similar mitochondrial DNA haplotypes, which suggests they are descendants from a common ancestor (called a clade; Douglas et al. 2011). In addition, a recent analysis of nuclear genetic differences between ancestral and contemporary bison detected five distinct populations: historic plains bison; Yellowstone bison; plains bison from Wind Cave National Park; wood bison from Elk Island National Park, and wood bison from the Mackenzie Bison Sanctuary (Stroupe et al. 2022). Most bison herds are subject to artificial selection due to confinement in fenced areas, protection from predators, removal of large bulls for ease of handling, vaccination and veterinary care, and other factors that contribute to domestication (Freese et al. 2007, Hedrick 2009, Boyd et al. 2010a). Thus, it is important that conservation herds, to the extent feasible, promote wildness and natural selection (also known as survival of the fittest), such as mate competition and predation, to retain adaptive capabilities (White and Wallen 2012; see Chapter 7).

Physical Characteristics

Bison are the largest terrestrial mammal in North America, with plains bison generally being smaller than wood bison. Bison stand about 5 to 6 feet tall (1.5 to 1.8 meters) at the shoulder and range from 7 to 11 feet long (2.1 to 3.4 meters; nose to tail). Adult males, called bulls, reach adult size by about six years of age and can weigh 2,200 pounds (1,000 kilograms) or more. Female bison, referred to as cows, reach adult size by about four years of age and can weigh 1,100 pounds (500 kilograms) or more. Calves weigh about 30 to 70 pounds (14 to 32 kilograms) at birth, 300 to 400 pounds (135 and 180 kilograms) after 8 to 9 months, and 500 to 700 pounds (225 and 315 kilograms) by 20 to 22 months of age. Males are larger than females after about 4 months.

Adult bison have thick brown fur that lightens somewhat in summer. The fur over the head, neck, and front quarters is long (about 6 inches; 15 centimeters) and thick with coarse guard hairs and wooly underfur that provides good insulation and makes them quite resistant to cold temperatures. Fur on the flanks and hindquarters is about 1 inch (3 centimeters) thick. Newborn calves have reddish tan fur that gradually darkens to brownish black between 3 and 4 months of age. Bison have large forequarters, smaller hindquarters, relatively short legs, and large rounded hooves made of a hard protein material called keratin that enable them to run up to 35 miles per hour (55 kilometers per hour) in spurts and more slowly for long distances. They are agile, strong swimmers, and can jump over objects about 5 feet (1.5 meters) tall. Bison have massive heads, thick short necks, and a ‘hump’ of large, muscular shoulders that enable them to sweep away deep snow using a sideways motion of their head to expose forage underneath. Both sexes have permanent horns with a bone-like core and black cover of modified hair protein that emerge laterally from the sides of the head and curve upwards and inwards over their heads.

Bison have teeth with highly crowned premolars and molars and a zigzag enamel pattern to break up plant materials for extracting energy and protein. They lack upper incisors and use their tongue to pull vegetation into their mouth where lower incisors push it against a dental pad on the upper part of their mouth to crop (cut) it. Teeth wear with age, so older bison become less efficient at obtaining nutrients and accumulating the fat and protein reserves needed to survive (Garrott et al. 2002, 2003). Bison have large eyes on the sides of their head that provide vision in a wide arc to detect movements of predators and other animals. They have good hearing across a range like humans and an acute sense of smell. Bison use an array of vocalizations including grunts, snorts, coughs, and bellows by males during the breeding season, snorts by females looking for calves, and bawling by calves separated from their mothers.

Social Organization

Bison are gregarious and form fluid, dynamic groups (called herds) of variable size throughout the year that form, merge, and break-up as individuals interchange frequently while they feed, rest, and move across the landscape (Geremia et al. 2015b). The basic social organization is matriarchal, with mixed groups primarily consisting of adult females, calves, and immature bison of both sexes. Mature bulls are solitary or in small bachelor groups for most of the year, which is called sexual segregation. Group size and composition (sex, age) varies among areas and seasons due to the breeding season, birthing events and calf protection, seasonal changes in food distribution and quality, snow conditions and energetic costs, and predation risk and competition. Older, larger females tend to be dominant over younger females during social interactions and displace them from chosen foraging sites. Dominance is related to age, weight (mass), body condition (amounts of fat and protein), and experience. Dominant females tend to give birth earlier and have calves that are heavier at weaning. These calves are usually dominant over other calves born later. Mature males are dominant over females.

Bison are polygynous with mature males 5 years and older joining female groups and attempting to breed multiple females from late June through September (called the rut). Younger bulls are capable of breeding but are generally excluded by larger, older males. Breeding is somewhat synchronous, with most copulations occurring during a 2- to 4-week period in August. Males guard or 'tend' individual females to keep other males away during estrus and until females accept copulations. Competition between males is intense as they engage in threat displays, such as bellowing and huffing or pawing the ground, or violent fights to establish dominance. Competitors often make short charges at each other, clashing and shoving with their heads in fierce pushing matches, with occasional hooks, thrusts, or swipes with their horns. These fights can be dangerous and result in injuries or death. Thus, males typically only breed from ages 6 to 12 years old, with peak reproductive success between ages 7 and 9 and little reproductive effort after age 12 (Berger and Cunningham 1994, Wilson et al. 2002). Females can breed throughout their adult life, provided they obtain sufficient nutrition to replenish their body condition each summer; however, fecundity is highest between 3 and 13 years old (see Chapters 3 and 5). The variance in reproductive success among individual bison is higher in males than females with as few as 10% of the males conducting 50% of the breeding each year, while about 50% to 70% of adult females breed each year (Berger and Cunningham 1994, Wilson et al. 2002). After the breeding season, mature males segregate themselves and females with their young move to autumn and winter ranges from October through March. Young bison tend to remain in groups with their mothers for two to three years and move in maternal family units.

Life History

Populations are aggregations of animals from the same species that interact. The number of animals in a population depends on the number added through births and movements into the population (immigration) minus the number removed through deaths and movements out of the population (dispersal or emigration; Caughley and Sinclair 1994). Whether a population grows depends on whether animals have sufficient resources, such as food, to survive and reproduce; although disease, predation, and severe weather can significantly depress growth in some circumstances (see Chapters 3 and 5). Populations of bison with abundant resources tend to grow quickly due to high reproduction and survival. Numbers of bison in a population can increase by as much as 20% in one year when forage and other conditions are optimal (Berger and Cunningham 1994, Gogan et al. 2010). However, population growth slows if the number of animals increases so there are fewer resources for everyone which can cause decreased nutrition, body condition, reproduction, and survival (Eberhardt 2002). This concept is referred to as density dependence.

Female bison begin breeding at 2 to 4 years old and continue to breed every 1 to 3 years thereafter depending on their body condition. Few yearlings breed and pregnancy rates vary in 2- and 3-year-olds depending on their body condition. Pregnancy rates are usually high (90%) in prime-aged females 4 to 13 years of age until their teeth deteriorate from wear (Berger and Cunningham 1994). Bison older than 16 years generally can no longer process forage efficiently due to worn teeth and, as a result, pregnancy rates may decrease quickly due to lower body condition which makes it less likely they become pregnant (Cook et al. 2004a, 2016). Other factors that can lower pregnancy rates include poor forage conditions and diseases such as brucellosis (Geremia et al. 2015c).

The estrus cycle in bison lasts about 3 weeks in late July or August when females become receptive to breeding for about 1 to 2 days (9 to 28 hours), after which they may cycle and ovulate again. Females sometimes segregate themselves prior to calving, but many give birth within the herd. Females usually give birth to a single calf (twins are rare) during late March through early June after a gestation period of about 9.5 months. There is synchrony in calving among females, with about 80% of the births occurring during a 1- to 2-month period. This strategy coincides lactation with the growth of nutritious forage and reduces (or dilutes) predation risk on each individual calf because they are one of many (Rutberg 1984). Birth synchrony in bison is more common in areas where wolf predation on calves is high (Gates and Larter 1990). Newborn calves can stand and nurse within 30 minutes of birth. They begin grazing and drinking water within one week but continue to nurse for 7 to 8 months, some longer.

Adult female bison can live more than 20 years; males about 15 years. Adult males have higher mortality (lower survival) than adult females due to their dangerous and exacting competitions for mates during the rut. The survival of prime-aged female ungulates is generally greater than 90% in areas with good forage and few human harvests or predators (Gaillard et al. 1998, 2000; Eberhardt 2002). Snowpack conditions seem to have little effect on prime-aged females except in the most extreme circumstances. However, survival decreases rapidly in older animals 12 to 15 or more years of age as tooth wear reduces foraging efficiency and snowpack conditions worsen (Garrott et al. 2003). The survival of calves is more variable among years (40% to 90%) because severe winters with deep or hard snowpack can kill many of them through malnutrition and starvation and increase vulnerability to predation (Gross et al. 2010). Mature males expend tremendous amounts of energy and eat less during the rut. Thus, they enter winter with relatively lower fat reserves than females, which could make them more susceptible to starvation during severe winters (Cook et al. 2004a, 2016).

Movements

Bison are thought to be more active during the day (diurnal). They are quite mobile and tend not to remain in the same area for long periods. Factors reported to influence bison movements include the availability of water, bison density, biting insects, breeding season, human disturbance, learned behaviors, predators, seasonal vegetation changes, and snow accumulation and melt. Bison spend a large portion of each day foraging, typically moving slowly across the landscape in loose, dispersed groups as they feed (Plumb and Dodd 1993). Minimum group sizes during 1970 to 1997 in YNP occurred in early spring while maximum group sizes occurred during the breeding season in late July and August (Taper et al.

2000). Feeding bouts are interspersed with rests to digest forage. In some areas, bison return to previously grazed areas every couple of weeks in a somewhat cyclical type of pattern (Geremia et al. 2022). Bison can travel 20 miles (32 kilometers) or more in a single day when moving to a distant foraging area or different range. When these longer movements are made through snow, they often travel in single file to reduce energy expenditures by trailing bison (Meagher 1973).

Bison in several free-ranging populations make seasonal round-trip movements (migrations) between summer and winter ranges, some of which are quite long (90 to 150 miles; 150 to 240 kilometers; see Chapter 4). Migrants often gain access to more abundant and nutritious food or safer areas with fewer predators to raise young. Many ungulates migrate to higher elevations each spring to forage on nutritious plant growth through the summer but return to lower elevations each autumn to avoid deep snowpack that limits food availability and increases energetic costs and predation risk during winter (Fryxell 1991). However, migrants also face additional risks compared to non-migratory residents, such as traversing dangerous environmental features like swollen rivers with fast currents during spring snow melt, and an increased risk of predation while traveling between seasonal areas of use (Fryxell et al. 1988).

Migratory behavior likely is transmitted across generations by calves learning from their mothers and social groups (Bracis and Mueller 2017, Jesmer et al. 2018, Merkle et al. 2019). Over many generations, bison occupying diverse landscapes may develop many different migratory strategies to cope with seasonal changes in the resources required to survive and reproduce (Parker et al. 2009, Lowrey et al. 2020, 2021). As a result, population substructure exists in some bison populations, with different segments of the population traditionally using different portions of the landscape for various activities, such as breeding and calving, or migrating to different seasonal ranges.

Adult male bison often travel considerable distances and may colonize unoccupied areas, especially when bison density increases to relatively high levels. Many of these males return to their previous range for the rut and, thereafter, may be followed by mixed-sex groups into the expanded range (Meager 1989b, Gates and Larter 1990, Gates et al. 2005, Gogan et al. 2010). Bison in the Northwest Territories moved to previously unoccupied habitat as density increased and population growth slowed. After this range expansion, population growth increased because of more available forage and other resources (Gates and Larter 1990, Larter et al. 2000).

Habitat Use and Diet

Obtaining adequate energy, protein, and nutrients is essential for the survival and reproduction of bison. Nutrition strongly influences growth and development, pregnancy and lactation, disease resistance, and survival (see Chapter 5). Bison were most abundant on the grasslands of the Great Plains and prairies in western North America. However, they also lived year-round in arid desert grasslands, mountains up to about 7,100 feet [2,165 meters] elevation or higher (Cannon et al. 2020), and northern forests and flood plains in Alaska and Canada. Bison are primarily grazers in all seasons and consistently select grasses and grass-like plants, such as sedges and rushes, which are collectively called graminoids. Grasses dominate diets in grassland, prairie, and shrub-steppe habitats, while sedges are prominent dietary components for bison living in mountains and northern forests and meadows. Reports suggest forbs (broad-leaf, non-woody plants) and browse (parts of woody plants) generally comprise a small portion of bison diets. In montane (mountain) and temperate environments, the depth and hardness of snowpack during winter limits access to grasses and determines how much energy bison use to displace snow during foraging and travel. Snow density (water content) and crusting or ice layers can substantially reduce forage availability and increase energetic costs (Messer et al. 2009).

Bison have a four-chambered stomach (including a rumen) that contains microorganisms, such as bacteria and protozoa, to break down and ferment plant materials and produce volatile fatty acids that provide them with energy (Robbins 1993, Van Soest 1994). Bison obtain energy through the fermentation of dietary carbohydrates and protein through the digestion of rumen microbes (Van Soest 1994). Most plants eaten by bison in temperate climates are dormant and not growing during the winter season. The digestibility and energy and protein content of these dead and dried grasses is low and results in a longer fermentation time in the rumen to extract energy, protein, and nutrients (Robbins 1993, Van Soest 1994). Bison regurgitate and re-chew their food (cud) to break ingested plants into smaller fragments before re-swallowing so more nutrients can be absorbed (Robbins 1993, Van Soest 1994). They can also recycle urea to the rumen where microbes convert it into protein for digestion when forage intake is insufficient to meet demands for body maintenance during winter (DelGuidice et al. 2001, Parker et al. 2009). As a large ruminant, bison are capable of digesting and subsisting on lower quality forage than smaller ruminants, such as deer and pronghorn (Robbins 1993, Van Soest 1994). Having a larger rumen means bison do not have to be as selective for high quality forage as smaller ruminants (Caughley and Sinclair 1994).

Predation and Competition

Potential predators of bison include wolves and grizzly bears, though bison are formidable opponents. Wolves kill bison by coursing through areas and searching for vulnerable individuals to attack, primarily debilitated, young, or old animals (Mech et al. 2015). Wolves can subsist by almost exclusively killing bison, which comprised about two-thirds of their diets in Wood Buffalo National Park in northern Alberta, with wolves tending to attack individual wood bison in groups with calves (Carbyn and Trottier 1987). Bison calves comprised more than 80% of the bison killed by wolves in the Northwest Territories (Gates and Larter 1990). Bears opportunistically kill newborn calves in spring and occasionally kill adult bison; see Chapter 6). Bison females often advance slowly or make short quick charges to defend calves from single predators. Groups of bison may coalesce in front of or around calves to protect them from multiple predators, such as a pack of wolves.

Competition occurs when individuals use a resource, such as consuming forage, or exclude other individuals from accessing the resource and, in turn, decrease the ability of the other individuals to survive and reproduce (Begon et al. 2005). There is the potential for competition among bison for forage or other resources as their numbers and density increase and resources become more limited, which is called intraspecific competition. There also can be competition with other ungulate species that have similar diets, ranges, and timing of the use of resources, which is called interspecific competition (Caughley and Sinclair 1994). Interspecific competition is usually reduced through differences in habitat and forage selection. As large ruminants, bison are often the least selective of forage plants and ingest the lowest quality diets. Several studies of bison found their selection of forages during grazing complements the diet selection of other ungulates, such as pronghorn.

Diseases

The are several diseases of health concern for bison, including anaplasmosis, anthrax, bluetongue, bovine spongiform encephalopathy, bovine viral diarrhea, brucellosis, foot and mouth disease, hemorrhagic septicemia, malignant catarrhal fever, paratuberculosis (Johne's disease), and tuberculosis (Aune et al. 2010, Adams and Dood 2011, Sweeney et al. 2014). The risk of these diseases has limited the recovery of bison due to concerns about their transmission to livestock. Anaplasmosis is a rickettsia bacteria transmitted by blood-sucking insects, such as ticks, that infect red blood cells and cause anemia (low red blood cell count), malnutrition, muscle wasting, and weakness (Aune et al. 2010). Anthrax is spread by ingesting or inhaling endospores with the bacterium *Bacillus anthracis* from alkaline calcium-rich soils and has infected populations of bison in the Northwest Territories and the Yellowstone area. Bluetongue is a viral disease transmitted by midges that causes fever, sore mouth (stomatitis), lameness, and reproductive failure, but it is not widely reported in bison. Bovine spongiform encephalopathy ('mad cow disease') is caused by misfolded proteins called prions and transmitted by direct animal-to-animal contact or indirectly through contact with infectious particles persisting in the environment. The disease causes progressive weight loss and is fatal. Bison are susceptible to this disease, but no wild bison have exhibited signs (Aune et al. 2010).

Bovine viral diarrhea is transmitted by direct animal-to-animal contact. It is widespread in bison populations and causes pneumonia and abortions. Brucellosis is a bacterial disease transmitted by contact with infectious reproductive materials that causes abortions. It is endemic in the Yellowstone area and Wood Buffalo National Park (Aune et al. 2010). Foot and mouth disease is a viral disease, transmitted by direct contact, inhalation, or ingestion, that causes fever, sore mouth, and foot lesions and lameness. Hemorrhagic septicemia is a bacterial disease, transmitted by ingestion or inhalation, that causes hemorrhaging, difficulties breathing, and death. Malignant catarrhal fever is a viral disease, transmitted by direct contact with domestic sheep, which causes lethal infections in bison. It has caused substantial mortality in some fenced bison populations (Aune et al. 2010). Paratuberculosis (Johne's disease) is a bacterial disease, transmitted by contact or ingestion of bacteria, which causes diarrhea, weight loss, and death. It is not present in wild bison but occurs in some commercial operations (Aune et al. 2010).

Tuberculosis is a bacterial disease transmitted by inhalation and ingestion that causes lower pregnancy rates (due to poorer nutrition) and fetal losses. Plains bison were infected with tuberculosis from cattle and relocated bison spread it to wood bison in the Wood Buffalo area during 1925 to 1928, where it contributed to a substantial decrease in abundance combined with brucellosis. Adult bison infected with both diseases had lower survival (75%) and calf survival was only 47% (Larter et al. 2000, Joly and Messier 2004). About one-half of wood bison are infected with brucellosis and tuberculosis, with prevalence rates of 31% and 49%, respectively (Aune et al. 2010).

Adaptive Behaviors and Capabilities

Historically, bison in temperate, montane climates evolved patterns of movement and habitat use to exploit predictable seasonal changes, moving to higher elevations with growing nutritious forage during the warm summer and returning to lower elevations with less snowpack during the cold winter. The behavior, morphology, and physiology of bison enhance their survival by reducing the energetic costs of maintaining their body temperatures (thermoregulation) and moving through snow (Telfer and Kelsall 1984, Robbins 1993). Adult bison also have large reserves of fat and muscle to sustain them through the long period of undernutrition during winter (DelGuidice et al. 2001). However, there is considerable random variation in weather among years, and severe winters can still influence their nutrition and body condition (DelGuidice et al. 1994). Calves have a much smaller body size with shorter legs and limited body reserves that makes them more susceptible to starvation during winter (DelGuidice et al. 2001).

Bison are ecosystem engineers that modify habitats and create heterogeneity across the landscape by changing vegetation phenology and composition through grazing, recycling and redistributing nutrients and seeds, trampling vegetation and creating wallows that favor early successional species and, through these processes, creating a diversity of habitats for numerous species, including birds, insects, plants, and small mammals (Knapp et al. 1999, Truett et al. 2001). Bison also convert grass to meat for predators, scavengers, and decomposers. As a result, they can shape the way energy, fire, nutrients, other ungulates, predators, scavengers, small mammals, soil, and water move across the landscape (Knapp et al. 1999, Sanderson et al. 2008).

Today, there are roughly 470,000 bison in North America, but most are managed in captivity and not tolerated as free-ranging wildlife on public and private lands (Hedrick 2009, Boyd et al. 2010a). Only one population of plains bison (Yellowstone) and three populations of wood bison (Greater Wood Buffalo National Park, Mackenzie Bison Sanctuary, and the Aishihik bison herd in Yukon's Nisling River watershed) are considered ecologically restored, with viable populations subject to natural selection (Gates and Ellison 2010, Gates et al. 2010). The number of plains bison in conservation herds has remained around 20,000 since the 1930s and there are about 11,000 wood bison in conservation herds (Freese et al. 2007, Boyd et al. 2010a, Potter et al. 2010). Most other conservation populations are small (less than 500 animals), isolated with only human assisted dispersal (gene flow) events, and not subject to the forces of natural selection. Thus, biologists have not restored the role of bison as a foundation species and ecosystem engineers (Freese et al. 2007, Sanderson et al. 2008).

Current Situation

More than 10,000 plains bison live in conservation herds managed by the U.S. Department of the Interior (USDI), including on Bureau of Land Management, National Park Service (NPS), and USFWS units (Sweeney et al. 2014). The NPS supports about three-quarters of these bison, but about one-half are in the Yellowstone and Grand Teton national park populations that are chronically infected by brucellosis. Bison in Grand Canyon, Grand Teton, Wrangell-St. Elias, and Yellowstone are unconfined and wide ranging. However, bison in Badlands, Chickasaw, Tallgrass Prairie, Theodore Roosevelt, and Wind Cave are fenced, and herd size is periodically managed through capture operations and culling for relocation to American Indian tribes[2], other states, and conservation groups. In addition, the Bureau of Land Management supports two free-ranging herds in Utah in collaboration with the state's Division of Wildlife Resources (Sweeney et al. 2014). There are public hunts for wild bison in Alaska, Arizona, Montana, Utah, and Wyoming, as well as Alberta, British Columbia, and Saskatchewan. Tribal subsistence hunting occurs in Montana, the Northwest Territories, and the Yukon (see Chapter 8).

The USFWS supports a metapopulation of spatially separated, relatively small herds of bison on their refuge system (Fort Niobrara, Neal Smith, Rocky Mountain Arsenal, Sullys Hill, and Wichita Mountains), while the National Elk Refuge co-manages the Jackson herd with Grand Teton National Park. Bison on the refuges are fenced and, as a result, herd size is managed by periodic capture operations and culling based on genetic criteria to maintain sustainable populations (Sweeney et al. 2014). Managers are developing a plan to occasionally move bison among herds to offset the effects of isolation, such as inbreeding and genetic drift. About 95% of bison removed from these herds are provided to American Indian tribes, with the remainder given to states and non-governmental organizations to augment or establish bison herds (Sweeney et al. 2014). The National Bison Range, which used to be managed by the USFWS, is now managed by the Confederated Salish and Kootenai tribes of the Flathead Nation (Public Law 116-260).

There are about 11,000 wild wood bison in Canada, but about 6,000 are in herds chronically infected by brucellosis and/or tuberculosis (Hedrick 2009). These bison also are hybridized with plains bison due to relocations of plains bison to Wood Buffalo National Park during 1925 to 1928. Some of these bison were relocated during 1963 and 1965 to Mackenzie Bison Sanctuary and Elk Island National Park to establish new herds. As a result, all wild wood bison populations are wood-plains hybrids (Hedrick 2009).

Threats to bison conservation and restoration include the loss of genetic integrity, exclusion from available habitat, non-native diseases, land development and fragmentation, and intractable management across multiple jurisdictions (Halbert and Derr 2008, White et al. 2015c, 2017b; see Chapter 10). Every viable, wild population within the original range of bison has a regulated disease, such as brucellosis or tuberculosis, that restricts its distribution and restoration (Freese et al. 2007). In addition, a warming climate is affecting precipitation and snow melt patterns, as well as the frequencies of droughts and wildfires, which could lead to invasive annual plants dominating native vegetation communities and

[2] American Indian tribes include bands, nations, or other organized groups the Secretary of the Interior includes in the Federally Recognized Indian Tribe List Act of 1994, as amended (25 USC 5130-5131).

negatively affecting productivity and water, energy, and nutrient cycles (Cole and Yung 2010, Wilmers et al. 2013; see Chapter 10).

Stack of bison hides, location unknown.
Photograph by J. R. Douglass in 1874. National Park Service collection.

Chapter 2—Historical Trends

Introduction

This chapter summarizes the history and population trends of Yellowstone bison in the Greater Yellowstone Ecosystem (GYE), which encompasses about 20 million acres (8 million hectares) in Wyoming, Montana, and Idaho with YNP as the core (Meagher 1973, Keiter 2020). The GYE includes the headwaters of the Columbia, Snake, and Yellowstone rivers, and the Continental Divide crosses the area from west to southeast. It also includes Grand Teton and Yellowstone national parks, and the Beaverhead-Deerlodge, Bridger-Teton, Caribou-Targhee, Custer Gallatin, and Shoshone national forests (Keiter 2020). The central plateau of YNP is within a volcanic caldera and extends from the Pelican and Hayden valleys with a maximum elevation of 8,200 feet (2,500 meters) in the east to the geothermally influenced Madison headwaters area (7,200 feet, 2,195 meters) in the west (Figure 1). Winters are often severe, with temperatures reaching -44 degrees Fahrenheit (°F) (-42 degrees Celsius) and snowpack exceeding 6 feet (1.8 meters) in some areas. The northern region of YNP is drier and warmer, with average snow depths ranging from about 3.5 feet (1 meter) at higher elevations to less than 1 foot (0.3 meter) at lower elevations (Meagher 1973).

The Gallatin and Absaroka Mountain ranges dominate the northwestern and eastern boundaries of YNP, with the Washburn Range, Central Plateau, Solfatara Plateau, and Mirror Plateau encompassing the intervening high points. The Pelican Creek watershed is located to the south of this terrain and drains directly into Yellowstone Lake. The Gibbon and Firehole Rivers, both tributaries of the Madison River, are located to the south and west along with the smaller Duck and Cougar creeks in the Madison Valley. In the northeastern area of the park, Soda Butte and Slough creeks drain into the Lamar River, which transects the Lamar Valley (6,700 feet [2,040 meters] in elevation). The moderately hilly topography on top of Mount Everts and the Blacktail Deer Plateau in north-central YNP is bounded on the north by the Black Canyon of the Yellowstone River and on the south by Folsom and Prospect Peaks. The Yellowstone River flows through a wide valley northwest of Gardiner, Montana, and is generally less than 5,495 feet (1,675 meters) in elevation.

The primary habitats used by bison in YNP are characterized by relatively high-elevation grasslands, meadows, shrub steppe, and riparian corridors surrounded by moderately steep slopes of the local mountain ranges and plateaus. In general, the central region of the park is higher in elevation, colder, and snowier. Snow typically begins accumulating in late October, density (depth and water content) peaks in April, and snow melts by late May. Crusting of snow frequently occurs in some areas, such as the Pelican Valley, due to prevailing westerly winds (Watson et al. 2009). Grass growth begins in mid-May or early June (Gogan et al. 2005). Bison often use geothermally influenced areas with less snow cover during winter and wet grasslands and meadows along rivers in the Hayden and Pelican valleys and in the Madison headwaters area to the west. The northern region of the park is drier, mostly outside the volcanic caldera, and has fewer geothermally influenced areas and wet meadows. The extensive grasslands in this area gradually decrease in elevation from east to west between Cooke City and Gardiner, Montana (56 miles [90 kilometers]). Bison often use grasslands in valley bottoms, sagebrush steppe in surrounding foothills, and wet meadows on plateaus and in valleys. Typically, snow begins accumulating in mid-November, density peaks in mid-March, and snow melts by mid-April. Grass growth begins in mid- to late-April (Gogan et al. 2005).

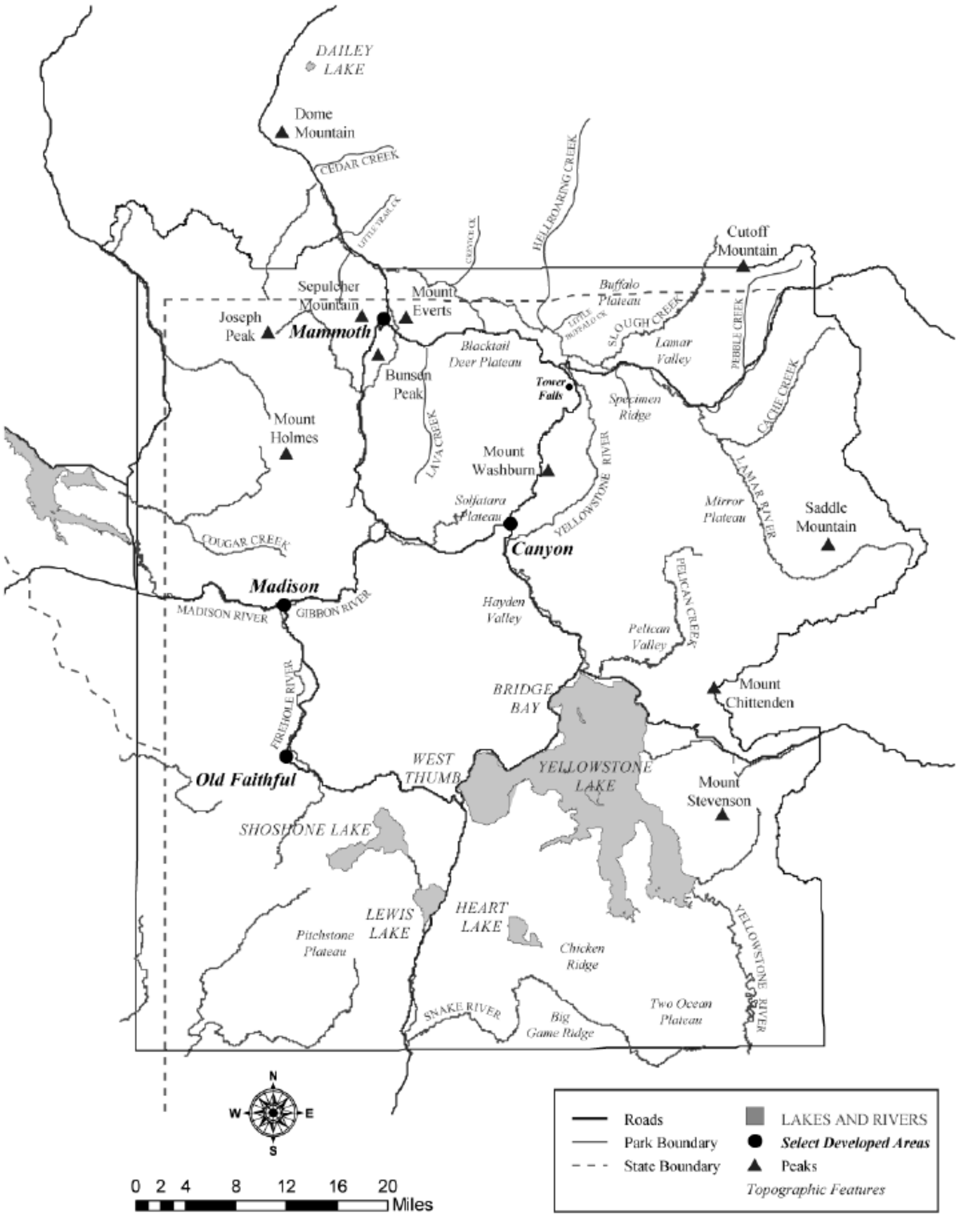

Figure 1. Yellowstone National Park and nearby areas of Montana with geographic features and place names.

Distribution

Archaeological evidence indicates bison have lived in the GYE for more than 10,000 years and historical narratives suggest they were abundant and widely distributed into the 1830s (Schullery and Whittlesey 2006, Whittlesey et al. 2018, Cannon et al. 2020, Whittlesey and Bone 2020). Bison were much more numerous at lower elevations in river valleys and on the surrounding plains, but many apparently migrated into the mountains during summer to access nutritious forage, and a smaller number lived year-round in the mountains, including the area encompassed by present-day YNP (Cannon et al. 2020, Whittlesey and Bone 2020). Archaeologists have found bison remains at indigenous precontact sites near

Gardiner, Montana, in the Hellroaring Drainage, near Tower Junction, in the Lamar Valley, and on the shoreline of Yellowstone Lake in present-day YNP (Schullery and Whittlesey 2006, Cannon et al. 2020).

Colonial and tribal hunters extirpated bison from the southwestern portion of the GYE by 1840, including the Snake River plain west of the Continental Divide (Franke 2005, Schullery and Whittlesey 2006, Whittlesey and Bone 2020). As a result, the Bannock tribes in present-day southeastern Idaho began making seasonal trips across the northern portion of the GYE to hunt bison to the north and east (Smith and Greenwald 2006b, Whittlesey and Bone 2020). Along this diffuse trail system, Bannock tribes hunted bison and other wildlife in the Madison, Hayden, and Pelican valleys of the central Yellowstone area and the Paradise and Lamar valleys and Blacktail Deer and Buffalo plateaus in northern Yellowstone area (Schullery and Whittlesey 2006, Smith and Greenwald 2006b, Whittlesey and Bone 2020). This trail network was also used by the Flatheads, Nez Perce, and Shoshone (Franke 2005). The Eastern Shoshone primarily lived in the Green and Wind River areas to the south but traveled seasonally through the Yellowstone area to access bison further north. They began hunting in the Yellowstone area more frequently as bison became scarce on the plains following colonization and settlement (Franke 2005, Krahe et al. 2006). In addition, the Crow tribe resided in the northeastern portion of the GYE and hunted in large portions of the present-day YNP and surrounding national forests (Smith and Greenwald 2006a).

Despite this increased hunting pressure, there were still many hundreds to thousands of bison left in the central and northern Yellowstone area during the 1860s and early 1870s, depending on the season and migration patterns (Whittlesey and Bone 2020). For example, Chief Plenty Coups of the Crow Nation recounted he was part of a hunting party in about 1860 that saw a herd of 200 to 300 bison in present-day YNP moving across the Yellowstone River and chased them on horseback along a creek where some bison were trapped against a cliff and killed. This location was near the expanse known as Buffalo Flat (also called Buffalo Tables or Plateau) where, in 1870, prospector Bart Henderson reported in his diary observing "thousands of buffalo quietly grazing," which was subsequently confirmed by James Gourley, another party member (Nabokov and Loendorf 2002, Keigley 2019, Whittlesey and Bone 2020).

Influence of Native People

Tribes of indigenous people, including the Bannock, Blackfeet, Crow, Kootenai, Nez Perce, Salish, and Shoshone, lived as part of the natural community in the GYE for more than 10,000 years (Nabokov and Loendorf 2002, Stark et al. 2022). Bison were an important food source for many of these tribes. Jump sites, where large groups of bison were driven over cliffs and killed, are found throughout North America from Alaska south to New Mexico and Texas; with a concentration of sites in the Dakotas, Montana, and Wyoming (Clawson et al. 2013). Communal hunters also drove bison along creeks or drivelines into cliffs, pitfalls, or traps where they were killed with arrows, clubs, spears, or guns. Hunters made game drivelines and traps from brush, poles, or rocks at several sites in the Yellowstone area (Norris 1881a,b). Bison kill sites have been found in YNP along terraces by Slough Creek and near Steamboat Point by a cliff above Yellowstone Lake; they also have been described near cliffs above the Buffalo Plateau (Nabokov and Loendorf 2002). There are at least 10 bison kill sites in the Paradise Valley of Montana north of YNP, including a large complex of drive lines called the Emigrant Buffalo Jump (Cannon et al. 2001, 2020). This practice decreased after the use of horses became prevalent in the 1600s and hunters could travel further and be more efficient at killing bison; however, jumps and drivelines continued to be used in the Yellowstone area until at least the 1860s (Clawson et al. 2013, Whittlesey and Bone 2020, Taylor et al. 2023). Hunting parties also lit fires to influence the movements of game and regenerate habitat (Confederated Salish and Kootenai Tribes 2005, Yonk et al. 2018). Indigenous people dried some meat and mixed it with berries and fat to create pemmican that lasted for many months. They also used hides for clothing, sinew as thread, bladders for containers, hooves for glue and implements, teeth for decorations and exchange, and bones for tools and weapons (Kuhnlein and Humphries 2017).

Diseases introduced by colonists, settlement of their lands, slaughter of wildlife populations, and government oppression decimated tribes in the GYE by the mid-1870s (Nabokov and Loendorf 2002). Federal treaties limited tribal use of traditional lands and confined them to reservations where they depended on government rations and were urged to adopt farming and ranching lifestyles (Nabokov and Loendorf 2002, Krahe et al. 2006, Smith and Greenwald 2006a,b). When YNP was established in 1872, the eastern portion overlapped the Crow Reservation until Congress removed this land from the Reservation in 1882 (Norris 1881b, Smith and Greenwald 2006a). By 1880, federal agents and soldiers had relocated most indigenous people in the Yellowstone area to reservations and discouraged them from using YNP for traditional hunting and gathering activities; though Indian parties hunted along the park periphery until about 1893 (Norris 1881b, Harris 1889, Meagher 1973, Franke 2005, Krahe et al. 2006, Smith and Greenwald 2006a,b). As a result, tribal foraging, hunting, and spiritual activities in and near the park waned during the 1890s (Nabokov and Loendorf 2002, Stark et al. 2022).

Effects of European American Settlement

Settlements were sparse and isolated in the American West through the 1840s but the discovery of gold in California during 1848 led to a mass western movement of settlers and livestock. There was an influx of miners and settlers into the northern portion of the GYE during the 1860s and 1870s when gold was discovered. This led to the building of settlements in the Gardiner basin north of the YNP boundary from 1880 to 1900 and a railroad line to near the northern park boundary (Cinnabar) in 1883 (Haines 1974, Whittlesey 1995). Settlers removed native vegetation in the Yellowstone River valley to create homesteads and grow crops. Farmers and ranchers erected fences to contain livestock and exclude wildlife from cultivated areas. Similar actions occurred in other river valleys emanating from the park.

Ranchers brought livestock into the GYE by 1867, and numerous ranches were established during the 1870s in areas historically used by bison. There were no restrictions on numbers, seasonal use, or type of livestock (cattle, horses, sheep) grazing within or outside the park, leading to many more fences, habitat degradation from overgrazing, and soil erosion (Pitcher 1905, Skinner 1925, 1928; Rush 1932). These effects increased after 1879 when the completion of the transcontinental railroad led to a substantial increase in livestock numbers and additional pressures on remaining wildlife (Franke 2005). There were about 35 to 40 million cattle in western states by the mid-1880s and about 10 million sheep in Montana and Wyoming from 1885 to 1915 (USDA 2020).

Livestock grazed without any restrictions within the park between Mammoth, Wyoming, and Gardiner, Montana, and several small cattle ranches operated in northern YNP from 1882 to 1884 (Rush 1932, Meagher and Meyer 1994, Meagher and Houston 1998, Yonk et al. 2018). In 1900, the superintendent established regulations to impound and dispose of loose livestock found grazing or being herded in YNP (Benson 1910). However, the park and concessionaires grazed as many as 3,000 horses on the Blacktail Deer Plateau until 1916 and 200 to 300 thereafter until sometime in the 1930s (Rush 1932, Yonk et al. 2018). Smaller bands of sheep and cattle grazed at numerous sites in the park through the 1930s for meat and milk, including near the Buffalo Ranch in the Lamar Valley (Rush 1932, Whittlesey 1994, Meagher and Houston 1998, Yonk et al. 2018). Also, grazing by cattle in areas outside the park, such as the Yellowstone River valley, continued and combined with cultivation substantially degraded native vegetation communities on the valley floor by the mid-1920s (Rush 1932). Range managers considered all the grasslands on the northern winter range for ungulates overgrazed by the 1930s, primarily due to heavy use by cattle and horses (Rush 1932, Houston 1982).

In addition, there was a massive slaughter of bison in the GYE, including in the newly established (1872) YNP, by colonial hunters for the hide and robe trade during the 1870s and 1880s (Norris 1881a, Wear 1885, Harris 1889, Whittlesey et al. 2018, Whittlesey and Bone 2020). In 1872, Lieutenant Gustavus Doane reported about 45,000 bison robes were shipped from Fort Benton, where hides from the

Yellowstone area were sent down the Missouri River for sale in the eastern market. This number of robes equates to about 135,000 dead bison, and the Crow tribe reportedly harvested another 10,000 bison that autumn (Whittlesey and Bone 2020). In 1875, a single fur trader in Bozeman, Montana, purchased 12,450 buffalo robes, which equates to about 62,250 dead bison, many of which likely came from the GYE (Avant Courier 1875, Whittlesey and Bone 2020). In addition, Philetus Norris, superintendent of YNP, reported "scores if not hundreds of moose and bison were taken out of the park in spring of 1875" and "hundreds if not thousands of each of these other animals [moose, bison] have been thus killed since its discovery in 1870" (Norris 1877). He added "[w]ithin a decade the buffalo, the bison, and, in fact, the most of these larger animals will be extinct or extremely rare elsewhere in the United States; and if our people are ever to preserve living specimens of our most beautiful, interesting, and valuable animals, *here*, in their native forests and glens of this lofty cliff and snow encircled "wonder-land," is the *place* and *now* the *time* to do it" (Norris 1877). In 1881, the Avant Courier newspaper in Bozeman, Montana, reported "at least 100,000 buffalo hides will be shipped out of the Yellowstone country this season" (Whittlesey and Bone 2020). Another observer identified only as Carl estimated about 524,000 bison were killed in Montana during 1880 to 1882. By 1884, there were few bison hides and robes left to be shipped out of the territory (Adams and Dood 2011, Whittlesey and Bone 2020).

Protection and Stewardship

Bison were extirpated from the Yellowstone River valley north of YNP by the 1860s but there were still at least 600 bison in the park during 1880, likely due to its remoteness and isolated mountain valleys too distant from the railroad to attract many hide hunters (Franke 2005). Bison were observed in the Crevice, Hellroaring, and Slough creek areas of northern YNP, Amethyst Mountain to Pelican Creek and Yellowstone Lake in central YNP, and on the Madison Plateau and along the Firehole and Madison rivers in west-central YNP. However, the number of bison isolated in YNP continued to diminish due to hunting in the park for food and poaching for hides and trade (Norris 1881a, Franke 2005, Whittlesey and Bone 2020). Bison were removed from their northern wintering areas during the 1880s and from the Madison headwaters area (along the Firehole River) and Hayden Valley by 1895 (Meagher 1973, 1989b; Meagher and Meyer 1994).

In 1883, the Secretary of the Interior issued regulations "to prohibit absolutely the killing, wounding or capturing at any time, of any buffalo, bison, moose, elk, ..." in YNP (Teller 1883). In 1884, the legislature of the Territory of Wyoming passed *An Act to Render Operative and Effectual the Laws of the Territory of Wyoming Within that Portion of the Yellowstone National Park Lying Within said Territory and to Protect and Preserve the Timber, Game, Fish and Natural Objects and Curiosities of the Park* (Harris 1889). Section 8 of this Act provided for the protection of wildlife in the park but poaching continued due to a lack of enforcement (Conger 1883, Wear 1885, Skinner et al. 1942, Franke 2005). In 1885, superintendent Wear stated in his annual report that "[t]he game in the Park had been shot with impunity and marketed at the hotels without any interference on the part of the officers whose sworn duty it was to protect and prevent its destruction" (Wear 1885:3). As a result, Congress passed a law with a provision the Secretary of War could send troops to the park, if requested by the Secretary of the Interior, to prevent trespassers from entering the park "for the purpose of destroying the game or objects of curiosity therein" (Act of March 3, 1883, Ch. 143, 22 Stat. 603, 626-627; Harris 1889, Cramton 1932). Poaching continued due to a lack of enforcement so the U.S. Army sent a detachment of the First Cavalry to the park in 1886 under Captain Moses Harris to enforce regulations and prevent poaching (Conger 1882, 1883; Wear 1885, Harris 1889, Hampton 1971, Franke 2005).

In 1893, geologist Arnold Hague saw small bands of bison totaling about 300 on the Mirror Plateau, Specimen Ridge, Elephant Back Mountain, Pelican Valley, Hayden Valley, and Madison Plateau in YNP (Whittlesey and Bone 2020). To increase protection, Congress passed *An Act to Protect the Birds and Animals in Yellowstone National Park, and to Punish Crimes in said Park, and for Other Purposes* in

1894 (16 USC 24-30a, Ch. 72, 28 Stat. 73; also known as the Lacey Act or Yellowstone Game Protection Act). The House of Representatives report (53d Congress, 2d Session, Report 658, April 4, 1894) accompanying this Act, stated "out of the vast herds of millions of buffaloes that a few years ago coursed the plains of America a few hundred only remain, and they are now all in the Yellowstone Park, and one of the purposes of setting aside this park has been to preserve this little herd." … "A few days ago, poachers entered the park and commenced the slaughter of these animals. Prompt action is necessary, or this last remaining herd of buffalo will be destroyed." The Lacey Act established "[t]hat the Yellowstone National Park, as its boundaries are now defined, or as they may be hereafter defined or extended, shall be under the sole and exclusive jurisdiction of the United States" … "All hunting, or the killing, wounding or capturing at any time of any bird or wild animal, except dangerous animals, when it is necessary to prevent them from destroying human life or inflicting an injury, is prohibited within the limits of said park; ..." (16 USC 26).

Despite the Lacey Act, the number of bison in the park decreased from about 200 in 1894 to between 25 and 50 in 1896 and about 25 by 1901 due to continued poaching (Wear 1885, Pitcher 1905, Skinner et al. 1942, Meagher 1973). Soldiers increased efforts to patrol the park, herded ungulates back into the park, erected miles of fencing along the north boundary of the park to prevent ungulates from leaving, killed predators, and grew hay to feed ungulates during winter (Harris 1889, Benson 1910, Hampton 1971, Haines 1977, Franke 2005). To help with bison recovery, Congress appropriated $15,000 in 1901 for the establishment of a new herd of bison in the northern portion of YNP (Skinner et al. 1942). Managers relocated 18 females (some pregnant) from northwestern Montana (Pablo-Allard herd) and three males from Texas (Goodnight herd) to the northern portion of YNP in 1902 and added three calves from the Pelican Valley during 1903 to 1906 (Skinner et al. 1942, Meagher 1973, Meagher and Meyer 1994). These bison were kept in an enclosure about one mile south of the park headquarters in Mammoth, Wyoming, from 1902 to 1906-1907 and then moved to the newly established Buffalo Ranch in the Lamar Valley, where they were kept in a fenced area for a few years. Another calf from the Pelican Valley was added to the herd in 1909 (Baggley 1934, Skinner et al. 1942, Meagher 1973).

Managers began growing (1909) and irrigating (1911) hay in the Lamar Valley, which was fed to bison at the Buffalo Ranch during winter. From 1910 to 1915, bison were allowed to graze in the valley during the day but kept in a fenced pasture at night; after 1915, bison were left overnight in the valley near the ranch (Skinner et al. 1942, Meagher 1973). In the 1920s, managers began herding bison from the Lamar Valley to the Mirror Plateau, upper Lamar River drainage, Mount Norris, and Specimen Ridge during summer. Managers erected drift fences across the valley above Soda Butte Creek to keep bison out of the hayfields in the valley (Skinner et al. 1942, Meagher 1973). The bison used the Lamar Valley winter range during May and early June before moving to higher ranges for the summer. A few bison went over the plateau and into the Pelican Valley (Baggley 1934). The bison remained at high elevations until October or early November, when they returned to the Lamar Valley (Baggley 1934). Managers removed all but a few mature bulls from the herd to ease management and 391 bull calves (about 50%) were castrated during 1917 (or 1918) through 1931 (Baggley 1934, Skinner et al. 1942). Under this stewardship, bison numbers increased from about 120 in 1910 to 765 by 1925 (Skinner et al. 1942). 'Buffalo stampedes' were held for several years in the Lamar Valley during the mid-1920s through 1929 for the enjoyment of important visitors (Baggley 1934).

Through 1938, rangers on horseback rounded up bison in late autumn and drove them into the Lamar Valley for feeding, captures, and culling; thereafter, staff used hay to bait bison into the valley and capture facility (Meagher 1973). During 1924 to 1952, park staff grew and harvested about 11,540 tons of hay in the Lamar Valley (average = 398 tons per year; range = 0 to 1,021 tons per year; Skinner et al. 1942). Staff fed bison in the Lamar Valley about 8,241 tons during winter (average = 284 tons per year; range = 9 to 836 tons per year) along with 113 tons of cottonseed cake during 1931 to 1933. Feeding mostly occurred during January through March (range = December 7 to April 17; Skinner et al. 1942).

This supplemental feeding facilitated rapid herd growth of about 16% per year (Fuller et al. 2007a). Managers substantially reduced supplemental feeding in the Lamar Valley after 1940 and the practices of feeding and herding bison in the Lamar Valley ceased in 1952, after which bison moved about freely (Skinner et al. 1942, Meagher 1973).

There were about 23 to 30 remaining native bison during 1902 to 1907 that spent winter in the Pelican Valley in central YNP but moved to the Mirror Plateau and upper Lamar River area during summer (Meagher 1973). 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 (Skinner et al. 1942, Meagher 1973, Plumb and Sucec 2006). The annual report of Superintendent Toll in 1929 indicated "[t]here seems to be a gradual intermingling of the wild [Pelican] and tame [Lamar] herd. It has reached a point where it is difficult to distinguish the buffalo of the wild herd from those of the Lamar Valley herd" (Toll 1929:29-30; Skinner et al. 1942). Numbers of bison spending winter in the Pelican Valley increased from about 32 in 1908 to 72 in 1916 and between 100 and 125 during 1920 to 1930 (Skinner et al. 1943, Meagher 1973).

There were about 830 bison in the Lamar herd by 1935. Managers relocated 71 of these bison to the Hayden Valley and Firehole River area in central YNP during 1936, creating the Mary Mountain herd. Bison moved back-and-forth between the Firehole River drainage and Hayden Valley areas, though most spent summer in the Hayden Valley (Meagher 1973). Many bison from the Hayden Valley moved westward across the Mary Mountain divide to spend winter in the Lower Geyser basin along the Firehole River where snow depths were lower due to geothermal influences (Meagher 1973, Taper et al. 2000). There was a steady increase in the size of this herd (about 10% per year) as bison expanded into areas not inhabited for 40 years or more (Meagher 1973, Fuller et al. 2007a).

Population Reduction Efforts

Congress established the NPS with the Organic Act of 1916, which directed park managers to "conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations" (54 USC 100101a,b). The NPS assumed management of YNP in 1918 and continued many of the agricultural husbandry practices initiated by the U.S. Army for decades, including predator control and the cultivation and feeding of hay to bison and other ungulates in the northern portion of the park (Toll 1929, Olliff et al. 2013).

Brucellosis was detected in bison in the Lamar herd during 1917, most likely transmitted from cattle kept at the ranch until about 1919 or wild elk infected by cattle (Meagher and Meyer 1994). Serology is often used to detect antibodies circulating in the blood that indicate past exposure to *Brucella abortus* bacteria, although a positive test does not necessarily mean the animal is still infected or capable of transmitting the bacteria (Treanor et al. 2011). Female bison in YNP are usually infected with brucellosis bacteria when they are young, but do not shed it until they become reproductively active at about 3 years of age (Treanor et al. 2011). Infections may recur when bison experience chronic undernutrition and poorer body condition during winter, which reduces their immune defenses and increases their vulnerability to *Brucella* bacteria (Treanor 2013). Females are more susceptible during pregnancies because their immune responses are suppressed to safeguard developing fetuses (Treanor 2013).

Due to concerns about brucellosis, overgrazing, and other issues, in 1923 Congress authorized the Secretary of the Interior the discretion "to give surplus elk, buffalo, bear, beaver, and predatory animals inhabiting Yellowstone National Park to Federal, State, county, and municipal authorities for preserves, zoos, zoological gardens, and parks" (16 USC 36; 54 USC 100101, 100752). Under this authority, managers sent about 800 live bison to zoos and other federal agencies, private individuals, and states to establish herds. Managers sent Yellowstone bison to Wind Cave and Grand Teton national parks during

1916 and 1948, respectively, and to the National Bison Range during 1953 (Skinner et al. 1942, Halbert and Derr 2007, Stroupe et al. 2022). They also sent live bison to Thermopolis State Park, Wyoming, and private individuals in Independence, Kansas, and Cora, Wyoming (Skinner et al. 1942). Live shipments were halted in 1951 due to concerns about relocating bison infected with brucellosis.

In addition, managers shipped about 3,005 bison carcasses to tribes (90%), contract sales (7%), relief agencies (1%), and other entities (2%) during 1925 to 1954 (Skinner et al. 1942). Most of the meat from shot and culled bison was distributed to Indian tribes in Montana, Wyoming, Idaho, North Dakota, and South Dakota, including the Arikara, Hidatsa, and Mandan Tribes of the Fort Berthold Indian Reservation, Assiniboine and Gros Ventre Tribes of the Belknap Indian Reservation, Blackfeet Nation, Chippewa Cree Tribe of the Rocky Boy Reservation, Confederated Salish and Kootenai Tribes of the Flathead Nation, Flandreau Santee Sioux Tribe, Northern Cheyenne Tribe, and the Standing Rock Sioux Tribe (Skinner et al. 1942, Franke 2005, Smith and Greenwald 2006a). In some instances, tribal members processed animals shot in the park for distribution to their families and other tribal members (Skinner et al. 1942). However, there is no evidence of them being allowed to hunt within the boundaries of the park (Whittlesey 2013).

During the 1960s, bison were driven into traps near the Lamar Valley (Crystal trap) and on the Firehole River (Nez Perce trap) using helicopters (Meagher 1973). In total, managers shot or captured and shipped about 3,500 bison from the Lamar herd between 1930 and 1966 to reduce numbers and take out individuals with the disease brucellosis (Meagher 1973). Managers also removed about 860 Mary Mountain bison and 150 Pelican bison between 1954 and 1966. These removals by shooting, capture for slaughter, and capture for relocation reduced numbers to about 70 Lamar, 160 Pelican, and 188 Mary Mountain bison by winter in 1968 (Figure 2; Meagher 1973).

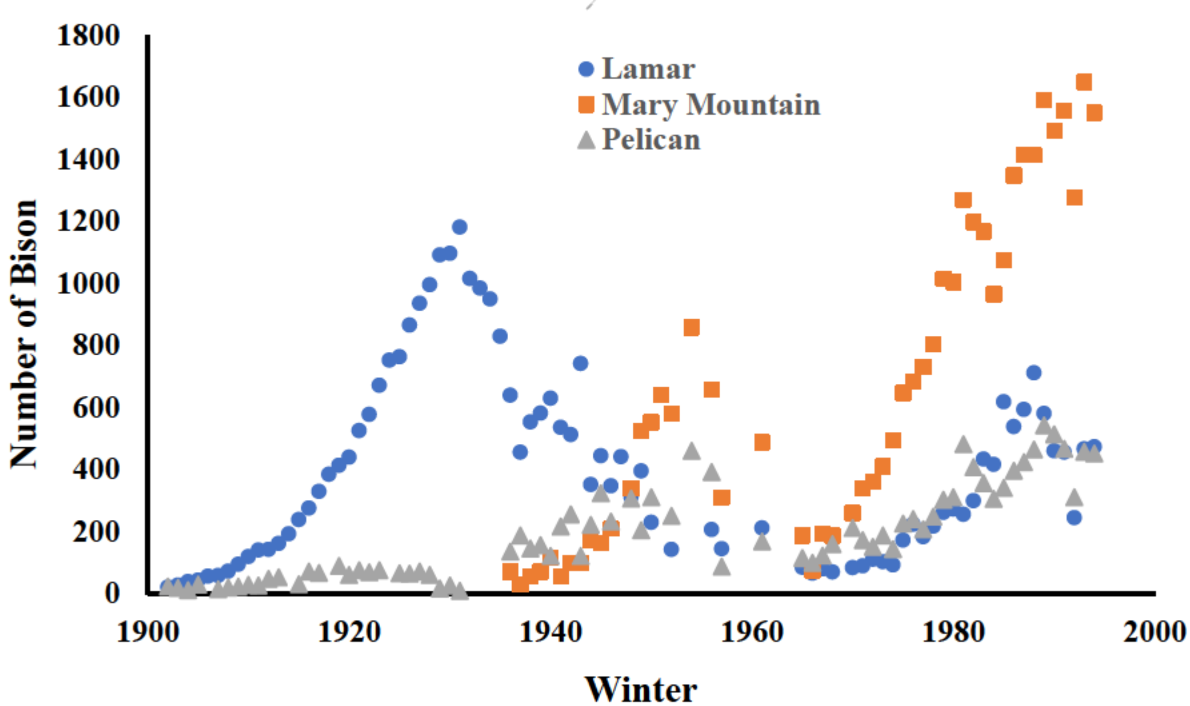

Figure 2. Winter counts of bison in the areas historically used by the Lamar, Mary Mountain, and Pelican herds in Yellowstone National Park (Meagher 1973, National Park Service, unpublished data).

Natural Regulation

In 1963, a special advisory board on wildlife management in national parks recommended allowing natural ecological processes to function with less human influence (Leopold et al. 1963). They suggested the NPS emphasize managing wildlife based on its mandate to preserve park resources unharmed and in their natural condition for the benefit and enjoyment of people; though they did not rule out human intervention when deemed necessary. In addition, park scientists began to question long-term beliefs about ungulate abundance and range deterioration in YNP based on prevailing range science standards (Houston 1982, Despain et al. 1986). For example, it appeared the use of testing and culling to eradicate brucellosis would eliminate wild, free-ranging bison concurrent with the disease (Plumb and Sucec 2006).

In 1969, park managers stopped culling ungulates and allowed their numbers to fluctuate naturally in response to food availability, predators, weather, and hunting outside the park (Despain et al. 1986, Olliff et al. 2013). Bison numbers increased exponentially under this management approach and, by 1994, there were about 4,100 bison, with almost 3,000 in central YNP and larger winter movements toward the park's northern and western boundaries (Plumb et al. 2009). 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 1989b, Taper et al. 2000, Meagher et al. 2002). Pelican bison began moving west to the northern shore of Yellowstone Lake and along the Yellowstone River to the Hayden Valley (see Chapter 4). Eventually, bison spending winter in the Pelican Valley stopped moving to the Mirror Plateau and upper Lamar River area during most summers and primarily remained in the Hayden Valley (Taper et al. 2000, Meagher et al. 2002). Thus, there was likely considerable mixing of descendants from the native (Pelican) and introduced (Lamar/Mary Mountain) lineages (White et al. 2022a).

In addition, some bison began moving from the Hayden Valley to the Firehole River area and along the Madison River towards the western boundary during winter. Others began moving to northern YNP, likely in response to increasing bison numbers and deep snow depths that reduced forage availability (Taper et al. 2000, Meagher et al. 2002, Bruggeman et al. 2009c). A few bison migrated to both the western and northern boundary areas during the same winter period. As a result, there was probably further mixing of descendants from the native and introduced lineages and distinguishing among descendants of Lamar, Pelican, and Mary Mountain bison based on their wintering areas in the park became impossible. Instead, biologists began counting and referring to bison that spent summer in the central and northern regions of YNP as the central and northern herds (Taper et al. 2000, Olexa and Gogan 2007, White et al. 2022a).

Livestock producers were concerned about bison movements outside the park because many animals have been exposed to the disease brucellosis, which can induce abortions between January and mid-May in Yellowstone bison, and be transmitted among bison, cattle, and elk through contact with infectious birthing tissues (Cheville et al. 1998, Jones et al. 2010). About 60% of adult female bison in YNP test positive for antibodies indicating previous exposure to *Brucella* bacteria, but only about 10% of adult female bison are infectious and could potentially shed live bacteria that spread the disease. These percentages have remained relatively consistent for the past 40 years (Hobbs et al. 2015). Most bison are infected early in life before reproductive maturity but recover from infection and have some level of immunity to brucellosis; though re-emergence of symptoms does occur in some animals (Treanor et al. 2011).

In 1995, the State of Montana sued the federal government over concerns Yellowstone bison infected with brucellosis bacteria would jeopardize the State's brucellosis-free status for cattle and, in turn, interstate and international trade (Bidwell 2010). A brucellosis-free classification allows producers to export cattle to other states or nations without testing. Historically, the entire state lost this classification if regulators detected brucellosis in two or more livestock herds within a 2-year period or ranchers did not depopulate a livestock herd exposed to brucellosis within 60 days. This reclassification had significant adverse economic consequences on producers state-wide (USDA, APHIS 2010, 22014). As a result, Montana wanted to maintain a negligible risk of brucellosis transmission from bison to cattle to assure other states and countries their livestock were brucellosis free (State of Montana 2000).

Staff from the U.S. Departments of Agriculture (USDA) and Interior (USDI) and the State of Montana worked with a court-appointed mediator to lessen their differences and develop an Interagency Bison Management Plan (IBMP) by December 2000 (USDI, NPS, and USDA, USFS and APHIS 2000a,b). The goals in the plan included "specific commitments relating to the size of the bison herd, both within and outside Yellowstone National Park; a clearly defined boundary line beyond which the agencies will not tolerate bison; provide for public safety and the protection of private property; agency actions showing a commitment toward the eventual elimination of brucellosis in bison; protection of livestock from the risk of brucellosis; actions to help protect the brucellosis class-free status of Montana; and maintenance of a viable population of wild bison in Yellowstone National Park from biological, genetic, and ecological terms" (USDI, NPS, and USDA, USFS and APHIS 2000b:8). The original members of the IBMP were the Animal and Plant Health Inspection Service (APHIS; Veterinary Services), Montana Department of Livestock (MDOL), Montana Fish, Wildlife and Parks (MFWP), NPS (YNP), and U.S. Forest Service (USFS; Custer Gallatin National Forest [CGNF]).

Negotiators of the IBMP chose a population target of 3,000 bison in late winter and early spring to reduce migration outside YNP (Cheville et al. 1998, USDI, NPS, and USDA, USFS and APHIS 2000b). This target equates to about 3,500 or more bison after calving during summer, depending on the composition and growth rate of the population (Angliss 2003). Under the plan, bison could only migrate into small areas adjacent to YNP during a short period in winter to "prevent the reestablishment of a free-ranging bison herd in places where bison have been absent for more than a century" (State of Montana 2000:27-28). The management of bison under the IBMP also included actions such as capture, test-and-slaughter, vaccination, and hazing animals back into YNP to constrain their abundance and distribution while attempting to suppress brucellosis prevalence. In addition, the Montana Legislature designated Yellowstone bison a species requiring disease control due to chronic brucellosis infection and directed MDOL to remove wild bison that migrate into the State and jeopardize compliance with livestock disease control programs (81-2-120 [1-4] Montana Code Annotated [MCA]; Administrative Rules of Montana 32.3.224). The Legislature also designated Yellowstone bison a species in need of management because they could pose a threat to persons or property from transmitting brucellosis or damaging property (87-1-216 [1] MCA). The Legislature directed MFWP to administer public hunts on lands adjacent to YNP (87-1-216 MCA) and ensure there are no free-ranging bison not contained by fencing or some other barrier elsewhere in the State. Similar designations and regulations do not exist for elk populations also chronically infected with brucellosis.

Interagency Bison Management Plan

Federal and state negotiators designed the IBMP to adaptively progress through a series of management steps that initially tolerated only bison testing negative for brucellosis exposure on winter ranges outside YNP but would eventually tolerate limited numbers of untested bison on small winter ranges adjacent to the park when cattle were not present. During step 1, the agencies agreed to: 1) enforce spatial and temporal separation between bison and cattle; 2) use hazing by humans on horseback, all-terrain vehicles, or in helicopters to prevent bison from leaving the park; 3) if hazing was unsuccessful, capture all bison attempting to leave the park and test them for brucellosis exposure; 4) send test-positive bison to slaughter; 5) vaccinate all test-negative bison except adult females during the third trimester of pregnancy (mid-January through May); 6) temporarily hold all test-negative bison at the north boundary for release back into the park in spring; 7) release up to 100 test-negative bison at the west boundary and allow them to use habitat adjacent to the park until May 15; 8) conduct research on *Brucella* persistence in the environment to determine an adequate temporal separation period between bison and cattle; 9) conduct research on the safety and efficacy of strain RB51 vaccine; and 10) conduct research and development of a remote vaccine delivery system. Montana also agreed to encourage voluntary vaccination of cattle that might graze on bison-occupied winter ranges outside the park. If 100% voluntary vaccination was not achieved in one year, Montana agreed to make the vaccination of all female cattle greater than 4 months of age mandatory (USDI, NPS, and USDA, USFS and APHIS 2000b, White et al. 2011).

Step 2 was to begin when cattle no longer grazed during winter on the Royal Teton Ranch adjacent to the north boundary of YNP, which was anticipated in winter 2003. Management actions initiated in step 1 would continue, except that up to 100 test-negative bison would be released at the north boundary and allowed to use habitat adjacent to the park until April 15, and any calf and yearling bison that could not be captured at the west boundary would be vaccinated using a remote delivery system. Step 3 was expected to begin by winter 2006 once the agencies had determined an adequate temporal separation period between bison and cattle, gained experience in managing bison in allowable zones outside the park, and initiated a vaccination program for all calf, yearling, and adult female bison in the population, including remote delivery vaccination inside YNP. The agencies would tolerate up to 100 untested bison to freely range in both the north and west boundary areas. The agencies would use capture facilities in these areas to maintain the population near 3,000 bison, enforce tolerance levels (less than 100 bison), and ensure no bison were outside the park after the respective spring cut-off dates. The agencies could also pursue a quarantine facility to better manage bison by developing a process to certify test-negative bison as brucellosis-free (USDI, NPS, and USDA, USFS and APHIS 2000b, White et al. 2011).

This plan was never completely implemented because new information indicated some of the premises regarding brucellosis transmission were incorrect and these intrusive methods could have adverse effects on the bison population and were not likely to be effective, feasible, or socially acceptable (White et al. 2011, Halbert et al. 2012, White et al. 2015a,b). Federal and state disease regulators initially thought elk played a minor role in brucellosis transmission to cattle, and bison migrating outside YNP would transmit brucellosis to cattle and jeopardize interstate and international trade (Bidwell 2010). However, elk have transmitted brucellosis to cattle at least 27 times since 1998 with no transmissions attributed to bison (National Academies of Sciences, Engineering, and Medicine 2017). Despite these occurrences, there have been no changes in class-free brucellosis status, economic sanctions by other nations or states, or sustained efforts to restrict the abundance and distribution of elk from these areas (White et al. 2015a,b).

Circumstances also changed with fewer cattle near the park, and federal and state disease regulators taking steps to lessen the economic impacts of brucellosis outbreaks in cattle (USDA, APHIS 2010, 2014). In addition, since 2006 several tribes have hunted bison on national forest lands adjacent to the park pursuant to long-standing treaties with the federal government. The Confederated Salish and Kootenai Tribes of the Flathead Nation and the Nez Perce Tribe became members of the IBMP in 2009 due to their treaty rights for hunting bison. Many tribes have rights reserved through treaties with the federal government to hunt on unoccupied lands of the U.S. so long as game is found thereon. The word "unoccupied" denotes an area free of residence or settlement by non-Indians (*Herrera v. Wyoming*, 139 S. Ct. 1686 (2019)). The InterTribal Buffalo Council (ITBC) also became a member of the IBMP in 2009. The ITBC was formed in 1990 to restore bison to tribal lands and approved in 2010 as a federally chartered Indian organization by the Bureau of Indian Affairs under Section 17 of the Indian Reorganization Act.

In subsequent years, several other American Indian tribes asserted their treaty rights to harvest bison migrating from YNP onto unoccupied lands on the CGNF in Montana, including the Shoshone Bannock Tribes, Confederated Tribes of the Umatilla Indian Reservation, Yakama Nation, Blackfeet Nation, Northern Arapaho Tribe, and the Crow Nation. Federal treaties create laws that supersede state legislation due to the Supremacy Clause of the U.S. Constitution (Article IV, § 2; *Antoine v. Washington*, 420 US 194 (1975)).

In 2008, the U.S. Government Accountability Office issued a report recommending the IBMP partners develop clearly defined, measurable objectives as to how the plan's goals would be achieved (Government Accountability Office 2008). In response, the partners included objectives in an Adaptive Management Plan with monitoring metrics for measuring progress and potential management responses to improve progress if necessary (Partner Agencies, IBMP 2008). The IBMP agencies adaptively adjusted the IBMP to decrease captures and shipments of bison to slaughter by increasing hunting opportunities outside the park. Management action 2.2.b indicates "adjacent to YNP, emphasize management of bison as wildlife and increase the use of state and treaty hunts to manage bison numbers and demographic rates, limit the risk of brucellosis transmission to cattle, and protect human safety and property" (Partner Agencies, IBMP 2008). The IBMP partners revised the plan again in 2011 to include "[o]bjective 1.4: recognize tribal treaty rights for hunting bison." Management action 1.4a is to "[a]llow bison to occupy National Forest System lands and other areas determined suitable within the designated tolerance area (Zone 2) and maximize timing and geographical extents to increase tribal hunt opportunities." Management action 1.4b is to "[c]oordinate management activities that could potentially impact opportunities for tribal members to exercise their treaty rights." In addition, the management (tolerance) zones for bison in Montana were expanded through adjustments to the plan in 2016, which was an important step toward eventually reestablishing year-round bison presence to support treaty hunting on lands in these areas (Figures 3 and 4; Bullock 2015, IBMP Agencies 2016).

The Adaptive Management Plan guides the operating procedures for the IBMP each year. These procedures are included in an Operations Plan that describes how each partner agency will contribute to implementing the Adaptive Management Plan and reducing conflicts among agency/tribal actions and between bison and the public with regards to safety and property. The intensity of management operations each winter usually depends on the timing and extent of bison migration to lower elevation winter ranges in and outside the park, which are driven by bison density and unpredictable variations in snow conditions and available forage (White et al. 2011, Geremia et al. 2014). Thus, the operations plan includes recommendations regarding contingencies for situations when few bison migrate or many bison migrate, as well as restraints to ensure population viability and a low risk of brucellosis transmission from bison to cattle. Such recommendations are derived from an annual report on the status of bison for the superintendent of YNP, which is shared with the IBMP members, hunting tribes, and the public before the annual operations plan is developed (Geremia 2022).

In 2010, APHIS changed its regulations and reduced the risk of Montana losing its brucellosis-free status and experiencing associated economic costs. The new regulations allow livestock producers to deal with brucellosis outbreaks in cattle on a case-by-case basis and eliminated the need to remove whole herds and test cattle across the entire state (USDA, APHIS 2010, 2014). In addition, Montana established a Designated Surveillance Area for brucellosis, defined by occurrence of the disease in elk, which saves livestock producers more than $5.5 million each year in testing and other costs (MDOL 2011). To prevent brucellosis-infected livestock from being moved into other states, all calves within the surveillance area are vaccinated for brucellosis, all cattle are uniquely marked so relocations or sales can be traced, and all reproductive cattle are tested for brucellosis exposure prior to movement elsewhere (MDOL, https://liv.mt.gov/Animal-Health/Reportable-Animal-Diseases/Brucellosis).

Bison Tolerance Zone - North

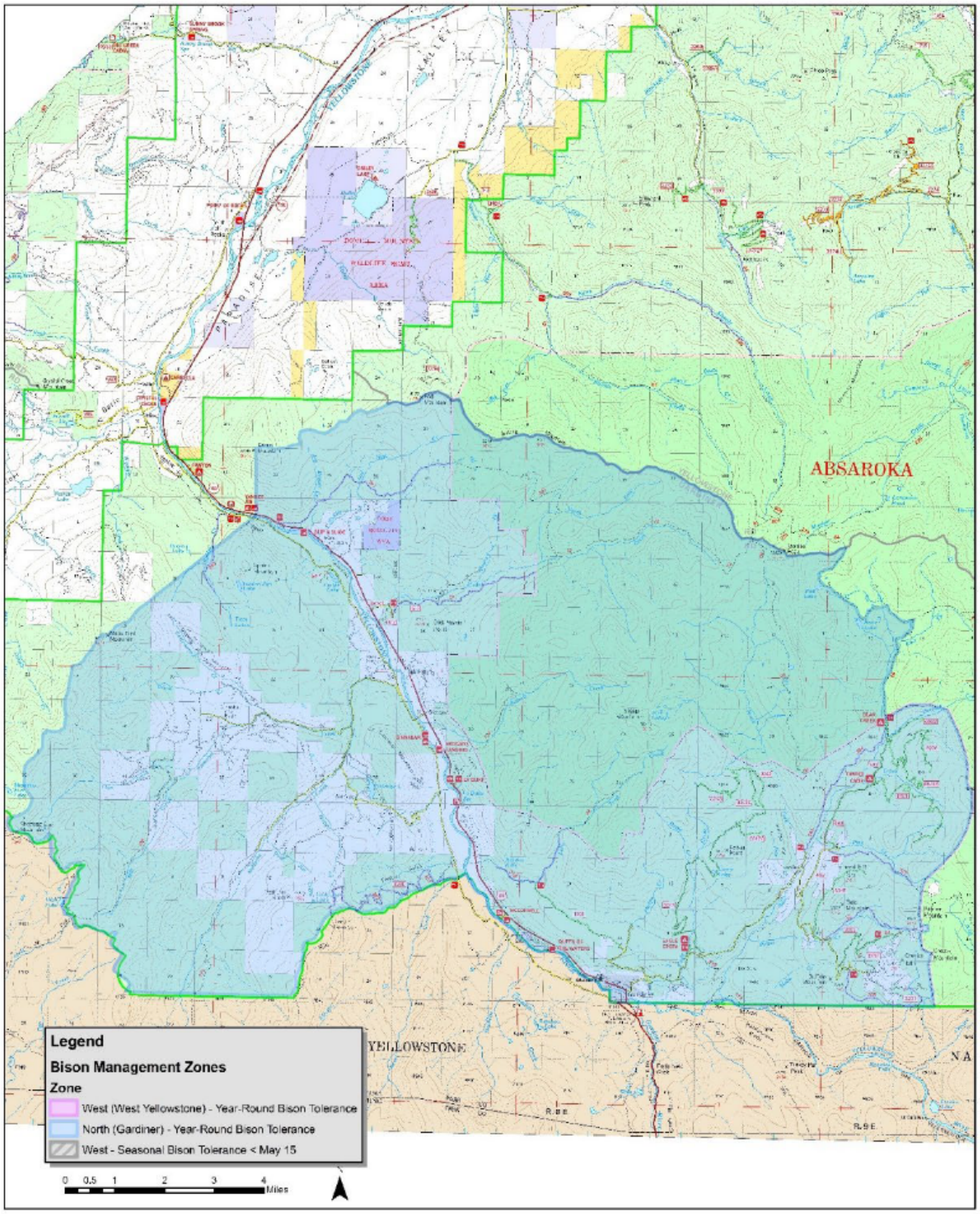

Figure 3. Northern management area in Montana for the Interagency Bison Management Plan (Randy Scarlett, Custer Gallatin National Forest, and Julie Anton Randall, Eco Mare Terra International).

Bison Tolerance Zone - West

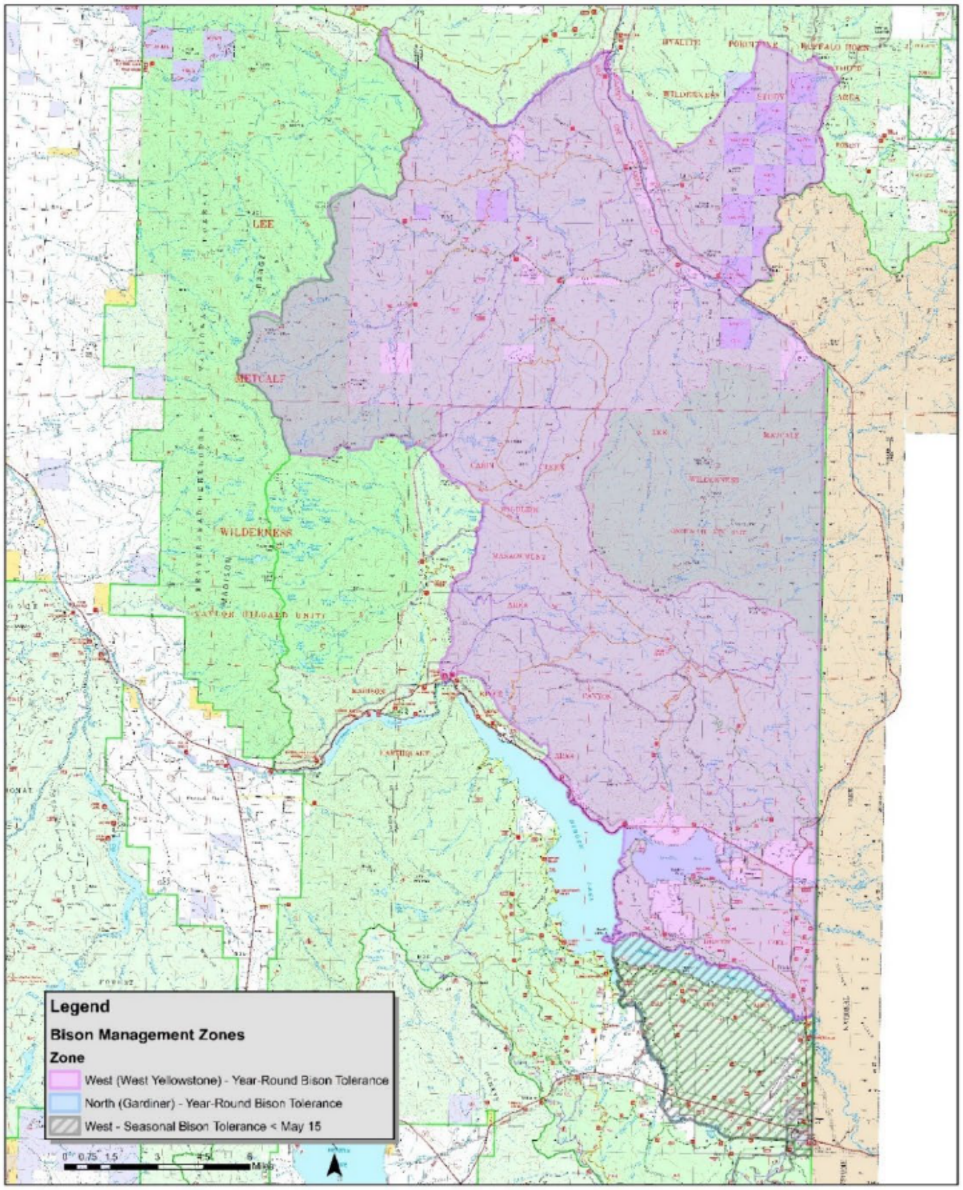

Figure 4. Western management area in Montana for the Interagency Bison Management Plan (Randy Scarlett, Custer Gallatin National Forest, and Julie Anton Randall, Eco Mare Terra International).

By 2013, the number of tribal members hunting in an area called Beattie Gulch just outside the northern boundary of YNP increased, leading to issues such as 'firing lines' that prevented bison from distributing across the larger landscape, wounding of bison that returned to the park, concentrations of gut piles near roads and residences, and human safety issues. The CGNF worked with MFWP, hunting tribes, and private property owners to assess safety concerns associated with the hunt and implement management changes to address issues. In 2013, the CGNF issued a permanent shooting closure for a portion of Beattie Gulch between the Yellowstone River to the east, Old Yellowstone Trail South Road to the west, YNP to the south, and residential houses to the north. In addition, MFWP led efforts in 2013 to remove gut piles from bison harvested in Beattie Gulch to reduce the chance of grizzly bears congregating in the area.

In 2014, the NPS released a final environmental impact statement that evaluated a remote vaccination program to reduce the prevalence of brucellosis in Yellowstone bison (USDI, NPS 2014). The NPS concluded the implementation of park-wide remote vaccination would not achieve desired results and could have unintended negative effects such as injuries and changes in bison behavior that would negatively affect visitor experiences like watching wild animals. The NPS based this conclusion on the lack of an easily distributed and highly effective vaccine and limitations of current diagnostic and vaccine delivery technologies. Bison nutrition, body condition, pregnancy, and lactation can reduce the protective immune responses from vaccination. In addition, elk that are also infected and widely distributed would re-infect bison (USDI, NPS 2014). Following a review of brucellosis in the GYE, the National Academies of Sciences, Engineering and Medicine (2017) recommended not using aggressive measures to try and suppress brucellosis in bison until tools became available for an eradication program in elk. While Montana has implemented hazing and shooting efforts in recent years to disperse some elk in the Paradise Valley north of YNP, many elk still mingle with cattle during the brucellosis transmission period (Tilt 2020). The State has not implemented measures, such as adult vaccination, culling, and test-and-slaughter, in this area to prevent transmission from elk to cattle like they want the NPS to implement with bison in YNP (Rayl et al. 2019).

Adult female elk in a pasture with cattle in the Paradise Valley near the peak of the elk calving season in early June. Photograph by Cameron H. Sholly, National Park Service, 2023.

In addition to leaving numerous gut piles on the landscape, concentrated hunters near the northern park boundary often shoot near roads and houses and, occasionally, towards other hunters, houses, and cars. In 2015, MFWP began requiring successful bison hunters to place unused parts of carcasses at least 200 yards (183 meters) from roads, trails, and homes, and spread stomach contents on the ground to reduce attractions to scavengers. To decrease traffic congestion and carcasses along Old Yellowstone Trail South Road, the CGNF began allowing successful hunters access to the Beattie Gulch administrative road to retrieve bison. The hunting tribes agreed to a 150-yard (137-meter) buffer extending west from Old Yellowstone Trail South Road in Beattie Gulch where there would be no shooting, carcasses, or gut piles. The CGNF issued an official shooting closure for this area in 2016. These actions moved shooting and carcasses farther away from residences in the area, but safety remains a concern for property owners (Bear Creek Council 2019).

In 2016, an analysis of genetic data indicated elk were responsible for infecting cattle herds with *Brucella abortus* bacteria in the GYE, not bison. Elk exposed to brucellosis inhabit an area encompassing about 17 million acres (6.9 million hectares), whereas bison inhabit 1.5 million acres (607,000 hectares) near the core of the ecosystem (Kamath et al. 2016). Brucellosis control measures in bison do not affect the dynamics of unrelated strains in elk elsewhere. The National Academies of Sciences, Engineering, and Medicine (2017) recommended prioritizing efforts on preventing brucellosis transmission by elk, while maintaining separation between bison and cattle. State biologists concluded the primary strategy for managing brucellosis transmission risk from elk to livestock is to prevent mingling by hazing, hunting, fencing or removing haystacks and other attractants, or improving forage on public lands (Rayl et al. 2019). For over two decades, the IBMP partners have demonstrated these same techniques work with bison in the Gardiner and Hebgen basins, north and west of YNP.

In 2017, the Nez Perce, Salish and Kootenai, Umatilla, and Yakama tribes signed a memorandum of agreement to maintain a regular, predictable, safe, and respectful bison hunt in Beattie Gulch. The tribes agreed to closely coordinate and implement common hunt protocols, safety regulations, and enforcement to ensure the safety of hunters, wardens, and the surrounding community. The agreement limited the number of hunters from these tribes in the area to 25 or fewer at any time, with each hunting party having a designated lead hunter and a law enforcement officer from each tribe remaining on-site to coordinate the hunts. The law enforcement officers hold a daily pre-hunt coordination meeting with hunters to ensure safety and issue citations as necessary. The lead hunter for each party is responsible for ensuring hunters follow the hunt protocols and safety regulations, coordinating with other parties to determine an orderly engagement and harvest of bison, and ensuring a safe approach and shooting direction.

In 2018, the NPS, APHIS, and MDOL began a quarantine program (now called the Bison Conservation Transfer Program; BCTP) to identify brucellosis-free Yellowstone bison and transfer them to the Fort Peck Indian Reservation in northeastern Montana. Since 2019, the NPS and APHIS have sent about 300 brucellosis-free Yellowstone bison to the Assiniboine and Sioux Tribes at Fort Peck for one year of additional testing and eventual release. The ITBC has subsequently transferred more than 170 bison of Yellowstone-origin from Fort Peck to at least 23 tribes across 12 states. In 2021 and 2022, YNP doubled the capacity of this program through a partnership with Yellowstone Forever, the Greater Yellowstone Coalition, and Defenders of Wildlife to lower the number of animals sent to slaughter and increase the restoration of bison to tribal lands (USDI, NPS 2018, 2023).

In 2019, a local organization named the Bear Creek Council asked the IBMP agencies to consider recommendations for a safer hunt with fewer impacts to residents in and near Gardiner, Montana. The IBMP agencies hosted a field trip to hunting areas, discussed concerns with local citizens, reviewed the current shooting closures and hunting regulations, and agreed to continue work to address these concerns while respecting tribal rights. In 2020, the CGNF proposed permanent firearm discharge closures on about 23 acres (9 hectares) for human safety near Beattie Gulch and the McConnell area north of

Gardiner, Montana. In 2023, staff from the CGNF, State of Montana, and USFWS, and members of the Nez Perce and Shoshone-Bannock tribes, removed 53,000 pounds (24,040 kilograms) of gut piles and other parts from bison harvested in Beattie Gulch. The CGNF also adopted a new Land Management Plan that includes habitat improvement projects to create or connect suitable bison habitat with enough bison present and distributed year-round to provide a self-sustaining population on the national forest in conjunction with bison herds in YNP (USDA, USFS 2022).

Current Situation

Bison have an iconic status in North America because their lives were interwoven with indigenous people for thousands of years and their movements across the vast landscape were a symbol of wildness (Robbins 2023). Bison were central to the colonization and settlement of the continent and their decimation inspired conservation movements in the early 1900s to restore populations of wildlife, including the establishment of the NPS (Franke 2005, Plumb and Sucec 2006, Stark et al. 2022). However, few parks and refuges are sufficient in size with necessary components to support viable, wild bison populations through the year with minimal human influence (White et al. 2015c). In addition, it is difficult to forge partnerships with adjacent jurisdictions that have different authorities, statutory mandates, and management philosophies (White et al. 2017b). Thus, the greatest impediment to bison restoration outside parks and refuges is intolerance due to conflicts with humans, including competition with livestock, conversion of valleys to irrigated cropland or ranchland, disease issues, and damage to crops and private property (Aune and Wallen 2010, White et al. 2015c).

The actions and adaptive management changes implemented by the IBMP partners during 2001 to 2023 helped them meet the goals of the plan as bison numbers increased to 5,000 during the 2000s and 6,000 by the summer of 2022 (IBMP Partners 2022). There has been no transmission of brucellosis from bison to cattle, fewer conflicts with people and property, high visitor enjoyment and economic contributions to gateway communities, increased tribal and public hunting opportunities, and more brucellosis-free bison sent to tribal lands (White et al. 2015a,b; Geremia 2022). During 2001 to 2011, prior to IBMP members making adaptive adjustments to emphasize treaty hunting, bison summer counts averaged about 3,900 and ranged between 3,000 and 5,000. During 2012 to 2022, with an emphasis on treaty hunting, counts averaged about 5,000 bison and ranged between 4,200 and 6,000 (Geremia 2022).

Despite this success, brucellosis continues to be 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 (Bidwell 2010). There is resistance from livestock producers to lessen existing constraints on bison distribution and alleviate the intrusive approach to managing them; even though fencing, hazing, and hunting have proven effective at preventing brucellosis transmission from bison to cattle and these techniques are used by the State of Montana on elk mingling with cattle (White et al. 2015a,b; Rayl et al. 2019). In addition, there has been little progress in the development of vaccines, delivery systems, and diagnostics for brucellosis in bison and elk to suppress the disease 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 (White et al. 2015a). Likewise, there is no substantive progress in developing a vaccine that blocks infection in cattle. Current cattle vaccines are only 65% to 70% effective against abortion and 10% to 15% effective against infection (Olsen et al. 2010). Thus, brucellosis directly limits the potential for further recovery of bison in the GYE and the degree of tolerance for bison outside YNP in future years will depend on mediating conflicts between bison and humans (Plumb et al. 2009, Bailey 2013).

Female bison and calves in Yellowstone National Park.
Photograph by Neal Herbert, National Park Service, 2015.

Chapter 3—Status of the Population

Introduction

Whether a bison population increases or decreases in abundance depends on factors influenced by the number of animals in an area (density), such as reproduction and survival, and other factors not related to density, such as climate and year-to-year variations in weather (Caughley and Sinclair 1994). Prime-aged females usually have high and relatively constant survival and reproduction, but calf survival is variable from year-to-year due to factors that affect food availability, growth, and energetic costs (Gaillard et al. 1998, 2000). Population growth slows if the density of animals increases and there is a sustained period of fewer resources for everyone, especially young animals (Caughley and Sinclair 1994). Lower nutrition and body condition initially contributes to lower survival of young, followed by reproduction beginning at an older age, and then lower adult reproduction and survival (Eberhardt, 2002, Parker et al. 2009).

Environmental factors not related to density, such as severe droughts and winters, can exacerbate these demographic responses by affecting food availability, energetic costs and, in turn, reproduction and survival; especially for calves and older adults (Coulson et al. 2001). The climate of YNP includes long cold winters and shorter cool summers (Meagher 1973, Houston 1982). Major snowstorms typically begin in November and continue through March or later. More snow accumulates on the higher-elevation mountains and plateaus (3 to 6 feet; 1 to 2 meters) than in the lower-elevation valleys (1 to 2 feet; 0.3 to 0.6 meter), most of which extend well outside the park. Snowpack melts during April and early May at lower elevations but can persist into June at higher elevations and in forested areas. Rainfall and thunderstorms occur from May through July. Thereafter, the climate is drier until winter storms begin.

New growth of grasses and forbs begins in spring following snow melt and progresses from lower elevation valleys and basins upslope to higher-elevation mountains and plateaus (Thein et al. 2009). Depending on elevation and precipitation, grasses stop growing in middle to late summer and become dormant through the winter (Thein et al. 2009). Deep wet snow increases energy expenditures and cycles of icing and thawing increase the hardness of the snowpack and make it more difficult for bison to access forage (Messer et al. 2009). Decreased forage intake by pregnant females can contribute to lower birth weights and survival of their calves which enter winter with lower fat reserves and are more susceptible to starvation (Cook et al. 2004a, 2016). Deep snow conditions also increase the susceptibility of bison to predation and the number of bison that migrate outside the park where they are vulnerable to harvest (Becker et al. 2009a, Geremia et al. 2011). In combination, these factors can result in substantial mortality and low recruitment during some winters that affect population trends.

This chapter summarizes information about the status of the Yellowstone bison population, including estimates of abundance, age and sex composition, births, deaths, and recruitment. Reproduction and survival have an overriding influence on the population dynamics of Yellowstone bison because there are not movements into (immigration) or out of (emigration) the population. Thus, rates of birth and death determine the number of bison, and these rates are strongly influenced by the effects of brucellosis on reproductive success and removals of bison migrating into Montana (White et al. 2011, Geremia et al. 2015c).

Counts and Classifications

Historically, park staff opportunistically counted or estimated numbers of Yellowstone bison observed during horse and ski travels, round-ups of animals in northern YNP, or occasional airplane or helicopter flights. There was little consistency in efforts from year-to-year (Meagher 1973). During the 1960s, biologists counted bison and collected age and sex composition during population reduction operations (Meagher 1973). From 1970 to 2010, park biologists routinely conducted two airplane counts of Yellowstone bison each summer (June and July/August) and recorded the number of calves and adults in observed groups. They used consistent counting methods, with the same observer and pilot from 1970 to 1997 (Hobbs et al. 2015). Biologists estimated the detection of bison was about 88% to 97% of the true number because most bison were in large, easily observed groups (Taper et al. 2000, Hess 2002). From 2000 to 2010, biologists concurrently recorded the composition of bison groups from the ground.

Bison abundance in the central and northern regions of YNP increased exponentially for two decades following the cessation of culling in 1969 and bison in both regions responded to increased density by expanding their ranges (see Chapter 4; Taper et al. 2000, Fuller et al. 2007a). The population continued growing thereafter, with sporadic decreases following substantial management removals (White et al. 2011, Hobbs et al. 2015). Biologists counted between 2,900 and 6,000 bison after calving each summer between 2001 and 2023 (Figure 5). The population maintained an annual growth rate of about 15% after accounting for (censoring) hunter harvests and management removals (Geremia 2022). The growth rate was substantially lower after some winters with high removals of bison, such as in 2006, 2008, and 2011, but the population recovered (Fuller et al. 2007a,b; Geremia et al. 2009; White et al. 2011, Geremia 2022, 2023). Yellowstone bison have modest reproductive rates and high survival rates for a wild population exposed to numerous predators and relatively severe environmental conditions. Thus, bison numbers increase rapidly when environmental conditions are suitable (Hobbs et al. 2015).

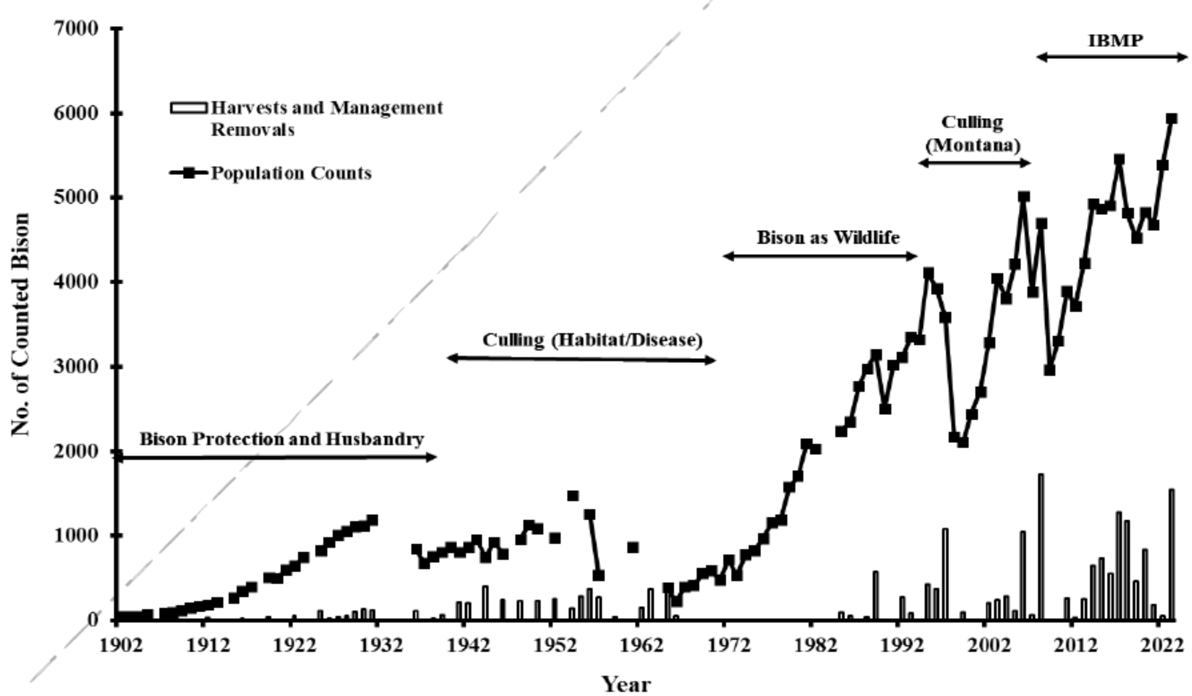

Figure 5. Counts and removals of bison in Yellowstone National Park and nearby areas of Montana during 1901 through 2023.

Telemetry

Efforts to monitor wildlife populations in the park were revolutionized in the 1960s when biologists fit telemetry collars on elk and grizzly bears. This technique enabled biologists to collect important information for management, including activity patterns, cause-specific mortality, dispersal, migration, population estimation, range use, recruitment, resource selection, and survival (White and Garrott 1990). There was a tremendous advancement in scientific knowledge that led to better-informed decisions and benefits to the scientific community and visitors. However, telemetry is intrusive because it requires capturing animals and attaching a device to them, such as a radio collar (Mech and Barber 2002). Scientists try to minimize these effects because an underlying assumption is that animals with devices behave like other animals (White and Garrott 1990). Biologists and engineers have developed lighter-weight, less visible, and less bulky attachment devices, timed detachment devices, longer battery life, and GPS or satellite collars (Mech and Barber 2002). They also use less invasive sampling methods, such as noninvasive genetic sampling, remote cameras, and stable isotope analysis, to gather information when possible. During 2000 to 2023, biologists captured and fit roughly 300 adult female bison in YNP with telemetry devices to monitor their behavior, demographics, movements, reproduction, resource selection, and survival (Geremia et al. 2015b,c; 2021).

Reproduction

The annual cycle of reproduction for Yellowstone bison begins when females ovulate and become receptive to mating during mid-July through mid-September (Meagher 1973, Kirkpatrick et al. 1991, Olexa and Gogan 2007). Breeding occurs when bison generally are in good nutritional condition from feeding on nutritious forage and replenishing muscle mass and fat. Gestation lasts about 285 days (9.5 months; Meagher 1973). Most calves are born during late April and May when grasses are initiating new growth, which provides mothers and their calves with nutritious forage to support nursing, restore nutritional condition, and grow prior to winter (Gogan et al. 2005, Jones et al. 2010). Yellowstone bison give birth to a single calf; twins are rare (Meagher 1973). Calves *in utero* and at birth may be slightly biased towards males, with reports of 108 males per 100 females during the early 1930s (Rush 1932), 112 males per 100 females during the 1940s (Meagher 1973), and 106 males per 100 females during 2001 to 2014 (Geremia et al. 2015a,c).

Calving overlaps with spring migrations from winter to summer ranges, and parturition locations likely depend on when migrations begin depending on snow melt and vegetation green-up (Bjornlie and Garrott 2001, Bruggeman et al. 2009c, Geremia et al. 2015b). Birthing locations of radio-collared females during 2004 to 2007 were widely distributed along migratory transition ranges in northern YNP, such as the Blacktail Deer Plateau, and central YNP, such as the Madison River drainage (Jones et al. 2009). Bison most often gave birth within or near a group of bison (89% of observed events) rather than in isolation (Jones et al. 2010). Parturition lasted 51 to 159 minutes, and most females left the birth site within two hours (range = 5 to 420 minutes) after nursing the calf, consuming birth tissues, and cleaning the site by eating vegetation and licking the soil; Jones et al. 2009).

The earliest calves are born in late March or early April each year and most calving tapers off in early June, though a few births occur through the summer (Taper et al. 2000, Gates et al. 2005, Gogan et al. 2005, Jones et al. 2010). There was a relatively high degree of synchrony in birthing events during 2004 to 2007, with 80% occurring in 32 days between April 25 to May 26 (Jones et al. 2010). Fifty percent of births occurred by May 6, 80% by May 16, 95% by May 27, and calving was finished by June 5 (Jones et al. 2010). Many females birthing within a short period may decrease the risk of predation to their calves through dilution, being one of many potential prey (Rutberg 1984). There are different environmental conditions for bison living in the central and northern regions of YNP. Central YNP has harsher winter conditions, such as deeper snow pack, later snow melt, and later grass growth, that decrease body condition in females (Geremia et al. 2015c). As a result, calving in central YNP occurs about 14 days later than in the north (Gogan et al. 2005; see Chapter 5).

Three-quarters of reproductive failures by radio-collared females, including stillborn calves, placenta retention with no calf, and death of the mother and calf during birth, occurred by the end of April (Jones et al. 2010). The survival of *Brucella abortus* bacteria on exposed reproductive tissues decreases rapidly with increasing exposure to sunlight (ultraviolet radiation), warmer temperatures, and dry weather. Survival times were about 60 to 80 days in February, 20 days in mid-May, and 5 days in June. Fetuses and other tissues are removed by scavengers within 3 to 18 days (Cook et al. 2004b, Jones et al. 2010, Aune et al. 2012). Scavengers in and near YNP include bears, coyotes, eagles, foxes, ground squirrels, magpies, ravens, and wolves.

Biologists report pregnancy rates as the proportion (0.90) or percentage (90%) of females pregnant (Caughley and Sinclair 1994). During the 1920s to the 1940s, only an occasional yearling bred in the herd introduced into the Lamar Valley in northern YNP, which was fed hay during winter. Most females bred as 2-year-olds and calved as 3-year-olds, with pregnancy rates of about 50%. Pregnancy rates for females 4 years and older varied between 65% in 1931-1932 and 94% in 1949-1950 (Rush 1932, Skinner 1941 as cited by Meagher 1973). When bison in the Lamar herd were at low densities following the substantial herd reductions during the 1930s through the 1960s and not being fed hay, most females reached sexual maturity at 4 years old (Meagher 1973). A few 2-year-olds bred and about one-quarter of 3-year-olds. The adult pregnancy rate was about 57%, suggesting bison successfully bred in alternate years (Meagher 1973).

During 1989 to 1991, the pregnancy rate of bison in YNP was 48% and females in central YNP had significantly fewer pregnancies and calves than females in northern YNP (Kirkpatrick et al. 1993, 1996). About 70% to 85% of adult females in central YNP became pregnant in alternate years, apparently due to lactational suppression of ovarian function and failure to ovulate, likely because these bison could not replenish their body condition sufficiently to support pregnancy during summers when drought or competition with other herbivores limited their nutritional intake (see Chapter 5; Kirkpatrick et al. 1993, 1996). Likewise, during 1997 to 2003 bison 2 years or older in central YNP had pregnancy rates of about 65% and appeared to calve in alternative years; only 5% of yearlings were pregnant (Gogan et al. 2013). In a separate study, radio-collared females in central YNP produced a calf in 60% of the years between 1996 and 2012 (Geremia et al. 2009, 2015c). In contrast, radio-collared females in northern YNP tended to calve in sequential years, with 80% producing a calf each year. As a result, birth rates were higher in northern YNP (78%) than central YNP (63%; Geremia et al. 2009, 2015c).

Overall, 57% of radio-collared 3-year-old females gave birth during 1996 through 2012, which increased to 75% for females 4 to 14 years of age. Birthing rates decreased to about 50% for bison 15 to 20 years old (Geremia et al. 2015a,c). Birth rates of ungulates tend to decrease as numbers in an area increase towards the food-limited capacity of the environment to support them (Eberhardt 2002). However, biologists did not detect effects of bison density on birth rates as the number of bison in northern YNP increased from 400 to 4,500 and the number in central YNP varied between 800 and 3,600 (Geremia et al. 2009, 2015c). Perhaps density dependent effects were masked somewhat by the lactational suppression of pregnancy, alternative year calving in central YNP, and the effects of brucellosis on birth rates (Gogan et al. 2013). Regardless, birth rates were lower following winters with deep or hard snow pack that limited forage availability and increased energetic costs (Geremia et al. 2015c).

Brucellosis infection decreases pregnancy rates because bison infected while pregnant tend to abort their first and, sometimes, second pregnancies thereafter (Fuller et al. 2007b, Geremia et al. 2015c). The probability of adult females giving birth was 80% before being infected with brucellosis but only 48% during their first pregnancy after infection (Geremia et al. 2015c). Initial research in central YNP suggested the probability of giving birth was depressed (~64%) for years following exposure to *Brucella* bacteria, perhaps from infection of the uterus delaying ovulation (Geremia et al. 2009, 2015c). However, previous brucellosis infection did not have long-term effects on pregnancy rates of females in a separate study during 1997 to 2003 or in wood bison (Joly and Messier 2004, Gogan et al. 2013). Regardless, the Yellowstone bison population has sustained rapid population growth (~15% after accounting for management removals) despite this chronic disease (Fuller et al. 2007a,b; Geremia et al. 2009, 2015b).

Causes of Death

The overwhelming cause of death for Yellowstone bison is human-caused mortality through management removals when they migrate to the park boundary, such as capture and shipment to meat processing facilities (slaughter) or tribal and public hunting. Managers removed about 13,670 bison from the Yellowstone population during 1985 to 2023 by shipping bison to slaughter (64%) and hunting (36%; White et al. 2011, Geremia 2022). This total includes about 10,550 bison since 2001 under the IBMP (61% slaughter; 39% harvest), which exceeds deaths from natural causes. The NPS captured and culled bison in the Stephens Creek Administrative Area in northern YNP during the winters of 1997, 2003, 2004, 2006, 2008, 2011, 2014 to 2020, 2022, and 2023. Managers removed about 31% of the bison population in the winter of 1997, 21% in 2006, 37% in 2008, 23% in 2017, 24% in 2018, and 26% in 2023 (White et al. 2011, Hobbs et al. 2015, Geremia 2023). These removals included a disproportionate number of yearling and adult females and calves, with about 1.3 females removed for every male during the 2000s (White et al. 2011, Hobbs et al. 2015). Since 2012, the IBMP agencies have tried to decrease shipments to slaughter (46%) and prioritize harvests (54%; Table 1). Public and tribal hunters harvested about 2,930 bison during 2001 through 2022, and 1,175 bison in the winter of 2023 (Geremia 2023).

Natural causes of mortality for bison include abandonment (neonates) and stillbirths, accidents, birth defects, diseases, drowning, geothermal features, injuries, predation, severe weather, and starvation (winterkill). Starvation was the main cause of natural mortality in the 1960s, prior to wolf restoration, with calves and older animals in poorer condition being more susceptible (Meagher 1973). There was substantial starvation in severe winters with deep, prolonged snow pack, which also contributed to low recruitment and reproduction (Meagher 1973). Predation has become a larger factor following wolf restoration and grizzly bear recovery (Smith et al. 2004, Becker et al. 2009a,b). During 1993 to 2010, biologists from Montana State University found 656 bison carcasses in central YNP during winter, including 225 wolf predations, 181 winterkills, 153 due to unknown causes, 46 grizzly bear predations, 20 thermal/mud entrapments, 10 vehicle strikes, 7 accidents/injuries, 7 birth/pregnancy complications, 6 due to unknown predators, and 1 coyote predation (Geremia et al. 2015c).

Diseases

There were several outbreaks of hemorrhagic septicemia in the Lamar herd that killed 15% of the bison in 1911 and 9% in 1919 and 1923 but there have been no subsequent outbreaks (Baggley 1934, Skinner et al. 1942, Plumb and Sucec 2006). Park staff detected bovine brucellosis in bison tested at the Buffalo Ranch in 1917 (Mohler 1917 as cited in Meagher and Meyer 1994). By 1931, about 60% of bison in the Lamar herd tested positive for exposure to the disease (Tunnicliff and Marsh 1935 as cited in Skinner et al. 1942). Test and removal operations during the 1930s and 1940s reduced the prevalence of brucellosis exposure to about 15% in 1948 (Skinner et al. 1942).

Biologists found parasites such as lungworm (*Dictyocaulus*) in about 11% of bison sampled during the 1960s, as well as tapeworms (*Moniezia benedeni*; Meagher 1973). They also detected antibodies for anaplasma (11%), bovine respiratory syncytial virus (31%), bovine viral diarrhea (31%), and parainfluenza 3 virus (36%) during sampling in 1991-1992 but no animals displayed signs of active infections (Taylor et al. 1997). Hematologic, serologic, histopathologic, and fecal evaluations of Yellowstone bison killed in 1991 were normal, with some evidence of modest intestinal parasite loads of blood worms (*Strongylus*), round worms (*Trichuris*), and cestode tapeworms (Zaugg et al. 1993).

Biologists monitor animals placed in the Bison Conservation Transfer Program (quarantine) for diseases of high health concern, including Johne's disease (paratuberculosis) and *Mycoplasma bovis*, with no detections of these diseases (Register et al. 2021).

In 2008, there was an anthrax outbreak in a herd of about 3,500 wide-ranging domestic bison in southwestern Montana that killed about 8% of the bison, including 28% of mature males (Blackburn et al. 2014, Nekorchuk et al. 2019). Anthrax is caused by the spore-forming bacterium, *Bacillus anthracis*, and can cause large, rapid, and deadly outbreaks, usually during hot, dry weather preceded by flooding or substantial rainfall. Outbreaks have not occurred in YNP, but hot, dry conditions often coincide with the breeding season for bison when they aggregate in the Lamar and Hayden valleys. The unpredictability and potential severity of an anthrax outbreak requires preparedness, and the NPS has developed a framework for responding effectively and rapidly to an outbreak (Treanor and White 2019).

Table 1. Numbers of bison removed from YNP or nearby areas of Montana from 1985 to 2023 (White et al. 2011, Geremia 2022, 2023).

	Number of Bison Counted Previous July-August			Sent to Slaughter/ Management Removals		Hunter Harvest[a]		Sent to Quarantine		
Winter	**Northern Herd**	**Central Herd**	**Total**	**North Boundary**	**West Boundary**	**North**	**West**	**North**	**West**	**Total**
1985[b]	695	1,552	2,247	0	0	88	0	0	0	88
1986	742	1,609	2,351	0	0	41	16	0	0	57
1987	998	1,778	2,776	0	0	0	7	0	0	7
1988	940	2,036	2,976	0	0	2	37	0	0	39
1989	1,058	2,089	3,147	0	0	567	2	0	0	569
1990	432	2,075	2,507	0	0	1	3	0	0	4
1991	818	2,203	3,021	0	0	0	14	0	0	14
1992	822	2,290	3,112	249	22	0	0	0	0	271
1993	681	2,676	3,357	0	79	0	0	0	0	79
1994	686	2,693	3,329	0	5	0	0	0	0	5
1995	1,140	2,974	4,114	307	119	0	0	0	0	426
1996	866	3,062	3,928	26	344	0	0	0	0	370
1997	860	2,724	3,584	725	358	0	0	0	0	1,083
1998	455	1,715	2,170	0	11	0	0	0	0	11
1999	489	1,622	2,111	0	94	0	0	0	0	94
2000	540	1,904	2,444	0	0	0	0	0	0	0
2001	590	2,118	2,708	0	6	0	0	0	0	6
2002	719	2,564	3,283	0	202	0	0	0	0	202
2003	805	3,240	4,045	231	13	0	0	0	0	244
2004	888	2,923	3,811	267	15	0	0	0	0	282
2005	876	3,339	4,215	1	96	0	0	0	17	114
2006	1,484	3,531	5,015	861	56	32	8	87	0	1044
2007	1,377	2,512	3,889	0	4	47	12	0	0	63
2008	2,070	2,624	4,694	1,288	160	59	107	112	0	1,726

	Number of Bison Counted Previous July-August			Sent to Slaughter/ Management Removals		Hunter Harvest[a]		Sent to Quarantine		
Winter	Northern Herd	Central Herd	Total	North Boundary	West Boundary	North	West	North	West	Total
2009	1,500	1,469	2,969	0	4	1	0	0	0	5
2010	1,837	1,464	3,301	3	0	4	0	0	0	7
2011	2,246	1,652	3,898	6	0	unk[c]	unk	53	0	59
2012	2,314	1,406	3,720	0	0	15	13	0	0	28
2013	2,669	1,561	4,230	0	0	148	81	0	0	229
2014	3,420	1,504	4,924	258	0	258	69	60	0	645
2015	3,424	1,441	4,865	511	0	201	18	7	0	737
2016	3,627	1,282	4,910	101	0	378	24	49	0	552
2017	4,008	1,451	5,459	753	0	389	97	35	0	1,274
2018	3,969	847	4,816	697	0	285	90	99	0	1,171
2019	3,337	1,190	4,527	348	0	109	3	0	0	460
2020	3,667	1,162	4,829	445	0	223	63	105	0	834
2021	3,427	1,243	4,670	0	0	153	34	0	0	187
2022	3,830	1,564	5,394	27	0	6	7	10	0	50
2023	4,507	1,432	5,939	94	0	1,130	42	282	0	1,548

[a] Total bison shot by game wardens and hunters from 1973 through 1991, and state and tribal hunters after 2000 outside the park.
[b] Winter from November 1984 to April 1985.
[c] unk = unknown

Survival

The probability a bison is still alive at some future time, such as 1 year later, is called the survival rate which, historically, biologists reported as a proportion or percentage of animals surviving (Caughley and Sinclair 1994). More recently, survival is usually modeled and described as a probability in a way that controls for bias caused by unknown fates. The likelihood of survival from year-to-year depends on an ungulate's age. It is usually lower from birth through the first year of life but quickly increases to a maximum when animals reach adult body size; survival then remains high through prime age after which it decreases (Eberhardt 2002, MacNulty et al. 2020, Smith 2021). The maximum lifespan of bison in YNP is 20 years old or more for adult females but only about 12 years for adult males because of higher energetic costs and increased risk of injury when sparring for mates during the breeding season (Geremia et al. 2015c).

Annual adult female survival derived from life-table analyses of archaeological bone assemblages at bison jump sites in western North America from 10,200 B.C. to 960 A.D. averaged 73% (0.73), with prime-aged survival (6 to 11 years old) averaging 85%. These rates are lower than contemporary populations, likely because of an abundant and diverse predator assemblage and hunting pressure that no longer affects most modern populations (Clawson et al. 2013). The natural survival of radio-collared females during 1996 to 2012 was 96% for prime-aged 2- to 9-year-olds, 84% for 10- to 15-year-olds, and 78% for 16- to 20-year-olds (Geremia et al. 2015c). Biologists estimated the survival of prime-aged males at 94% (Geremia et al 2009, Wallen et al. 2015b).

Overwinter survival is influenced by bison density and winter severity, both of which affect forage availability (Geremia et al. 2009). Thus, calf survival can be highly variable from year to year (Fuller et al. 2007b). Calf survival was estimated at 75% during the first month of life and 87% for the rest of the year, which is high compared to other ungulates in YNP, such as elk (less than 30%) following the recovery of grizzly bears and wolves (Barber-Meyer et al. 2008, Geremia et al. 2015a,c; Wallen et al. 2015b). The survival rates of adult females in central YNP appear to decrease quicker after 10 years of age because of accelerated tooth wear from ingesting high levels of fluoride and abrasive silica during the consumption of plants, soil, and water in geothermally influenced areas (Garrott et al. 2002, Geremia et al. 2009). About 30% to 40% of the mandibles (jaws) collected from elk and bison killed by wolves in the Madison headwaters area had moderate to severe signs of necrosis (Becker et al. 2009a, Garrott et al. 2009b). The northern region of YNP has far fewer geothermal features and different soils containing less silica.

Brucellosis infection does not appear to affect natural bison survival which remains high and consistent in exposed females (Dobson and Meagher 1996, Fuller et al. 2007b, Geremia et al. 2015b). However, chronic brucellosis infection in the Yellowstone population indirectly lowers the survival of bison because of culling over concerns about transmission to cattle when they attempt to move to lower-elevation areas outside the park (Geremia et al. 2009, 2015b). Management culls are the major source of mortality for bison in YNP due to the capture for slaughter and hunting of bison migrating to the park boundary. Annual survival for radio-collared females 2 to 11 years old decreased to about 83% when biologists included management deaths (Geremia et al. 2009, 2015a,c). Both survival and calving are lower for bison during and after some severe winters, with a population growth rate of less than 4% after severe winters in 2005-2006, 2007-2008, and 2010-2011 compared to an average growth rate of 15% during the IBMP era (Geremia 2023). However, numbers of Yellowstone bison increased during the IBMP era despite these severe winters and the total removal (culls, harvests, quarantine) of about 11,470 bison from 2001 through 2023 (Geremia 2022, 2023).

Recruitment

The number of calves that are produced and survive has a big influence on bison population trends. The annual birth pulse adds hundreds of calves to the population each spring and abundance can increase rapidly if most survive. However, calves are more vulnerable to predation and unpredictable weather conditions, such as severe winters, due to their smaller size and lower body condition. As a result, a moderate portion of calves may die during their first year if conditions are not favorable or bison density is high with more competition for forage (Coughenour 2005, Fuller et al. 2007b, Parker et al. 2009). Adult female bison in YNP have modest pregnancy (70%) and high survival (90%) rates (Geremia et al. 2015a,c). Females produce a single calf, suggesting there could be about 63 calves per 100 adult females at birth. However, this number typically decreases to less than 50 calves per 100 adult females after one month due to neonate mortality, and less than 40 calves per 100 adult females during the remainder of the year depending on the extent of predation, starvation, and other causes of death (Geremia et al. 2015a, Wallen et al. 2015b).

Calves that survive until their first birthday are considered ‘recruited’ into the adult population, which biologists report as a ratio such as 30 calves per 100 adults (or adult females) or 0.30 calves per adult (or female; Caughley and Sinclair 1994). Ratios are usually reported as calves per 100 adult bison rather than calves per 100 adult females because of the difficulty of accurately telling subadult males from females during aerial surveys or from a distance on the ground. Ratios are not ideal for assessing recruitment because they reflect four different processes: adult female survival; pregnancy; birth; and calf survival. However, they can be an informative index of recruitment when adult female survival and pregnancy and birth rates remain relatively constant (Caughley and Sinclair 1994).

Calf to adult ratios of bison based on aerial surveys in May and June from 1970 to 1997, prior to the restoration of wolves, ranged between 15 and 40 calves per 100 adults in northern YNP and 15 to 30 calves per 100 adults in central YNP, with the ratios decreasing as snow pack or drought increased (Fuller et al. 2007b). Calf to adult ratios in June and July from 2000 to 2019, after the restoration of wolves, ranged between 15 and 22 calves per 100 adults (average = 20) in northern YNP and 10 and 22 calves per 100 adults (average = 15) in central YNP (Geremia 2022). Concurrent ground composition surveys of calf to adult ratios from 2003 to 2022 ranged between 14 to 37 calves per 100 adults (average = 29) in northern YNP and 16 to 34 calves per 100 adults (average = 25) in central YNP (Geremia 2022). These results suggest fertility and/or neonate survival may be slightly higher in northern YNP than in the central portion of the park where winter conditions are more severe, and females may have lower body condition during late gestation (DelGuidice et al. 1994, 2001). There also is an indication summer calf to adult ratios based on ground composition surveys decreased (average = 27) in northern YNP during 2014 to 2022 when the herd count exceeded 3,400 bison compared to 2006 to 2013 (average = 35) when the herd was growing and counts ranged between 1,300 and 2,700 bison. During the earlier period, there were substantial reductions in elk numbers in northern YNP and dispersal of bison from central to northern YNP (White et al. 2105c). Continued monitoring will be necessary to determine if this trend continues and the causation.

Brucellosis decreases recruitment because infected females produce substantially fewer calves due to abortions of their first one or two pregnancies, and recovered females produced about 10% to 20% fewer calves than females not exposed to the disease (Hobbs et al. 2015). This decreased recruitment only depressed the estimated growth rate of the population by about 5% compared to a population without brucellosis and contributed to a lower portion of juveniles in the population (Hobbs et al. 2015). Despite these effects, bison still have modest reproductive rates and high survival of calves compared to other ungulates in YNP because of lower rates of predation due to their aggressive and dangerous group defensive tactics (MacNulty et al. 2014). As a result, bison numbers can increase quickly when conditions are favorable (White et al. 2015c).

Age Distribution

Information on the age and sex structure of free-ranging bison populations, including in YNP, is limited because most populations are subject to periodic culling to regulate numbers (Gogan et al. 2010). Since 1995, management culls (slaughter and harvests) were the major source of mortality for radio-collared females and their associated calves in YNP. These culls were not age-specific but focused on female-juvenile groups that tended to migrate to the park boundary earlier and in larger numbers than adult males (Geremia et al. 2009, Geremia 2022).

The age structure of bison from central YNP culled at the western park boundary during 1997 to 2003 ranged from 1 to 16 years, with most animals between 1 and 11 years old (Gogan et al. 2013). The age and sex structure of Yellowstone bison has changed somewhat during the past decades, with the portions of males and older bison increasing in the population (Geremia et al. 2021). Since 2018, the sex ratio of Yellowstone bison has averaged 52% males and 48% females, though males outnumbered females in the central herd (average = 144 males per 100 females) and were underrepresented in the northern herd (average = 98 per 100; Geremia 2022). The age structure of the population was about 28% juveniles and 72% adults over the past five years. Juveniles averaged about 24% of animals in the central herd and 29% in the northern herd (Geremia 2022).

Emigration and Immigration

During the 1960s, there was little movement to unoccupied areas within or outside YNP (Meagher 1973). Beginning in the mid-1970s, however, Yellowstone bison began to expand their range in response to increasing densities, especially during and after severe winters (Taper et al. 2000, Meagher et al. 2002). In addition, bison began to emigrate (disperse) from central to northern YNP during the 1980s and 1990s in response to forage limitations from high bison density exacerbated by severe snow pack (Fuller et al. 2007a). There has been no movement of bison from other populations (immigration) into YNP. Further information on bison movements and range expansion is provided in Chapter 4.

Current Situation

The bison count during the summer of 2022 was the highest (about 5,940) recorded since the establishment of YNP and park biologists recommended removing animals near the northern park boundary through captures and harvests to reduce population growth, support the BCTP (quarantine) and tribal treaty hunts, and reduce conflicts from bison exiting the park (Geremia 2022). Biologists cautioned against removing more than 25% of the population (about 1,500 bison) to avoid unintended consequences on sustainability and future tribal hunting opportunities and transfers of live bison to tribes (Geremia 2022). The subsequent winter was severe, with deep and prolonged snowpack. More than 4,100 bison migrated north of Mammoth in YNP, and about 1,550 bison (27%) were removed from the population), including about 1,175 harvests, 282 for the BCTP, and 88 sent to slaughter (Geremia 2023). Removals consisted of 32% adult males, 32% adult females, 7% yearlings and 29% calves, which reduced the portion of juveniles in the population because a higher proportion (1.7 times) of calves was removed compared to their occurrence in the population (Geremia 2023). Brucellosis prevalence in 660 bison captured at Stephens Creek in northern YNP was 2% in calves, 44% in yearlings, 70% in adult females, and 68% in adult males (Geremia 2023).

Biologists counted about 4,945 Yellowstone bison after calving during the summer of 2023, which was slightly lower than the average count of 5,050 bison over the previous 10 summers (Geremia 2023). During the prolonged and severe winter of 2022-2023, counts of bison decreased by 14% in northern YNP and 16% in central YNP. However, the population maintained a 15% growth rate (after accounting for management removals) because calving remained at the long-term average of about 46 calves per 100 adult females, which offset reduced adult female survival (82%) during the previous winter (Geremia 2023). In other words, the bison population demonstrated demographic resiliency in response to a removal of 27% of the population. The ratio of adult males to females decreased from 52% to 49% in the central breeding herd and 45% to 42% in the northern breeding herd, probably due to reduced adult male survival during the severe winter. Juveniles (calves and yearlings) comprised 27% of the central herd and 30% of the northern herd during the summer count in 2023 (Geremia 2023).

Chapter 4—Seasonal Distributions and Movements

Bison moving single file through deep snow in Yellowstone National Park. Photograph by Jim Peaco, National Park Service, 2008.

Introduction

Snowpack up to 10 feet (3 meters) deep can accumulate in the mountains and on high-elevation plateaus in YNP (Newman and Watson 2009, Watson et al. 2009). Bison adapted to this predictable climate pattern by migrating seasonally, with most animals moving to lower-elevation winter ranges to avoid deep snowpack and returning to higher-elevation ranges in early summer following snow melt to obtain emerging, nutritious forage (Norris 1881a, Whittlesey and Bone 2020). These movements enhance reproduction by increasing access to nutritious foods during late pregnancy and lactation, which contributes to larger calves and higher growth rates. Nutritious forage also may enable females to restore their body condition before breeding again in late summer. Migration to areas with less snow decreases energetic costs during winter which, in turn, increases the likelihood of survival for females and their smaller calves (Wilson et al. 2002, Vervaecke et al. 2005, Gogan et al. 2010, 2013).

Movements of bison within their seasonal ranges are influenced by herd density, forage availability, snow accumulation and melt, terrain features such as rivers and slope, and human influences such as hazing and road grooming (mechanically compacted snow) or plowing during winter (Bruggeman et al. 2007, Geremia et al. 2011). Bison appear to move more during daylight and typically move along gentle gradients and avoid steep slopes (Bruggeman et al. 2006, 2007). They initially move from areas as snow pack increases and the displacement of snow becomes more energetically costly. As snow accumulates across the landscape, however, they necessarily must forage in areas with deeper snow (Bruggeman et al. 2009b). Thus, bison decrease movements to conserve energy as snow accumulates but increase movements in spring as snow melts and forage is exposed in more areas (Bruggeman et al. 2006).

Bison in central YNP tend to travel along rivers during winter, using a self-groomed trail network between foraging meadows and relatively snow-free pockets in geothermal basins (Bruggeman et al. 2007, 2009b). Groomed roads facilitate travel in some places, such as through rugged terrain or forests with substantial downed timber that hinders movements, but most of these road sections align with natural travel corridors bison would naturally use (Bruggeman et al. 2007, 2009a,b). Bison do not appear to preferentially use groomed roads during winter, when bison travel naturally decreases to conserve energy (Bjornlie and Garrott 2001, Bruggeman et al. 2006).

Historic Distribution and Spatial Structuring

Before settlement, the range of bison in the northern Yellowstone area probably extended from the upper Lamar River drainage downslope along the Yellowstone River into the Paradise Valley and towards the present-day town of Livingston, Montana (Skinner et al. 1942, Plumb et al. 2009). By the late 1800s, however, the valleys and foothills north of the park were occupied by ranches and settlements with fences and intense hunting impeding migratory movements by bison out of the park and into these areas (Skinner 1925, 1928; Rush 1932, Skinner et al. 1942; see Chapter 2). Explorer and guide Thomas Hofer saw bison and elk from northern YNP migrate along the Yellowstone River to lower elevations for winter in the late 1870s (Hofer 1918 as cited in Whittlesey and Bone 2020). In 1893, geologist Arnold Hague indicated some bison that spent summer in YNP migrated to lower elevations in Idaho and Montana during winter (Hague 1893 as cited in Whittlesey and Bone 2020). However, other bison spent winter inside YNP near Slough Creek, on the Hellroaring Mountain foothills, and in the Lamar Valley in the north; near Amethyst Mountain and Alum Creek (Hayden Valley) in central YNP; and along the Madison River in west-central YNP (Yount 1881, Whittlesey and Bone 2020).

During the mid- to late 1800s, mixed groups of Yellowstone bison apparently used at least four primary summer and winter areas in the present-day park and nearby areas. Some bison spent summer north of the Lamar Valley in the Absaroka Mountains and on the Buffalo Plateau. These bison moved to the Lamar Valley or north to other valleys for winter (Meagher 1973). Other bison spent summer on the Mirror Plateau south of the Lamar Valley and in the upper Lamar River drainage along the east boundary of the park. These bison moved to the Lamar or Pelican valleys for winter (Meagher 1973). Some bison spent both summer and winter in the Hayden Valley in central YNP, with movements west to the Madison headwaters area (Firehole River) and south to the Elephant Back Mountain area, including near Beach and Dryad lakes (Meagher 1973). In addition, some bison spent summer on the Madison and Pitchstone plateaus in southwest YNP and moved to the Madison headwaters area or south to the Snake River plains for winter (Meagher 1973).

After near eradication, the remnant herd of indigenous bison in YNP spent winter in the Pelican Valley while the herd reintroduced from northwestern Montana and Texas spent winter in the Lamar Valley after about 1910 (Meagher 1973). Bison from both herds moved to the Mirror Plateau and upper Lamar River drainage during summer, where they mingled to some extent through the breeding season (Meagher 1973). In 1936, managers relocated about 71 bison from the Lamar Valley to the Hayden Valley and

Firehole River in central YNP. These bison began moving between the two areas and formed the Mary Mountain herd which bred primarily in the Hayden Valley (Meagher 1973). By 1939 some of these bison were using the Madison Plateau during summer and mixed herds frequently used this area and the Pitchstone Plateau by the 1950s (Meagher 1973). During a severe winter in 1943, about 130 bison migrated west from the Lamar Valley and downslope along the Yellowstone River into Montana, about 30 miles (48 kilometers). Most of these bison returned to YNP within 10 days, but a few (sex not reported) continued into the southern Paradise Valley near Carbella, and one was found on a ranch 8 miles (13 kilometers) south of Livingston (Skinner et al. 1942).

Bison distributions during the 1950s and 1960s were similar, with three spatially separated herds (Lamar, Mary Mountain [Firehole-Hayden], Pelican) during winter. Individual bison tended to use the same breeding and winter ranges among years, especially mature females (Meagher 1973). The winter ranges were not isolated, however, and there were temporary shifts by small groups of bison among ranges with some interbreeding of bison from different herds the following summer (Meagher 1973). Bison usually began migrating from their winter to summer ranges in late May or early June. Some bison occasionally returned to areas of their winter range for a few weeks during summer but the reasons for these movements were unclear (Meagher 1973). Autumn migrations usually began after storms at higher elevations, with final movements to winter ranges by mid-November (Meagher 1973).

The Pelican winter range included the valley along Pelican Creek and lower portions of Astringent Creek and adjacent hot springs to the west. It also included geothermally influenced areas interspersed between the Mushpots and Mudkettles in the north, Pelican Springs in the east, and Vermillion Springs in the west (Meagher 1989b). In the severe winter of 1956, about two dozen bison in a mixed group trailed single file through deep snow along the Yellowstone River to the Hayden Valley. However, this movement was not repeated in subsequent years. The winter range for the Mary Mountain herd included the Hayden Valley and areas along the Firehole River about 15 to 20 miles (24 to 32 kilometers) west, with movements between these areas along the Mary Mountain divide and Nez Perce Creek. Most bison began winter in the Hayden Valley but, as winter progressed, more bison would move west to the Firehole River area where snow pack was lower because of geothermal influences in the Lower and Midway geyser basins (Taper et al. 2000, Meagher et al. 2002). The Lamar winter range included the areas from Hellroaring Creek, east across the lower elevations of the Buffalo Plateau, along Slough Creek, and through the Lamar Valley to Soda Butte Creek (Meagher 1989b). The core of this range was east of the Yellowstone River near Tower Junction for about 6 miles (10 kilometers) to the canyon at the western end of the Lamar Valley (Meagher 1989b, Taper et al. 2000).

The summer distributions of bison changed somewhat during the 1950s and 1960s as managers reduced their abundance substantially through removals, with fewer bison spending summer north of the Lamar and Yellowstone rivers in northern YNP and on the Madison and Pitchstone plateaus in southwestern YNP (Meagher 1973). Bison from the Lamar and Pelican valleys continued to move onto the eastern portion of the Mirror Plateau in June, using meadows from Raven Creek north to Timothy and Flint creeks, and some bison used the area north to Specimen Ridge (Meagher 1973, Taper et al. 2000). Many bison would cross the Lamar River and move east into the Cache, Calfee, and Miller creek areas, eventually continuing upward into the Absaroka mountains along the eastern boundary of the park by late July or early August (Meagher 1973, Taper et al. 2000, Meagher et al. 2002). Mixing of bison from the Lamar and Pelican herds occurred during the breeding season, suggesting they could be considered one interbreeding population with several semi-distinct herds (Meagher 1973). In August, bison would gradually move back to the Mirror Plateau before returning to the Lamar and Pelican valleys by late November (Taper et al. 2000, Meagher et al. 2002). Most bison from the Mary Mountain herd (Hayden Valley/Firehole River) concentrated in the Hayden Valley during the breeding season (Taper et al. 2000).

Range Expansion and Redistribution

During the 1970s and 1980s, bison began to expand their winter ranges to lower elevations as herd numbers increased. These movements occurred well before bison density approached estimates of food-limited carrying capacity based on summer forage production (Coughenour 2005, Bruggeman et al. 2009c, Plumb et al. 2009). The stimulus initiating these movements was deep snow pack that severely limited access to forage at higher elevations, resulting in decreased foraging efficiency and decreasing body condition (Meagher 1989b, Taper et al. 2000, Meagher et al. 2002, Bruggeman et al. 2009c, Plumb et al. 2009). In 1976, the primary wintering area for the Lamar herd was covered by deep, crusted snow, which induced a mixed group of about 60 bison to move west (downslope) along the Yellowstone River to Tower Junction and then the Blacktail Deer Plateau. A half-dozen males continued further west to Mammoth, Wyoming, about 20 miles (32 kilometers) total distance (Meagher 1989b). The bison returned to the Lamar Valley in spring, after which these movements were repeated by groups of males during the next several winters. In 1983, mixed groups of bison began migrating west to the Blacktail Deer Plateau, Mammoth, and the northern boundary of the park near Gardiner, Montana, where there was far less snow (Meagher 1989b).

More bison began making this migration earlier in subsequent winters, with many of them using the road plowed for vehicles between Tower Junction and Mammoth (Meagher 1989b). About 250 bison migrated from the Lamar Valley to the Gardiner basin during the winters of 1986 and 1987, which was about 40% of the Lamar herd. By 1984, large mixed groups of bison began remaining in the Lamar Valley and along lower Slough Creek and Soda Butte Creek during summer, rather than migrating to higher elevations (Taper et al. 2000, Meagher et al. 2002). More bison spent summer in this traditional winter range as the number of bison increased which, in turn, increased the number of bison migrating to lower elevations during winter (Meagher 1989b).

The few bison that migrated beyond the park boundary during winters in the 1970s to mid-1980s were hazed back into the park or killed by Montana game wardens or park staff to prevent the mingling of bison and cattle (Meagher 1989b). As the number of bison migrating outside YNP increased in the mid-1980s, park staff attempted to deter their movements by baiting with hay, cattleguards, fencing, hazing (herding), and scare devices. These efforts failed and MFWP initiated a public hunt for bison (Meagher 1989a,b). Managers removed about 3,120 migratory bison from the population during 1985 through 2000; 25% harvested by hunters and 75% captured and shipped to meat processing facilities (White et al. 2011). These removals generated intense public, political, and scientific debate about bison conservation and disease containment (Cheville et al. 1998).

Prior to the 1980s, bison in central YNP spent winter either in the Pelican Valley or in the Hayden Valley and Firehole River drainage (Meagher 1973, 1989b). Despite increasing numbers, bison rarely moved the 11 miles (18 kilometers) between the Pelican and Hayden valleys, probably due to occasional herd reductions by managers and deep intervening snow pack (Taper et al. 2000, Meagher et al. 2002). Over time, however, the density of bison increased as the size of each herd increased (Taper et al. 2000). During 1982, snow pack was above average and contributed to a winterkill of about 300 bison, which was 20% of the bison in central YNP (Meagher et al. 2002). A mixed group of bison moved west from the Pelican Valley to the northern shore of Yellowstone Lake and then westward from Mary Bay into the Hayden Valley, which was already occupied by bison from the Mary Mountain herd (Meagher 1989b, Taper et al. 2000, Meagher et al. 2002). In addition, bison moved from the Firehole River area north to the meadows west of Madison Junction, where bison had not migrated since the severe winter of 1956 (Meagher et al. 2002).

These movements began earlier in subsequent winters, with higher numbers of bison moving from the Pelican Valley to the Hayden Valley through winter (Taper et al. 2000, Bjornlie and Garrott 2001, Meagher et al. 2002). As the number of bison in central YNP increased, more bison began moving from the Hayden Valley west to the Firehole River drainage and associated geyser basins, including about 1,880 bison in 1996 (Bruggeman et al. 2009c, Geremia et al. 2014). About one-third to two-thirds of the bison in central YNP began to migrate to the Madison headwaters area each winter, with numbers peaking in late March or early April, and some of these bison remained in this area into summer (Bjornlie and Garrott 2001, Bruggeman et al. 2006, 2009c). As bison numbers continued to increase, more bison began to move north along the Firehole River to meadows along the Madison and Gibbon rivers, and some bison continued west along the Madison River to the western boundary of the park (Meagher et al. 2002). Managers hazed these bison back into the park or shot them to stop movements into Montana (Taper et al. 2000).

Bison began to use roads with compacted snow for vehicle travel along these routes (Meagher 1989b, Taper et al. 2000, Meagher et al. 2002). During the 1990s, bison moved from Madison Junction east and north along the Gibbon River to the Norris Geyser basin and then continued further north along the groomed road corridor to Mammoth and the northern boundary of the park (Meagher et al. 2002, Fuller et al. 2007a, Bruggeman et al. 2007, 2009c). About 350 bison migrated along this route during the severe winter of 1997 (Taper et al. 2000, Meagher et al. 2002). Mixed groups of bison also moved from central to northern YNP across the Washburn Range, Solfatara Plateau, and Mirror Plateau during autumn and winter (Bruggeman et al. 2009c). Concurrent with the westward expansion of their winter range, many bison from the Pelican Valley remained in the Hayden Valley during the following summer and through the breeding season before returning to the Pelican Valley in autumn (Taper et al. 2000). As a result, fewer bison moved to the Mirror Plateau and east boundary of YNP each summer until these regular, annual movements ceased by the mid-1980s (Taper et al. 2000, Meagher et al. 2002). Instead, up to 3,000 bison began congregating in the Hayden Valley during summer and the rut, with smaller numbers in the Madison headwaters area (Meagher 1989b, Taper et al. 2000, Meagher et al. 2002, Bruggeman et al. 2009c).

Population substructure can result from different segments of the population, such as the breeding herds in central and northern YNP, primarily using different seasonal use areas due learning and traditional use patterns (Meagher 1989b, Olexa and Gogan 2007, Halbert et al. 2012). Until the 1990s, bison spending winter in the central portion of YNP tended to migrate towards the western boundary and bison in northern YNP tended to migrate towards the northern boundary, with few movements between these regions of the park (Gogan et al. 2005). During 1997 to 2000, radio-collared females had high fidelity to either the central (Hayden Valley) or northern (upper Lamar River drainage/Mirror Plateau) breeding area and did not move between these areas during the peak rut from mid-July to mid-September. Only about 3% of these adult females moved between the central and northern regions of the park after the peak of the rut during mid-September through October, and about 5% to 8% moved between these regions during winter (Olexa and Gogan 2007). Thus, the central and northern breeding herds appeared to function behaviorally and genetically as semi-distinct subpopulations (Olexa and Gogan 2007, Halbert et al. 2012).

The number of bison in central YNP increased from about 1,500 in 1998 to 3,500 by the summer of 2005. As bison density increased, mixed groups began to migrate or disperse to northern YNP during winter (Fuller et al. 2007b, Bruggeman et al. 2009c, Geremia et al. 2014). The impetus for these movements likely included higher bison density, intense hazing by managers to keep bison in the park along the western boundary, and groomed roads that enabled bison to rapidly travel north (Meagher et al. 2002, Geremia et al. 2011, White and Wallen 2012). In addition, there was a decrease in numbers of elk counted in northern YNP from more than 19,000 in the mid-1990s to about 3,900 by 2013 following the restoration of predators such as bears, cougars (mountain lions), and wolves and the continuation of liberal antlerless hunts in Montana until the mid-2000s (White et al. 2023). As elk numbers decreased, the number of bison in northern YNP increased from about 1,500 in 2005 to 4,000 in 2016. In contrast, the number of bison counted in central YNP decreased from about 3,500 in 2005 to 1,200 in 2018 (Geremia 2022).

During 2004 to 2017, about two-thirds of adult female bison fit with radio-collars in central YNP moved in groups with hundreds of other females and young bison to northern YNP during winter. About one-half of these collared females remained in northern YNP at least through the breeding season the following summer (White and Wallen 2012, Wallen and White 2015, White et al. 2022a). Thus, there was significant mixing, breeding, and gene flow between bison originating from these two regions of the park (Fuller et al. 2007a, White and Wallen 2012, Wallen and White 2015). Geneticists from Texas A&M University sampled mitochondrial haplotypes from bison in central and northern YNP during 2011-2012 and did not detect subpopulations. However, they did detect two independent lineages from the remnant indigenous bison and the female bison introduced into northern YNP from northwestern Montana in the early 1900s. Bison from these two lineages were intermixed in both the central and northern regions of YNP (Forgacs et al. 2016). Dispersal movements of bison from central to northern YNP have apparently slowed in recent years as bison density in northern YNP increased substantially. However, Yellowstone bison still appear to constitute a single population with two primary breeding segments (White and Wallen 2012, Wallen and White 2015, Forgacs et al. 2016, Stroupe et al. 2023; see Chapter 7).

Contemporary Migration Patterns

Bison currently occupy about 1.2 million acres (485,620 hectares) in the central and northern portions of YNP and nearby areas of Montana. Bison can roam freely across all wilderness and other undeveloped areas in YNP, which includes more than 99% of the park's 2.2 million acres (8,900 square kilometers). Montana expanded management (tolerance) zones for bison migrating outside YNP, which allows them to access additional resources during winter and year-round in some areas (Bullock 2015). In addition, the CGNF issued a Land Management Plan that allows for expanded tolerance of bison on the national forest, including a desired condition to have a self-sustaining population of bison on the forest year-round (USDA, USFS 2022). However, movements into Montana are often impeded by intense hunting near the park boundary during winter that induces surviving bison to return to the park (White et al. 2015b; see Chapter 8).

Most Yellowstone bison continue to migrate along elevation gradients in response to forage production and snow accumulation or melting (Geremia et al. 2015b). In spring (April through June), bison move upslope as snow melts and highly nutritious vegetation begins growing to spend summer in higher-elevation areas of YNP (Geremia et al. 2015b). When snow begins accumulating in autumn (November), however, foraging efficiency decreases and bison gradually move to lower elevations where less snow accumulates, and food is more accessible through winter (Geremia et al. 2015b). Most females in central and northern YNP have strong fidelity to their breeding ranges, with more variation in the use of wintering areas (Geremia et al. 2014). Since YNP is primarily mountainous, with limited areas of low-elevation winter range, some of these migrating bison eventually move across the park boundary into Montana; usually during late February and March in the north and April and May in the west (Geremia et al. 2014, 2015b). When the density of accumulated snowpack is well above average and forage production is well below average, more than 1,000 bison may migrate toward the boundary of YNP (Geremia et al. 2011, 2014). Substantially fewer bison migrate under more moderate weather and productivity conditions, even when there are more than 5,000 bison in the population (Geremia et al. 2011, 2014).

Bison in northern YNP move upslope during spring as snow melts and new vegetation growth occurs along the Yellowstone River corridor. Once bison reach the Lamar Valley and surrounding areas, however, thousands stop and repeatedly graze portions of the valley and nearby areas through summer rather than continuing to higher or more distant summer ranges (Geremia et al. 2019, 2022; see Chapter 5). Bison move back and forth along the Lamar River between its confluence with the Yellowstone River near Tower Junction in the west to Cache and Calfee creeks in the upper portion of the drainage about 20 miles (32 kilometers) east (Geremia et al. 2014, 2015b). Some bison move onto the higher-elevation Specimen Ridge and Mirror Plateau to the south, with sporadic trips further south to the Pelican and Hayden valleys (Geremia et al. 2014, 2015b). Thousands of bison congregate in the Lamar Valley for the rut, after which some mixed groups make short trips in early autumn to portions of their winter range, perhaps to assess forage availability or consume the remaining high-quality forage prior to grasses becoming cured and dry. These animals generally return to their summer range after a few weeks. Similar exploratory movements are made by bison in central YNP (Geremia et al. 2014, 2015b).

As snow begins to accumulate, most bison begin to move downslope along the Yellowstone River. The timing and extent of snow accumulation and melting in northern YNP varies widely from year to year, which makes it difficult for bison to predict where they will be able to access forage at similar times each year (Geremia et al. 2014, 2015b). Thus, bison use a conditional strategy and respond to changes in foraging efficiency as snow pack accumulates along the elevation gradient on their winter range; as a result, there are large variations in the distribution and movements of bison within and among years (Plumb et al. 2009, Geremia et al. 2014, 2015b). As a deeper snow pack accumulates and becomes denser, foraging efficiency decreases and bison gradually move westward to lower elevations using several pathways through Slough Creek, Tower Junction, the Hellroaring Mountain slopes, Blacktail Deer Plateau, Mammoth, and the Gardiner basin where snow pack is usually minimal and new vegetation growth begins early in spring (Geremia et al. 2011, 2014, 2015b).

Snow conditions in central YNP are more prolonged and severe, but also more similar among winters; as a result, foraging efficiency decreases in a predictable manner (Geremia et al. 2014, 2015b). Bison move to specific foraging areas each year to exploit these predictable seasonal changes and have more regular seasonal distributions (Geremia et al. 2014). However, new grass growth typically begins three weeks later in central than northern YNP (Thein et al. 2009). Thus, many bison in central YNP are just reaching their low-elevation wintering areas along the Madison River near the western boundary of the park when bison in northern YNP are already moving towards their summer ranges (Geremia et al. 2014, 2015b). Several hundred bison in mixed groups from central YNP often migrate along the Madison River and outside the western boundary of the park in April and May when new vegetation is emerging in the Hebgen Lake basin and females are in late gestation (Geremia et al. 2014, 2015b). After calving, these bison return to higher elevation summer ranges in the Madison headwaters area and Hayden Valley during June. Nearly all bison in central YNP move to the Hayden Valley during July and August for the breeding season. Afterwards, many of these bison travel back and forth to the northern shore of Yellowstone Lake and the Pelican Valley (Geremia et al. 2014, 2015b).

As snow accumulates during autumn, many bison gradually leave the Hayden Valley and migrate west across the Mary Mountain divide (trail) to the Firehole River in the Madison headwaters area (Bjornlie and Garrott 2001, Geremia et al. 2014, 2015b). From there, bison can move south into the geyser basins towards Old Faithful or continue downslope (north) to access meadows and geothermal areas along the Firehole, Gibbon, and Madison rivers. Bison often move back and forth through these meadows and thermal areas during the winter (Geremia et al. 2014, 2015b). Some bison continue west along the Madison River to the western boundary of the park, while others move to east and then north along the Gibbon River to the Norris Geyser basin. They then continue north along the roadway corridor to Mammoth. Some of these bison gradually move upslope (east) to the Blacktail Deer Plateau and lower Yellowstone River drainage, before returning downslope to lower-elevation areas in the Gardiner basin (Geremia et al. 2014, 2015b).

Current Situation

The spatial structure of the Yellowstone bison population is dynamic and has changed over time with variations in bison density, management practices, and learning by bison (Geremia et al. 2014). The primary response of bison to increases in abundance was range expansion to alleviate food limitations during severe winters by exploiting new areas (Taper et al. 2000). More bison migrated earlier during winter, and the extent of winter ranges increased, as population size and bison density increased (Bruggeman et al. 2009c, Plumb et al. 2009, Geremia et al. 2014). These movements appeared to be triggered and exacerbated by severe winters with deep, prolonged snow accumulation that limited access to forage on traditional winter ranges (Bruggeman et al. 2009c, Plumb et al. 2009). Range expansion by Yellowstone bison contributed to sustained population growth for two decades during 1976 to 1996 in both the central and northern regions of the park (Taper et al. 2000, Plumb et al. 2009).

The lack of tolerance for wild bison outside national parks is the primary factor limiting their further recovery in the GYE (White et al. 2015b). One of the most vexing problems for Yellowstone bison is the lack of available lower-elevation habitat north of the park. The valley bottoms in this area have accessible forage and less snow than surrounding mountains during winter but were already overgrazed by cattle in the early 1900s and are currently used for agricultural and residential development (Rush 1932, Hansen and Phillips 2018). Thus, large portions of the historical winter ranges used by bison are no longer available. Also, there are political and social concerns about allowing bison to migrate outside the park, including competition with livestock and other ungulates for grass, diseases such as brucellosis, human safety and property damage (including agricultural crops), and a shortage of funds for state management (Bailey 2013, White et al. 2015b). Thus, re-establishing large populations of wild, migratory bison is one of the greatest conservation challenges of our time (White et al. 2015b,c; Geremia et al. 2021).

Chapter 5—Resource Selection and Nutritional Condition

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Frost-covered bison bedded in Yellowstone National Park.
Photograph by Jacob W. Frank, National Park Service, 2018.

Introduction

Winter is a period of prolonged undernutrition for bison in mountainous YNP because grasses are cured, dormant, and low in digestibility, energy, and nutrients, while snowpack reduces access to forage and increases energy expenditures (Meagher 1973, Houston 1982). The body condition of bison decreases with inadequate nourishment for maintenance which triggers the break-down (metabolization) of fat reserves and protein for energy (Torbit et al. 1985, DelGuidice et al. 1994, 2001). This progression leads to animals losing about 10% to 20% of their body weight over the course of the winter depending on the severity of conditions (DelGuidice et al. 2001, Coughenour 2005, Parker et al. 2009). Some animals experience severe malnutrition and starvation once their fat reserves become depleted and too much muscle is metabolized for energy (Torbit et al. 1985, DelGuidice et al. 1994). It is essential for bison that survive to increase their energy and nutrient intake (nutrition) and replenish their nutritional (body) condition during the relatively short summer by feeding on nutritious vegetation (Parker et al. 2009). In most years, snowmelt and spring rains increase soil moisture and stimulate the production of abundant grasses which provide nutrition for supporting lactation, replenishing body condition, and perhaps producing a healthy calf the following spring (Parker et al. 2009).

Bison adapted to these predictable seasonal changes by developing a general foraging strategy to meet their energetic needs through the year (Treanor et al. 2015). In winter, they minimize energy costs and protein losses and reduce activity and daily food intake (Parker et al. 2009). In spring, females give birth and provide high-protein milk to calves by eating newly emerging forage high in digestible energy and protein (Parker et al. 2009). This nutritious milk is critical for calves to attain larger sizes with more reserves before the onset of winter (Parker et al. 2009). In summer, females maximize the intake of high-energy, high-protein forage to replenish their body condition, enable pregnancy during autumn, and support gestation through winter (Parker et al. 2009). Mature males eat little during the late-summer breeding season, which is energetically and physically draining, but increase forage intake after breeding to replenish some of their fat and protein reserves before winter (Parker et al. 2009). Likewise, females and calves continue high forage intake in late-summer and autumn to prepare for prolonged undernutrition through winter (Parker et al. 2009). Calves are more susceptible to starvation during severe winters due to their smaller body size with limited fat and protein reserves (Parker et al. 2009).

Habitat Use and Diet

Yellowstone National Park and nearby areas of Montana support a variety of plant communities due to variable topography, soils, and weather. About 1,150 native plants occur in YNP, including three plants found only in or near the park (Ross's bentgrass, Yellowstone sand verbena, and Yellowstone sulfur wild buckwheat) and 97 other rare plants. Vegetation is composed primarily of typical Rocky Mountain plants in montane forests, sagebrush steppe, alpine meadows, wetlands and riparian areas, and geothermal communities (Despain 1990). Yellowstone bison use numerous habitats through the year, including grasslands, sedge meadows, upland sagebrush steppe, burned and unburned forest, geothermally influenced areas, sub-alpine, river and stream riparian areas, old agricultural fields, and irrigated alfalfa pastures outside the park (Meagher 1973). The Hayden and Pelican valleys support highly productive grassland communities, while the Madison headwaters area includes several interconnected geyser basins and productive sedge meadows (Meagher 1973). The Lamar Valley supports extensive grassland meadows and dense sedge growth along rivers and streams, with sagebrush steppe on mountain foothills, and forests with wet meadows at higher elevations, such as on the Mirror Plateau (Meagher 1973). Park managers introduced many cool-season, nonnative grasses in the Lamar Valley during the early 1900s as bison forage (hay; Skinner et al. 1942). The riparian zone along the river through the Lamar Valley contains sparse stands of cottonwood trees with increasing densities of lodgepole pine, Douglas fir, and willow in the Lamar Canyon and near the confluence of the Lamar and Yellowstone rivers (Despain 1990, Meagher and Houston 1998).

Most management activities with bison in YNP occur in the high-desert environment of the Gardiner basin, which is not a particularly favorable winter range for bison because of its relatively poor soils on active mudflows, low annual precipitation, high winds, and heavy historical use by livestock and native ungulates (Rush 1932, Whittlesey 1995). An account from the Langford-Washburn-Doane Expedition of 1870 (Secretary of War 1874:5) describes native vegetation in the Gardiner basin as "[t]his desert region, inclosed [sic] by mountains covered with verdure, and on the banks of a large stream, is one of the anomalies common in the West, where the presence of limestones or sandstones, in horizontal strata especially, almost always mean want of water, and consequent desolation. We camped at the mouth of Gardiner's [sic] River, a large stream coming in through a deep and gloomy canyon from the south. This was our first poor camping place, grass being very scarce." This area has had relatively sparse vegetation since that time (Whittlesey 1995; USDI, NPS 2006b). Congress added a 7,600-acre (243-hectare) portion of the basin to YNP during 1925 to 1941, primarily to provide lower-elevation habitat for elk, pronghorn, and other animals during winter (Whittlesey 1995). Previously, settlers homesteaded, tilled and irrigated, ranched, or hunted for wild animals, primarily ungulates, on most of this area (Whittlesey 1995). This area was overgrazed, with nonnative grasses such as cheatgrass and erosion of the topsoil, by the 1920s due to heavy use by cattle and horses (Rush 1932).

Grasses and grass-like plants (sedge, rush) comprised 96% of diets (volume) through the year during the 1960s (Meagher 1973). Sedges were the main forage in all seasons, averaging more than one-half of rumen contents. During winter, bison in the Lamar Valley of northern YNP primarily fed on sedges in wet sites and bison in central YNP primarily fed on sedges in thermally influenced areas (Meagher 1973). Grasses averaged about one-half the diet during spring, while rushes represented one-third of the autumn diet. Forbs and browse comprised less than 3% of the diet (Meagher 1973). During winter in the late 1980s, graminoids (grasses, sedges, rushes) comprised most of bison diets with conifers, forbs, and shrubs comprising less than 5%. The diet of bison in northern YNP was primarily grasses (55% to 65%) compared to the Pelican Valley where bison primarily subsisted on sedges (75% to 80%; DelGuidice et al. 1994, 2001).

Seasonal changes in diet quality for Yellowstone bison, reflect predictable changes in the phenology (growth cycle) of grasses (Treanor et al. 2015). The summer ranges for bison in YNP are dominated by cool-season grasses and sedges. Young plants contain more digestible carbohydrates and less fiber during the growing season, which makes them more digestible and nutritious than older plants as the growing season progresses (Treanor et al. 2015). Thus, bison select areas with young plants high in nutrients during spring and summer, but transition to areas with higher plant availability during autumn and winter when grasses are past their growing period and there is relatively little variation in quality among areas (Wallace et al. 1995, Wallen et al. 2015b). Male bison in YNP may eat a slightly greater variety of plants while female diets may be somewhat higher in quality (Berini and Badgley 2017). The large rumens of adult male bison enable them to retain forage longer and efficiently convert large quantities of high-fiber forage into digestible energy. Females require somewhat higher quality forage than males because forage passes through their smaller rumens quicker and, as a result, they extract less useable energy. Thus, males may focus more on forage quantity while females may be somewhat more selective in terms of quality (Berini and Badgley 2017).

Foraging Behavior

Bison in YNP spend about 60% of daylight foraging; nighttime activity is not known (Rutberg 1986). Bison make multiple decisions prior to and during foraging, including the selection of a foraging area, patches within that area, and plants within each patch (Bruggeman 2006). The duration of foraging in an area depends on its perceived value compared to other recently visited sites based on the quantity and quality of available forage, snow cover, previous foraging experiences (learning), and competition with other bison and species of ungulates (Bruggeman 2006). Older, larger females are dominant over younger animals and often displace them from preferred foraging sites, resulting young bison spending about 5% less time ingesting forage (Rutberg 1986).

Yellowstone bison adjust their nutritional intake by moving across the landscape seasonally as the availability and quality of forage changes. They move from higher-elevation summer ranges to lower elevations during autumn through winter, and then return to the summer ranges in June (Geremia et al. 2015b). Grass quality has little influence on the selection of foraging areas used by bison during winter because plant tissues are dead, high in fiber, and low in nutrition. Instead, factors that influence the availability of forage, such as snow pack and bison density, become more important (Wallace et al. 1995, Bruggeman 2006). Bison tend to select foraging patches in areas with less snow because displacing snow reduces efficiency and contributes to increased energetic costs (Bjornlie and Garrott 2001, Harvey and Fortin 2013). They sometimes feed in meadows with higher snowpack but usually in small areas where forage is concentrated (Harvey and Fortin 2013). As an area becomes covered by deeper snow or occupied by numerous animals competing for forage, bison will eventually search for another area with less snow or fewer animals (Bruggeman 2006, Bruggeman et al. 2009c). As a result, large shifts in bison distribution may occur to lower-elevation meadows with more energy efficient foraging during severe winters. In other words, as snow pack increases, the available foraging area decreases (Bruggeman 2006, Bruggeman et al. 2009c). Bison in central YNP often choose to feed in geothermally influenced areas where the time and energetic costs of displacing snow are minimal, but the quantity of forage is relatively low and there are other costs to feeding, such as faster wear of teeth due to silica in the soil and high arsenic and fluoride concentrations in water and plants (Kocar 2002, Garrott et al. 2002, 2009b; Christianson et al. 2005, Geremia et al. 2009).

During spring, there are more energy-efficient foraging opportunities for bison at lower elevations because snow melt and vegetation growth start earlier (Thein et al. 2009). Thus, most calving occurs in these areas (Jones et al. 2010). The migration of bison to higher-elevation summer ranges coincides with new grass growth on the landscape (Thein et al. 2009 provides detailed descriptions and maps). Highly digestible graminoids eventually become widely distributed and energy intake by bison increases. During summer, bison tend to repeatedly graze productive areas, selecting grasses from dry uplands and grasses and sedges from moist sites (Wallace et al. 1995, Geremia et al. 2019). During 1998 to 2000, bison in the Hayden Valley foraged in upland grasslands until they had eaten 50% to 60% of the forage and efficiency decreased, after which they moved to ungrazed patches or grazed patches with regrowth (Olenicki and Irby 2003 as cited by Coughenour 2005).

In northern YNP, numbers of elk decreased by more than 70% during the 2000s following the recovery of large predators such as wolves, bears, and cougars. A much greater portion (80%) of the smaller northern Yellowstone elk population now spends winter on lower-elevation areas with less snow outside the park (White et al. 2012). At the same time, bison numbers in northern YNP increased from about 600 in 2000 and 900 in 2005 to 4,500 in 2022 due to high survival and calving combined with movements of bison from the central to the northern part of the park (White et al. 2015c, Geremia 2022). Bison began using grasslands in this area quite differently than elk during summer. They moved upslope as new vegetation growth occurred along the Yellowstone River corridor, but once they reached the Lamar Valley and surrounding areas, thousands stopped and repeatedly grazed portions of the valley and nearby areas through summer rather than continuing to higher or more distant summer ranges like elk (Geremia et al. 2019, 2022). Bison began using this winter range area for elk as a summer grazing area. In turn, far fewer elk now use this area during winter (White et al. 2012).

Many groups of bison move back and forth across the Lamar Valley during summer, repeatedly returning to the same areas every few weeks to intensively re-graze cool-season grasses that have proliferated from the abandoned hayfields cultivated in the early 1900s (Geremia et al. 2019). This behavior keeps the grasses growing in a short, spring-like condition that is nutritious. These grazing lawns of dense, short-statured plants sustain highly nutritious food by prolonging new plant growth and stimulating nutrient cycling and water-holding potential (McNaughton 1985, Geremia et al. 2019). The deposition of feces and urine into the soil releases plants from nitrogen limitation, and precipitation is the primary factor influencing plant growth (Frank et al. 2013 and references therein, Geremia and Hamilton 2019, 2022). Through this behavior, bison create and maintain grasslands that green-up earlier each year, grow faster and more intensely, and remain in a nutritious condition for a longer duration (Geremia et al. 2019, 2021).

Energetics

Bison meet the nutritional demands of growth, reproduction, and survival by selecting nutritious forage from spring to autumn and reducing nutritional needs and using body reserves during winter (DelGuidice et al. 2001, Treanor et al. 2015). Female bison usually have higher energy demands than males because of gestation and lactation, which peak in early to mid-summer and continue as females try to replenish their body condition prior to the next breeding season (Berini and Badgley 2017). The energy demands of males also peak in early to mid-summer as they attempt to restore their body condition before the breeding season in late summer. Both males and females spend less time foraging during the breeding season and prime-aged 6- to 10-year-old males can lose most of their subcutaneous fat from the strenuous competitions for mates (Plumb and Dodd 1993, Komers et al. 1994).

The availability of nutritious forage in spring during late gestation and lactation is a primary factor influencing the timing of parturition for ungulates in temperate, montane environments (Parker et al. 2009). Calving in northern YNP occurs about two weeks earlier than in central YNP, concurrent with the earlier snow melt and nutritious grass growth in the north (Gogan et al. 2005). Snow melt begins about 24 days earlier at lower elevations in northern YNP, so there are earlier foraging opportunities on new grass growth with less energetic costs while higher-elevation areas in central YNP are still covered with snow (Gogan et al. 2005, Thein et al. 2009). Thus, the central region of the park typically has a shorter growing season for bison to support lactation and restore body condition after winter.

Bison decrease their metabolic rates during winter through hormonal changes in response to less daylight and colder temperatures (Christopherson et al. 1979, Feist 2000). They generate heat through digestive fermentation of high fiber diets but decrease activities, energy requirements, and food intake during this prolonged period of under-nutrition (Gogan et al. 2010, Treanor et al. 2015). Despite these changes, foraging is still the major energetic cost to bison during winter (Bruggeman et al. 2006, 2009c). Bison in central YNP spend about two-thirds of their time during winter foraging, and displacing snow to access forage accounts for more than one-third of that time (Bjornlie and Garrott 2001, Bruggeman et al. 2009a-c). Digestible energy intake by adult female bison is greater in northern than central YNP, and lower in the Hayden Valley with deeper snows than in the Madison headwaters area where geothermally warmed basins reduce snow accumulation and afford easier access to vegetation (DelGiudice et al. 2001, Bruggeman et al. 2009a-c).

Travel comprises a relatively small part of Yellowstone bison activity (8% to 11%) during winter, with only about 7% to 12% of travelers displacing snow (Bjornlie and Garrott 2001, Bruggeman et al. 2009a,b). Bison travel through unbroken snow (6%), broken snow on trails created by other bison or species of ungulates (74%), and on roads plowed for wheeled vehicles or groomed for snowmobiles and coaches (20%; Coughenour 2005). Travel costs comprise about 11% to 14% of energy costs for bison (Coughenour 2005). About 80% of their travel occurs off road, though they learn to use plowed or groomed roads in some areas (Bjornlie and Garrott 2001, Coughenour 2005, Bruggeman et al. 2009a,b).

Body Condition

Protein requirements for pregnant bison increase in late winter and early spring when fetus growth accelerates (Robbins 1993). Females meet this demand by metabolizing fat and protein reserves and, in the process, lose a substantial amount of body mass (weight; Treanor 2012). If winters are severe and prolonged, and nutritional intake remains low until parturition, the survival of neonates can be reduced (Cook et al. 2013, Treanor et al. 2015). Body mass is a relatively good indicator of nutritional condition in bison and females in better condition tend to be more dominant, probably by obtaining better feeding opportunities and nutrition than subordinates. Dominant females tend to produce more and heavier calves, while old and immature females in poorer condition are not as fecund (Wilson et al. 2002, Vervaecke et al. 2005). Smaller neonates tend to grow slower because of lower nutrition and become small adults which, in turn, produce fewer and smaller calves (Treanor et al. 2015).

About 80% of calves in YNP are born from late April to late May when forage high in protein and digestible energy typically becomes available on low-elevation winter ranges (Jones et al. 2010, Treanor 2012, Treanor et al. 2015). Females in better condition tend to synchronize calving when nutritious plant growth is available to increase the quality of milk for lactation and, perhaps, to dilute predation risk on calves (Berger and Cain 1999). Lactation is nutritionally demanding, with protein requirements increasing 110% to 130%, and milk fat is primarily derived from food intake rather than body reserves (Robbins

1993, Parker et al. 2009). Thus, the growth of calves in the early months of life, which affects their ability to survive the upcoming winter, depends on the quality of food available to their mothers for milk production (Treanor et al. 2015).

The availability of high-quality forage during summer enables bison to replenish their body reserves for ovulation, breeding, gestation, and winter survival (Parker et al. 2009). Fat reserves are necessary for energy and protein during winter, especially for pregnant females during late gestation. In addition, the growth and survival of calves is positively affected by the nutritional quality of summer forage (Parker et al. 2009). Dominant females tend to have heavier calves at weaning, which increases their survival and likelihood of reproduction at a younger age (Vervaecke et al. 2005). In addition, dominant (heavier) males tend to have better success during competitions for mates and, as a result, higher reproductive success (Rutberg 1986, Vervaecke et al. 2005). Thus, bison increase forage intake during the growing season, which increases the integration of nutrients to replenish their body condition (Parker et al. 2009).

Reproductive success in adult female bison usually varies less than in males which compete for breeding opportunities. However, fewer females may ovulate and become pregnant after winters with severe malnutrition, or during droughts that limit forage availability, which reduce their ability to replenish body condition by the rut; especially lactating females (DelGuidice et al. 2001, Vervaecke et al. 2005). In other words, the body condition of female bison, based on their ability to access summer forage with adequate digestible energy to replenish fat and protein reserves, largely determines whether they will ovulate and become pregnant (Treanor et al. 2015). The portion of females in YNP conceiving as yearlings and calving as 2-year-olds depends on their level of body condition and generally ranges between 4% and 12% (Gogan et al. 2010). Females usually give birth to their first calf as 3- or 4-year-olds (Geremia et al. 2015c). During 1997 to 2003, pregnancy rates were higher in females in better body condition as indexed by weight (Gogan et al. 2013). Females in some herds or populations, including central YNP, may produce calves every two or three years because of the nutritional cost of gestation and lactation, and the difficulty in replenishing body condition prior to the next breeding season (Gogan et al. 2010).

Bison in YNP experience progressive nutritional deprivation through winter, with increasing catabolism (break down) of fat and muscle (DelGuidice et al. 1994). Winter forage intake helps reduce the rate at which these reserves are mobilized, and dominant females have higher foraging efficiency in snow-covered environments (Rutberg 1986, Vervaecke et al. 2005). Bison calves typically have 40% to 50% lower fat reserves and higher mortality rates than adults, especially during severe winters (DelGiudice et al. 2001). Under-nutrition and fat and protein metabolism are usually higher in bison spending winter in central than northern YNP because of the more prolonged and harsher winter conditions, especially snow depth and density that restricts nutritional intake (DelGuidice et al. 1994, 2001). Fat contents for adult female bison in March during the moderate winter of 1988 were 3% to 4% in central YNP and 5% to 7% in northern YNP (DelGiudice et al. 2001). The milder nutritional restriction of bison in northern YNP is likely due to shallower snow cover and greater access to forage compared to the more severe winter conditions in central YNP that limit access to forage, increase the energetic costs of foraging and movements and, in turn, lead to increased depletion of body fat and protein (Torbit et al. 1985, DelGiudice et al. 2001). Likewise, indices of nutrition were consistently lower for bison in the Hayden Valley than bison in the Madison headwaters area during 2005-2006 (Bruggeman et al. 2009c). Deep snows frequently become crusted in the Hayden and Pelican valleys due to prevailing westerly winds which increase the energetic costs of foraging and traveling and exacerbate nutritional deficiencies (Watson et al. 2009).

Effects of Grazing

Several independent researchers assert herbivory (grazing, browsing) and trampling by increasing numbers of bison in northern YNP are degrading grasslands, limiting the recovery of woody riparian vegetation, and degrading river channels in the Lamar Valley (Hunter et al. 2018, Beschta et al. 2020, Kauffman et al. 2023). Overgrazing (or overbrowsing) occurs when widespread, repeated foraging removes so much leaf tissue that plant productivity and regrowth decrease considerably, and soils become compacted and unproductive with fewer available nutrients (Crawley et al. 2021). Excessively grazed areas are vulnerable to erosion and invasion by nonnative plants due to less plant litter and more bare ground. Signs of overgrazing include changes in the variety (composition) of plants, the spread of nonnative plants, and poor body condition and lower productivity in ungulates (Crawley et al. 2021). Overgrazing usually occurs when the abundance of ungulates is kept artificially high by supplying supplemental food during winter in temperate climates or moving additional animals into an area during the plant growing season (Coughenour 2008, Crawley et al. 2021). These effects are usually observed in livestock, not wildlife populations, though impediments to movements (for example, fences and highways) or severe winter conditions can increase the effective density of wildlife in an area and lead to overgrazing (Coughenour 2008, Crawley et al. 2021).

There were vibrant, tall willow communities with beavers from the Blacktail Deer Plateau to the upper Lamar Valley during the late 1800s and early 1900s (Meagher and Houston 1998). However, the establishment of willows decreased after the 1930s and beavers disappeared which, over time, led to the incision (downcutting) of stream channels and a lower water table across the floodplains (Wolf et al. 2007). Much of northern YNP was characterized as "badly overgrazed" by the 1930s from as many as 3,000 horses on the Blacktail Deer Plateau and increasing numbers of elk in the Lamar Valley (Rush 1932:47-48). The horses were removed, and from 1935 to 1968, tens of thousands of elk were removed from the population via hunting in Montana, shooting in the park, and capture and culling in the park (Houston 1982). After these removals ceased, counts of northern Yellowstone elk increased rapidly, with the biomass of all ungulates in northern Yellowstone stabilizing around 8.8 million pounds (4 million kilograms) during the 1980s and 1990s (Geremia and Hamilton 2019). Elk dominated the ungulate guild, with more than 20,000 animals in the 1980s and 1990s (White et al. 2023). Aspen, cottonwood, and willow were extensively browsed, with little to no recruitment (Wolf et al. 2007). During severe winters in 1989 and 1997, large die-offs of elk suggested they were near a food-limited carrying capacity on the winter range, which included the Blacktail Deer Plateau to Lamar Valley area (Coughenour and Singer 1996, Singer et al. 1997, Taper and Gogan 2002, Coughenour 2005). During the twentieth century, many riparian communities in northern Yellowstone transitioned from a beaver-willow state to an elk-grassland state and browsing by elk is widely accepted as a primary cause of this transition (Hobbs and Cooper 2013, Peterson et al. 2020).

Nonnative grass species, including Kentucky bluegrass and timothy, were already prevalent in the grassland-dominated sites of the Lamar Valley by the 1930s from cultivating and feeding hay (Rush 1932, Skinner et al. 1942, White et al. 2022c). Between 1904 and 1952, about 575 acres (233 hectares) in the Lamar Valley were cleared of native vegetation and cultivated with nonnative grasses, including oats, smooth brome, slender wheatgrass, clover, dandelion, and timothy, to grow hay in support of bison restoration (Rush 1932, Baggley 1934, Skinner et al. 1942). These cool-season grasses grow best when the weather is moist and cool because they do not use water efficiently; rather they are well adapted for the cool, wet, nitrogen-rich habitats of the mid- to high-elevations of northern YNP. These grasses thrive when grazed and are usually more productive than native bunchgrasses (Geremia and Hamilton 2019, 2022). As a result, these planted cool-season grasses displaced native plants in wet areas across much of northern YNP and now dominate plant communities from Tower Junction to the upper Lamar Valley (Geremia and Hamilton 2019, 2022).

Predation from recovered large carnivores, liberal harvests of antlerless elk migrating into Montana, and food limitations from a 10-year drought decreased large ungulate biomass in northern YNP to between 4.4 and 6.6 million pounds (2 and 3 million kilograms) through the 1990s and early 2000s (Vucetich et al. 2005, White and Garrott 2005, Geremia and Hamilton 2019). As a result, elk density and browsing intensity decreased. Willow heights increased slowly from 2001 to 2016, but growth was hindered in areas where water tables were low due to stream channel incision; willows could not access sufficient groundwater (Beyer et al. 2007, Painter and Ripple 2012). As a result, most riparian communities did not recover to their historical tall distributions (Hobbs and Cooper 2013, Peterson et al. 2020).

Bison numbers increased rapidly in northern YNP after 2005 due, in part, to the dispersal of bison from central to northern YNP. The exact causes are unknown but potential contributing factors include: 1) high bison densities, intense grazing in some areas, and severe winters (1997, 2006, 2008) in central YNP that limited forage availability; 2) intense hunting during the 1980s and hazing of bison during the 1990s and 2000s along the western boundary to keep them in the park; 3) roads groomed for over-snow vehicles that facilitated rapid travel by bison to the north during winter; 4) higher wolf densities and predation of bison in central YNP during the early 2000s; and 5) a 50% decrease in numbers of elk spending winter in northern YNP by 2006 and a 75% decrease by 2013 (Taper et al. 2000, Meagher et al. 2002, Becker et al. 2009a,b; White et al. 2015c, Tallian et al. 2017). As a result, ungulate biomass in northern YNP again increased to near 8.8 million pounds (4 million kilograms; Geremia and Hamilton 2019, 2022).

To summarize, many riparian communities in northern YNP transitioned from a beaver-willow state to an elk-grassland state during the twentieth century due to elk browsing, well before the substantial increase in bison numbers during the last 15 years. Abundant bison are suppressing the regeneration of some riparian habitat in northern YNP that was extensively degraded by elk herbivory (Ripple et al. 2010, Painter and Ripple 2012, Peterson et al. 2020). However, it also appears the recovery of beaver populations may be necessary to raise the water table for widespread recovery of willows to occur in many areas on the Blacktail Deer Plateau and Lamar Valley (Hobbs and Cooper 2013, Peterson et al. 2020). Some colonization by beavers has occurred, but the elk-grassland state may prevail unless they recolonize a much greater portion of northern YNP (Peterson et al. 2020, Tyers 2020).

In addition, the climate of northern YNP has warmed and dried significantly since the 1980s, and this trend is forecast to continue (Tercek et al. 2015, Thoma et al. 2015, Hostetler et al. 2021). This warming has already changed the composition and distribution of vegetation and facilitated the spread of winter annuals in many areas, which likely will continue and could preclude a transition of most grasslands back to a willow-beaver state (Peterson et al. 2020). Warm-season nonnatives, including desert alyssum and cheatgrass, are gradually invading the warm and dry low-elevation range habitat types and have the potential to displace native plants and unbalance the functional integrity of plant communities (Renkin 2022, Wacker 2022). These plants grow in dry soils, where there is intense competition for moisture. Winter annuals can outcompete native plants by sprouting in the fall, with already germinated annuals then monopolizing early spring pulses of water (Renkin 2022, Wacker 2022). The abundance and distribution of winter annuals will likely depend on how much northern YNP 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 YNP (Geremia and Hamilton 2019, 2022).

Another uncertainty is the long-term effects of the record-breaking flooding events of June 2022 across northern YNP that changed the hydrology and vegetation along each river and stream in the drainage. This flooding was considered a 1-in-500-year event and northern parts of the park received 2 to 4 inches (5 to 10 centimeters) of rain in a 24-hour period, together with at least 5.5 inches (14 centimeters) of snow melt. This flood event caused extensive erosion along river corridors, realigned waterways in many places, and deposited extensive sediment (sand, silt) in many previously vegetated areas along river banks and on floodplains. In the long term, the deposited sediment should provide a substrate for the regrowth of cool-season grasses, forbs, and riparian plants like cottonwoods and willows. However, there also is the potential for the spread of less nutritious, nonnative winter annuals, such as annual wheatgrass, cheatgrass, and desert alyssum, into these disturbed areas, especially if conditions become drier. Recurrent and prolonged drought would lower soil moisture and organic matter, which could support the proliferation of winter annuals, particularly given the high concentration of nitrogen in the soil (Geremia and Hamilton 2019, 2022). It will take additional years of monitoring and research to determine if repeated intense grazing by numerous bison in the Lamar Valley combined with ongoing environmental changes is inducing another state transition in certain vegetation communities in northern YNP.

Grasslands dominate valleys in northern YNP and graminoids comprise most of the vegetation and ungulate diets (Geremia et al. 2019, 2022). Elk primarily feed on forbs and graminoids, which make up more than 85% of summer and winter diets, while browse makes up less than 10% of diets (Singer and Norland 1994, McGarvey and Geremia 2022). Bison also prefer graminoids, which make up about 97% of their diets (Meagher 1973, Singer and Norland 1994, McGarvey and Geremia 2022). Monitoring and research of grasslands in northern YNP during 2015 to 2022 by park biologists and collaborators indicated soil organic matter was stable and within ranges supporting nutrient cycling, water-holding potential, and physical structure. Grazed plant communities maintained primary production compared to fenced areas where grazing was precluded, although at least one area of the Lamar Valley had a gradual decline in production over time (Geremia and Hamilton 2019, 2022). Greenhouse studies of the dominant grasses in the Lamar Valley found they maintained growth while being grazed and transferred resources to root production during wet years (Geremia and Hamilton 2019, 2022). In addition, the grassland community contains the same native species at the same sites compared to what grew there in the 1980s (Frank 2022). These findings are indicative of a highly resilient grazing community of interacting plants and ungulates (Crawley et al. 2021). However, there is evidence the composition of plants in the grassland community has shifted somewhat in recent years, which may continue for the reasons described in the previous paragraph (Frank 2022; C. Geremia, NPS, unpublished data).

Current Situation

The warming trend in the GYE is predicted to continue, with an increase in average annual temperatures of another 2°F across all seasons, milder winters with fewer days below freezing, and earlier spring vegetation green-up (Hostetler et al. 2021). With less snow and an earlier snow melt, the growing season could start about two weeks earlier during some summers, but there would be more hotter days and more frequent droughts (Gross and Runyon 2020, Yellowstone Center for Resources 2021). These changes will modify the timing and production of forage, as well as ungulate body condition, movement patterns, and demographic rates, in complex and contrasting ways (Wilmers et al. 2013, Lachish et al. 2020). For example, shorter winters could increase the length of the growing season while hotter, drier summers could result in the senescence of vegetation earlier in the summer (Lachish et al. 2020). These conflicting changes could have substantial, but divergent, impacts on population trends by increasing and decreasing nutrition and body condition (Wilmers and Getz 2005, Lachish et al. 2020). Research on elk populations in the northwestern U.S. has already detected a decrease in recruitment from 1989 to 2010 due, in part, to changes in precipitation patterns and forage conditions (Lukacs et al. 2018).

Bison carcass with coyotes in Yellowstone National Park.
Photograph by Jim Peaco, National Park Service, 2015.

Chapter 6—Competition and Predation

Introduction

Seven ungulates other than bison live in YNP seasonally or year-round, including elk, pronghorn, bighorn sheep, mule deer, moose, mountain goats, and white-tailed deer. There are relatively few white-tailed deer in the park and moose and mountain goats generally use different areas and habitats than bison. Bison are the only large ungulate in the Pelican and Hayden valleys during winter, and there are relatively few elk in the Madison headwaters area after wolf restoration (Becker et al. 2009a,b). In contrast, northern YNP has thousands of elk during summer and hundreds of bighorn sheep, elk, mule deer, and pronghorn that overlap spatially to some extent with bison during winter (Singer and Norland 1994, McGarvey and Geremia 2022).

Large predators in the GYE include black and grizzly bears, cougars, and wolves. During 1995 to 1997, biologists released 41 wolves in YNP, and their abundance and distribution rapidly increased with a growth rate of about 20% per year (Smith et al. 2020). This restoration coincided with the continued increase and expansion of populations of grizzly bears and cougars in the northern Yellowstone area (White et al. 2017a, Ruth et al. 2019). As a result, a complete association of native ungulates and large predators again lived in the region by the mid-2000s, when there were about 3,500 bison in central YNP and 1,500 bison in northern YNP (Geremia 2022).

Competition

Competition may occur when animals consume a resource or exclude others from doing so and, in turn, decrease the ability of the other animals to survive and reproduce (Begon et al. 2005). There is the potential for intraspecific competition among bison for forage as their numbers and density increase and resources become more limited. There also may be interspecific competition with other ungulate species with similar seasonal diets, though small differences in habitat and forage selection can reduce this potential (Caughley and Sinclair 1994). Graminoids are important foods for many ungulates in YNP, including bison (97% of winter diet), elk (86%), and bighorn sheep (67%; Singer and Norland 1994). As bison numbers in northern YNP increased during the 1970s and 1980s, they expanded their geographic range and, in turn, their diet and habitat overlap with other ungulates increased (Meagher et al. 2002). There was a moderate overlap in diet and a large overlap in habitat with elk that could contribute to competition (Singer and Norland 1994, Coughenour 2005).

Elk—The northern Yellowstone elk population spends winter on more than 580 square miles (1,500 square kilometers) of grasslands, sagebrush steppe, and lodgepole pine forests adjacent to the Yellowstone River and its tributaries. About two-thirds of this winter range is within the northern portion of YNP, while the remainder is in Montana to the north. During the 2000s, predation, in combination with liberal hunter harvests in Montana and occasional severe weather, rapidly decreased numbers of northern Yellowstone elk by about 70% from a high count of more than 19,000 in the mid-1990s (Vucetich et al. 2005, White and Garrott 2005, Eberhardt et al. 2007). Managers at MFWP eliminated the late season hunter harvest of fertile, prime-aged female elk to increase adult female survival and reproduction and offset consistently lower recruitment due to predation (Proffitt et al. 2014). In turn, numbers of elk increased to between 5,000 and 7,500 after a low count of 3,915 in 2013 (MacNulty et al. 2020). A biologist from MFWP observed 6,651 northern Yellowstone elk in March 2023 (Yarnall 2023a).

Northern Yellowstone elk are partially migratory with most animals moving seasonally between summer and winter ranges and others remaining on the same range year-round. Many elk spend winter in the lower-elevation Gardiner basin and southern Paradise Valley, with numbers increasing during winters with deep snowpack at higher elevations (White et al. 2010, 2012). Spring migrations generally begin from late April to mid-May but vary among years based on the severity and duration of the previous winter which, in turn, affects snow melt and the growth of new forage (White et al. 2010). Elk initially follow the green-up of vegetation as snow progressively melts at higher elevations, with many elk migrating through the Sepulcher Mountain foothills, across Mount Everts, or along the Yellowstone and Gardner Rivers (White et al. 2010). Many female elk calve in these areas before moving between 6 and 93 miles (10 and 150 kilometers; straight-line distance) to a dozen different summer ranges throughout the park (White et al. 2010).

Autumn migration begins in late September to mid-October following snow accumulation, with two-thirds of movements starting within 72 hours of a major snowstorm on the summer range. For elk migrating to winter ranges inside the park, the autumn migration lasts about 7 days. For elk migrating to winter ranges outside the park, migrations last about 43 days (White et al. 2010). Many females with calves move to lower elevations in and outside the park where snowpack is lower and there are fewer predators and, in the 2000s, a larger portion (80% by 2020) of the smaller elk population began to migrate outside the park. Elk spending winter outside the park have higher survival and recruitment compared to elk spending winter inside the park where predator densities are much higher (White et al. 2012).

Elk and bison in northern YNP have high overlap in habitat on the winter range and moderate diet overlap (Singer and Norland 1994). Bison and elk diets overlap considerably because both eat substantial amounts of graminoids (Singer and Norland 1994). This indirect competition could limit the amount of forage available for bison, resulting in increased bison movements outside the park boundary with higher elk numbers (Coughenour 2005, Plumb et al. 2009). Biologists estimated the carrying capacity for bison in YNP at about 10,000 bison during summer and 6,500 during winter, near which foraging efficiency and bison condition should decrease (Coughenour 2005, Plumb et al. 2009, Wallen et al. 2015b). Modeling predicted a substantial decrease in numbers of northern Yellowstone elk after wolf recovery could release bison from competition and allow numbers in the northern herd to increase to about 4,900 (Coughenour 2005, Plumb et al. 2009). Indeed, counts of northern Yellowstone elk decreased from about 19,000 in 1994 to less than 4,000 by 2013, while bison numbers increased from about 500 in 1997 to 4,500 in 2022 (Figure 6; Tallian et al. 2017, MacNulty et al. 2020, Geremia 2022).

Pronghorn—During an aerial survey in April 2023, a park biologist counted 341 pronghorn in the Yellowstone population. This count was lower than those made in 2022 (448), 2020 (416), and 2019 (476; no count in 2021), suggesting severe winter conditions in 2022-2023 contributed to a significant decrease in pronghorn numbers (Northern Yellowstone Cooperative Wildlife Working Group 2023). The population is partially migratory with all pronghorn spending winter in the Gardiner basin and southern Paradise Valley, and about 80% of them migrating in spring to higher elevations in the park (White et al. 2007, 2022d). These movements enable pronghorn to use nutritious food when it is available and release the lower-elevation winter range from intensive use for a portion of the year (Barnowe-Meyer et al. 2017). Migrating pronghorn and their fawns have higher survival rates through summer than non-migrants that remain on the winter range year-round (Barnowe-Meyer et al. 2010, 2011). Non-migratory pronghorn stay in the vicinity of the Gardiner basin during summer and increase their use of the foothills from Sepulcher Mountain and Electric Peak, as well as the northwestern portion of Mount Everts. Most pronghorn use the same migration strategy and summer range each year (White et al. 2007, 2022d).

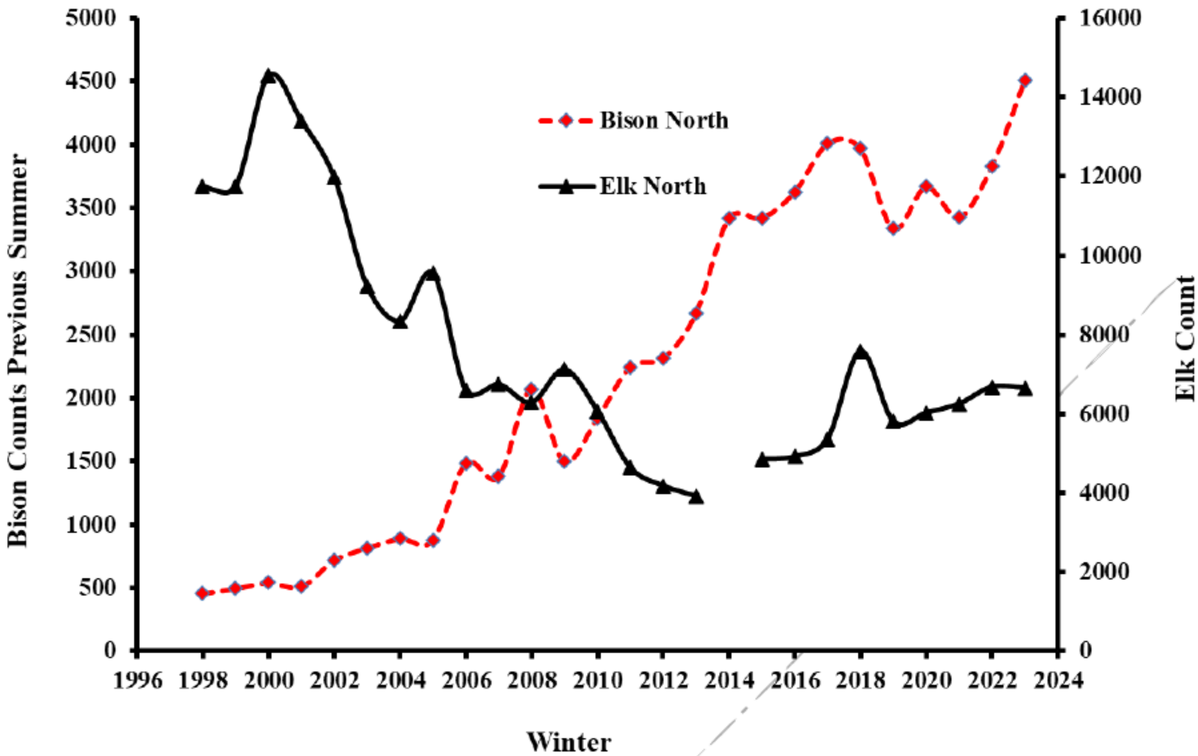


Figure 6. Counts of northern Yellowstone elk (winter) and the northern bison herd (previous summer) during 1997 to 2023 in Yellowstone National Park.

Migratory pronghorn gather at the southeastern end of the Gardiner basin winter range in late March and early April on an open flat north of Mount Everts and on its slopes. As snow recedes, these animals travel southeast about 7 miles (11 kilometers) over Mount Everts, which separates their winter and summer ranges. Pronghorn travel along grassland-sagebrush passageways through gaps in surrounding conifer forests, most of which are less than 328 yards (300 meters) wide with occasional constricted areas of 22 to 66 yards (20 to 60 meters). Once spring migrants reach the southeastern end of Mount Everts, they disperse somewhat to travel to their individual summer ranges. Most pronghorn generally follow the Yellowstone River to summer ranges farther east, including the Blacktail Deer Plateau, slopes of Hellroaring Mountain, Little America and Specimen Ridge, and the Lamar Valley and Soda Butte area. Spring migrations occur over 1 to 2 months during mid-March to mid-May with most pronghorn reaching their summer ranges during April. Females migrate when vegetation green-up begins but before giving birth in late May and June. Autumn migrations occur over 1 to 2 months from mid-September to mid-November with all pronghorn crossing Mount Everts and most reaching the Gardiner basin winter range during October. Animals mostly migrate after breeding but before snow covers their summer ranges. Most animals migrate between their seasonal ranges in less than one week by moving 3 to 9 miles (5 to 15 kilometers) each day (White et al. 2007, 2022d).

Pronghorn historically lived with many large groups of bison that created high quality foods by repeatedly and intensely re-grazing grasslands to keep nutritious forbs and grasses growing throughout the summer (Geremia et al. 2019, 2022). There was little overlap in diets because bison select more grasses and pronghorn prefer forbs and shrubs (Barnowe-Meyer et al. 2017). Pronghorn also associated with bighorn sheep, mule deer, and elk. These species have more dietary overlap with pronghorn but tend to select different areas and habitats in some seasons (White et al. 2022d). Competition for forage with high numbers of elk may have been a factor contributing to Yellowstone pronghorn numbers remaining at lower levels following a population crash in the early 1990s but there is no evidence of pronghorn competing with bison for forage (Singer and Norland 1994, White et al. 2022d).

Bighorn Sheep—About a dozen bands of bighorn sheep in the northern portion of YNP and nearby areas of Montana and Wyoming appear to function as a metapopulation with periodic movements and gene flow among them. Many of these bands are relatively small, slow growing, and low in productivity, with overall numbers remaining relatively stable over the past decade (White et al. 2008, 2021; White and Gunther 2013, Garrott et al. 2021). During a helicopter survey in March 2019, a biologist from MFWP counted 312 bighorn sheep from Point of Rocks in the southern Paradise Valley of Montana to Barronette Peak in the northeastern portion of YNP, which was slightly lower than the 10-year average of 358 sheep (Loveless 2019). The biologist observed a ratio of 14 lambs per 100 ewes, compared to an average of 28 lambs per 100 ewes during 1995 to 2017.

Most of the bighorn sheep in these bands are migratory and spend winter in lower-elevation areas before moving to higher-elevation summer ranges during May through October. However, some sheep remain resident year-round (Houston 1982, Keating 1982, Meagher et al. 1992, Legg 1996, Ostovar 1998). There is a group of bighorn sheep that spends winter on about 1,185 acres (480 hectares) of Mount Everts between the Yellowstone and Gardner Rivers (Keating et al. 1985). Counts have ranged between 36 and 110 bighorn sheep since 1995 (average = 63, with 65 counted in 2019; Loveless 2019). The core of this range is McMinn Bench, on the northwestern corner of Mount Everts, where bighorn sheep congregate for the breeding season (rut) from about mid-November to mid-December and continue to use the area through winter and spring green-up (Houston 1982, Garrott et al. 2021). Some bighorn sheep depart the Mount Everts winter range in late April or May, while others remain in the area through the year, including on McMinn Bench (Keating et al. 1985, Ostovar 1998). Lambing occurs in late May and early June (Lowrey et al. 2021).

Adult females that spend winter on Mount Everts have various lambing and summer ranges. Some ewes remain resident and give birth on McMinn Bench or Mount Everts. Others migrate south across Mount Everts, through the Blacktail Deer Plateau to Tower Junction, and then south along Antelope Creek and the Yellowstone River to Mount Washburn (28 miles; 45 kilometers). Most of these ewes give birth to lambs on cliffs along the Yellowstone River near Tower, Specimen Ridge, or the Grand Canyon of the Yellowstone before moving to Mount Washburn by middle to late June, where they spend the summer (Ostovar 1998). Another group crosses the Gardner River on or near the bridge by Eagle Nest rock in late May or early June and travels about 4 to 5 miles (6 to 8 kilometers) west to give birth on the east-facing cliffs of Sepulcher Mountain. Many of these ewes return with their lambs to McMinn Bench and Mount Everts in late June and early July (Ostovar 1998). A third group gives birth about 3 to 5 miles (5 to 8 kilometers) east of McMinn Bench on cliffs in the Black Canyon of the Yellowstone River before returning to spend summer on Mount Everts and nearby Rattlesnake Butte (Ostovar 1998).

Some adult males (rams) that spend winter on Mount Everts remain year-round. Others migrate about 18 miles (30 kilometers) southwest to the Gallatin Mountain Range during summer. These migrants travel south across Mount Everts, cross the Grand Loop Road near Bunsen Peak, and move west toward Quadrant Mountain, Little Quadrant Mountain, and Bannock Peak (Ostovar 1998). Other rams remain on Mount Everts during summer but then move northwest to the Electric Peak and Cinnabar areas (7 to 8 miles; 11 to 13 kilometers) or a few miles east to Deckard Flats for the autumn rut (breeding season) before returning to Mount Everts for the winter.

When bison in northern YNP expanded their winter range westward in the 1980s, their spatial overlap with bighorn sheep increased by about 28% and their diets were similar, primarily composed of grasses and sedges (Singer and Norland 1994). While this suggests the potential for competition, both species were at relatively low abundances during that period which likely limited competition between them

(Singer and Norland 1994). There is no subsequent information indicating bison are reducing the reproduction and survival of bighorn sheep.

Mule Deer—During a helicopter survey in April 2023, an MFWP biologist counted 1,032 mule deer (164 fawns, 825 adults, 43 unclassified) in the Gardiner basin area of Montana, compared to a range of 1,299 to 2,343 (average = 1,901) since 1995 (Yarnall 2023b). A ratio of 20 fawns per 100 adults was observed, which compares to an average spring recruitment estimate of 40 fawns per 100 adults (range = 18 to 56) since 1995. This count was lower than those made in previous years, suggesting severe winter conditions in 2022-2023 contributed to a decrease in mule deer numbers. This population is partially migratory, with about one-quarter remaining on the winter range year-round in the Gardiner basin (including on the Sepulcher Mountain foothills and slopes of Mount Everts) and three-quarters migrating 6 to 65 miles (10 to 104 kilometers) to summer ranges in and near YNP. Migrants travel to summer ranges during late April to mid-June over a period of 2 to 40 days and tend to use the same winter and summer ranges each year (Gogan et al. 2019).

Some migratory deer that spend winter east of the Yellowstone River in the Gardiner basin move east in spring to spend summer in the Hellroaring and Buffalo Creek drainages and the Slough Creek and Flint Creek drainages of the Lamar River. Other deer move south to the Firehole River drainage and Heart and Shoshone Lake areas (Gogan et al. 2019). Migratory deer that spend winter on the west side of the Yellowstone River primarily move south to spend summer in and near the Gibbon and Madison River drainages. Some migrants move through the Sepulcher Mountain foothills or over Mount Everts. Migrant deer begin traveling back to the winter range in the Gardiner basin during mid-October (Gogan et al. 2019).

As bison expanded their winter range westward in the 1980s, spatial overlap with mule deer increased by about 25% (Singer and Norland 1994). However, few deer spent winter in the park and their diets were quite different, with bison consuming more graminoids and mule deer more browse. Thus, there appeared to be little competition for forage during this period (Singer and Norland 1994).

Predation

Since the recovery of large predators in YNP during the early 2000s, there has been a large decrease in the number of bison in central YNP, a rapid increase in the number of bison in northern YNP, and more movements of bison from central to northern YNP (Wallen and White 2015). These movements were likely in response to high bison numbers in central YNP, intense hazing by the State of Montana along the western boundary to keep bison in the park, and groomed roads that allowed bison to rapidly travel north during winter (Wallen and White 2015). In addition, counts of elk in northern YNP decreased 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 (MacNulty et al. 2020). As elk numbers decreased, the number of bison in northern YNP increased from about 1,500 in 2005 to 4,000 in 2016-2017 (Tallian et al. 2017). In contrast, the number of bison in central YNP decreased from about 3,500 in 2005 to about 1,200 in 2018 (Geremia 2022).

Bears—From the late 1950s through the 1970s, most black bear and grizzly bear mortality inside YNP was due to human causes, primarily management removals of bears involved in conflicts with people (White et al. 2017a). Managers in YNP and surrounding national forests and states implemented changes to limit access to human foods (storage orders), limit motorized access, retire livestock allotments, and prevent the loss of secure habitat. Over time, these actions increased the annual survival and abundance of bears in YNP (White et al. 2017a). Most bear mortality in YNP from 1980 to present has been from natural causes, primarily old age and intra- and inter-specific strife (White et al. 2017a, van Manen et al. 2021, Gunther 2022). Today, there are about 965 grizzly bears (range = 800 to 1,100) occupying more than 27,200 square miles (70,500 square kilometers) in the GYE, with enough reproductive females to sustain a viable population over the long term (van Manen et al. 2021, Interagency Grizzly Bear Study Team, unpublished data, 2023). In addition, there are between 150 and 275 black bears in northern YNP (Bowersock 2020). Most black bears and grizzly bears rarely kill adult ungulates, but they are effective hunters of newborn calves and fawns, especially elk. They intensely search areas near female ungulates during the birthing season to locate calves and fawns in hiding.

Grizzly bears in YNP are carnivorous with ungulate meat comprising about 45% to 80% of their diets (Mattson 1997). They frequently obtain meat by scavenging carcasses, usurping wolf kills, and killing injured or older elk and calves (Stahler et al. 2020). Prior to wolf restoration, carcasses primarily were available in late winter (April) when bison and elk died from starvation (Green et al. 1997). Black and grizzly bears emerging from their dens after hibernating through the winter fed on this carrion. However, wolves changed this pattern by killing elk throughout the year (Wilmers and Getz 2005, Metz et al. 2020b, Stahler et al. 2020). Grizzly bears occasionally kill starving bison, those caught in extremely deep snow or downed timber, and a few healthy bison separated from the herd that attempt to flee rather than stand their ground (Craighead et al. 1995, Smith et al. 2000, Wyman 2002). They also opportunistically kill some calves (Varley and Gunther 2002). An adult male grizzly bear was observed killing a few adult bison in central YNP circa 2005 to 2007 by charging them head on and leaping over their heads to bite them in the neck (T. Wyman, YNP, personal communication). A different male grizzly was found dead in the Hayden Valley with what appeared to be a goring wound from a bison (K. Gunther, YNP, personal communication). Regardless, opportunistic predation by grizzly bears on adult bison is rare and has insignificant effects on bison population dynamics (Mattson 1997). Adult bison are formidable prey, often forming cohesive groups, with adults aligned and calves in the middle or behind the adults, to confront approaching predators (Gunther 1991, Smith et al. 2000, Varley and Gunther 2002).

Cougars—Colonists and settlers decimated the number of cougars in and near the northern portion of YNP by the 1930s, but cougars reestablished a viable population by the mid-1980s and then continued to increase to as many as 50 animals during the 2000s (Murphy 1998, Ruth et al. 2019, Anton 2020). Cougars are solitary hunters that stalk and ambush their prey. They are opportunistic and often select smaller prey to minimize the risk of injury during attacks (Ruth et al. 2019). About 55% of cougar diets in and near YNP consist of elk, primarily calves (65%) and adult females (34%). Cougars kill more elk calves as summer progresses and continue through winter as calves move around the landscape with groups of adult females (Stahler et al. 2020). After wolf restoration, cougars began killing more adult female elk, probably due to fewer available calves. Another 35% of their diet consists of mule deer, with the portion of this prey source increasing from 20% to 35% in recent years (Stahler et al. 2020).

Cougars sometimes lose kills to bears and wolves and need to kill more frequently, especially when they are raising kittens (Ruth et al. 2019, Stahler et al. 2020). As a result, their kill rates of elk increased after wolf restoration and were about twice the per capita kill rate of wolves (Ruth et al. 2019, Anton 2020, Stahler et al. 2020). Predation studies between 1998 and 2006 found cougars increasingly used elk (74%) and relied less on deer (14%) and other prey (12%; Ruth et al. 2019, Stahler et al. 2020). From 2016 to 2022, however, cougar diets shifted to less use of elk (49%), with increasing use of deer (35%) and about 16% other prey (Stahler et al. 2021). These patterns of prey selection are likely most influenced by changes in elk abundance and carnivore competition in northern Yellowstone (Stahler et al. 2020).

There are no records of cougars preying on bison in YNP, and few references to attempts elsewhere; though they occasionally scavenge on bison carcasses in YNP. Bison are likely too formidable for cougars to attack and kill given their social groupings, size, and thick necks and hair at the base of the skull where cougars typically deliver killing bites (D. Stahler, YNP, personal communication).

Gray Wolves—Wolves and bison historically coexisted over large portions of North America and, aside from humans, wolves are the only effective predator of bison (Smith et al. 2000, Gates and Ellison 2010). After being extirpated from YNP by the 1930s, 31 wolves from Canada and 10 wolves from northwestern Montana were relocated to YNP in the mid-1990s. Numbers increased to 174 wolves in as many as 16 packs over the next decade but eventually decreased to between 80 and 123 wolves in 7 to 10 packs (Smith et al. 2020). There were 108 wolves in 10 packs in YNP during December 2022, including 7 breeding pairs. Several packs used portions of the bison management area in and outside northern YNP during 2022 and 2023, especially during winter and spring when many hundreds of ungulates spent winter in the Gardiner basin and surrounding foothills.

Wolves in YNP typically hunt in packs during winter and travel long distances through relatively flat grasslands close to rivers and streams. This strategy facilitates scanning the landscape and detecting elk, their primary prey (80% to 95%), foraging in grasslands or near habitat transitions, such as edges between grasslands and forests, and allows wolves to scan groups for individual elk susceptible to attack (MacNulty et al. 2007). Wolves kill more bison (primarily calves) during spring (10%) and scavenge on bison carcasses frequently through winter (Metz et al. 2020a,b; Stahler et al. 2020). Bison in YNP cannot separate themselves from wolves because they need to feed in relatively open grasslands and meadows and, as a result, are relatively predictable in location. Bison are more vulnerable to predation during winter and groups avoid areas with deep snow and consume less forage when wolves are in the vicinity (Harvey and Fortin 2013).

Bison are more numerous than elk in central and northern YNP during winter. However, they are formidable prey because their large size, aggressiveness, and deployment of group defenses, whereby adults coalesce around and protect calves, make them more likely to injure or kill wolves (Carbyn and Trottier 1987, Smith et al. 2000, MacNulty et al. 2007, 2014; Becker et al. 2009a). Elk are about three times easier for wolves to capture than bison because they are more vulnerable, both behaviorally and physically (Garrott et al. 2009a, MacNulty et al. 2014). In turn, more wolves (9 to 13) usually are needed to successfully capture bison than elk (2 to 6 wolves; MacNulty et al. 2014). Although bison and elk calves are roughly the same size, bison calves are less vulnerable due to the group defense tactics of bison (see below; Garrott et al. 2009a). Thus, wolves generally avoid hunting bison when less dangerous (safer) prey are available because the potential costs exceed the gains (MacNulty et al. 2014). Capture success for wolves hunting bison is generally limited to large packs of about 11 or more wolves attacking smaller groups of 10 to 20 bison with calves (Tallian et al. 2017).

Wolves in YNP typically approach bison without attempting concealment and, ultimately, the outcome of the encounter depends largely on the reaction of the bison (Smith et al. 2000). Three-quarters of bison groups approached by wolves stand their ground and do not run; instead, they coalesce in tight groups and face the approaching wolves (Smith et al. 2000). Wolves often attempt to provoke bison to run by feinting and lunging or rushing at them (Carbyn and Trottier 1987, MacNulty et al. 2007). If bison stand their ground when harassed, the probe usually ends, and the wolves leave. If one or more bison run, wolves pursue them and focus on biting a vulnerable animal, such as a calf, in the neck to restrain and kill it (MacNulty et al. 2014). Bison groups are more likely to run as the number of attacking wolves increases and wolves are more likely to attack fleeing groups (Tallian et al. 2017). Wolves sometimes try to run bison into deep snow or terrain traps, such as downed timber or dense regeneration, where bison mobility is curtailed and wolves can overwhelm them (Smith et al. 2000, Garrott et al. 2009a). During 1995 to 1999, wolves killed more bison during late winter when they were susceptible because of undernutrition (poor condition) and elk were scarce (Smith et al. 2000, Becker et al. 2009a,b).

During 1995 to 2015 in northern YNP, wolves attacked elk on about two-thirds of their encounters and bison on about 40% of encounters. Wolves were less likely to attack bison groups larger than 15 and more likely to attack groups with calves rather than just adults (Tallian et al. 2017). Wolves also were more likely to attack bison when in larger packs, likely because they had a higher probability of provoking a flight response (Tallian et al. 2017). Less than 5% of observed wolf attacks on bison in northern YNP resulted in a kill and groups with more than 20 bison generally fended off wolves (Tallian et al. 2017). Bison only comprised 2% of the ungulates killed by wolves, with annual numbers ranging from zero to 10 (Tallian et al. 2017). The average age of bison killed by wolves was 8 years for females and 9 years for males.

Wolves kill more adult elk in winter when bears are hibernating and fewer adult elk during summer, so fewer carcasses are available for scavenging by bears at that time (Wilmers and Getz 2005, Metz et al. 2012, 2020b; Stahler et al. 2020). As elk numbers decreased and bison numbers increased in northern YNP, wolves began to scavenge on carcasses of bison that died during calving, from injuries sustained during the rut, starvation, or other causes (Tallian et al. 2017, MacNulty et al. 2020, Metz et al. 2020a,b). Scavenging increased as bison abundance increased, and bison carcasses now make up about 25% of the meat wolves eat during winter (MacNulty et al. 2020, Metz et al. 2020b). This scavenging reduced predation on elk from about 18 to 12 elk per wolf each year based on kill rates during winter (Metz et al. 2020a). Similarly, kill rates of elk and bison in central YNP decreased as carcass consumption increased (Becker et al. 2009a,b).

In the Madison headwaters area of central YNP, multiple packs averaging about 10 wolves (range to 4 to 21) killed about 80% elk and 20% bison (range = 0 to 29 bison) during winters from 1997 to 2007, even though bison were more abundant and their abundance increased through winter because of migration into the area from the Hayden Valley (Becker et al. 2009a,b). Wolves preferred elk calves and primarily killed them from early to mid-winter until they substantially reduced numbers. They killed vulnerable adult elk through winter and more bison, especially calves, during middle to late winter as increasing numbers migrated into the area (Becker et al. 2009a). Kill rates of bison increased substantially with the abundance of calves migrating into the area and as the duration and accumulation of snow pack increased from early to late winter (Becker et al. 2009b). Though wolves strongly preferred elk, and selected bison less than expected given their abundance, predation on bison enabled wolf packs to continue using the area during winter as elk numbers dwindled, which eventually resulted in the near extirpation of this non-migratory elk population (Garrott et al. 2009a).

Wolves in central YNP primarily killed older bison, with females averaging 11 years (range = 9 to 13) of age at death and males averaging 8 years (4 to 11) of age (Becker et al. 2009a). The body condition of bison decreased through winter in this severe snow pack and cold environment (DelGuidice et al. 2001, Becker et al. 2009a). Most kills of bison occurred in late winter when bison were in their lowest nutritional condition and likely susceptible and less able to defend themselves during prolonged attacks lasting several hours (Becker et al. 2009a,b).

Scavengers

Abundant and widespread scavengers in YNP limit the time birth and reproductive tissues from bison and elk, possibly with infectious *Brucella abortus* bacteria, persist in the environment (Cook et al. 2004b, Maichak et al. 2009, Aune et al. 2012). These scavengers include bears, coyotes, eagles, foxes, ground squirrels, magpies, ravens, and wolves (Jones et al. 2010). The recovery of bison, wolves, cougars, and grizzly bears in the Yellowstone area has increased the amount of carrion and, in turn, the abundance of scavengers that could remove brucellosis-infected tissues before they are discovered by susceptible bison, cattle, or elk (White et al. 2015a, Stahler et al. 2020). The Wyoming Game and Fish Department protects scavengers such as coyotes and red foxes on some elk feed grounds to reduce the time infectious tissues remain on the landscape (Cross et al. 2013).

Current Situation

Bison have become the dominant herbivore in YNP over the past two decades as elk numbers decreased following predator recovery and bison dispersed from central to northern YNP and proliferated. This transition has already had substantial effects on the ecosystem, affecting both top-down (predation) and bottom-up (plant production) processes. Higher numbers of bison have resulted in more prey and carrion throughout the year which, in turn, has decreased predation rates of wolves on elk and promoted a diverse scavenger community with microhabitats of intense nutrient release for decomposers and primary producers (Metz et al. 2020, Stahler et al. 2020). In addition, intense and repeated grazing by bison in some areas is altering plant composition and production (Geremia and Hamilton 2019, 2022; Geremia et al. 2019) which, in turn, could influence the potential for competition among various species of herbivores. Whether these changes will eventually transition these grassland communities and the herbivore association to another state is the subject of ongoing research.

Bison covered in snow in Yellowstone National Park.
Photograph by Neal Herbert, National Park Service, 2014.

Chapter 7—Ecological Role and Genetic Diversity

Adaptive Capabilities

Yellowstone bison exhibit wild behaviors like their ancestors, competing for food and mates, using group defensive strategies to protect their young from predators, migrating between seasonal ranges, and moving widely to explore new areas. They are extremely adaptable and quickly respond to changes in environmental conditions and management actions. Bison can withstand severe winter conditions with poorer forage availability better than smaller ungulates due to their large four-chambered stomach that effectively digests plants high in fiber (Wallen and White 2015). In addition, bison evolved in spatially and temporally variable environments and one of their defining characteristics is their mobility. They can traverse large expanses of habitat in large groups in relatively brief periods of time to respond to changed conditions, such as increased snow pack and decreased foraging efficiency (Plumb et al. 2009). They can break trails through snow more than 3 feet (1 meter) deep for long distances and then keep them in a self-groomed state through repeated use; thereby saving substantial energy for trailing bison when moving through snow (Meagher 1973, Gates et al. 2005). Bison also are formidable prey for wolves because their larger size and tendency to employ group defenses, whereby adults congregate around calves, increases the risk of injury for wolves during attacks (Becker et al. 2009a, MacNulty et al. 2014).

Ecological Role

Bison are ecosystem engineers that move and graze across the land to intentionally create intensely grazed areas, which improves their own food quality by changing the timing and duration of new grass growth, manipulating grass productivity by increasing nutrient cycling and redistribution, and altering the composition of plant communities (Geremia et al. 2019). In the Lamar and Hayden valleys they create grazing lawns, like those found in the savanna systems of the Serengeti, with areas of particularly intense, repetitive grazing, which resets plant growth and allows them to continue to eat high-quality foods longer through the summer (McNaughton 1985, Olenicki and Irby 2005 as cited in Coughenour 2005, Geremia et al. 2019). Research since 2012 indicates the cool-season cultivars in the Lamar Valley have healthy soil, water, and nutrients necessary for them to regrow (Geremia and Hamilton 2019, 2022). Grazed plants produce entirely new shoots off the root crown, the part of the plant immediately below the soil surface (Frank et al. 2013). 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, like newly growing spring vegetation (Geremia and Hamilton 2019, 2022).

Bison also manipulate grass productivity and quality by depositing urine and fecal material across the landscape, which redistributes nutrients and increases their availability to plants (nutrient cycling) to sustain the production of grasses and the health of the soil (Frank et al. 2013, Wallen et al. 2015b, Geremia and Hamilton 2019, 2022; Geremia et al. 2019, 2022). Their carcasses provide increased soil respiration and concentrations of nutrients that alter bacterial and fungal communities. These effects can substantially elevate soil nutrients and improve grass nutritional quality for multiple growing seasons (Gogan et al. 2010, Risch et al. 2020). The short, dense lawns of grasses on the summer range in the Lamar Valley remain productive and soils have the same level of nutrients from decade to decade because grazing facilitates the recycling of nutrients and organic matter back into the soil (Geremia et al. 2021).

Bison create habitats for a range of species from birds to small mammals to other ungulates by altering the composition of grasslands and promoting a variety of plants and more variation across the landscape that, in turn, creates a variety of habitats for plants and animals (Knapp et al. 1999, Wallen et al. 2015b).

Bison do not graze areas uniformly; rather light to moderate grazing occurs in areas along seasonal migration routes while intense grazing occurs on grazing lawns used through the summer. In northern YNP, bison graze about 80% of the area at low intensity, 10% at moderate intensity, and 10% at high intensity (Geremia and Hamilton 2019, Geremia et al. 2021). Thus, a mosaic of vegetation conditions occurs across the landscape which supports a wider variety of plants and animals because some need various habitats, while others favor disturbed or undisturbed habitats (Fuhlendorf et al. 2012). Bison also disperse seeds across the landscape in their fur and feces, which helps maintain the grasslands and meadows on which many species depend, such as nesting birds (Wallen et al. 2015b).

Bison create wallows, which are relatively circular depressions in the ground, by rolling from side-to-side on their backs to cover their body with dirt (dust bath) and relieve skin irritations, shed fur, or stop insects from biting. These depressions often fill with water and form ephemeral pools for wetland plants and amphibians (Gogan et al. 2010). In addition, the heavy bodies and sharp hooves of bison create depressions in the soil (tilling) and disturb roots of grasses and forbs, which prevents grassland succession to shrubs or trees. Bison also rub their horns on trees or shrubs along the periphery of grasslands and meadows, which inhibits growth and plant community succession (Wallen et al. 2015b).

Bison provide prey for predators and carcasses for scavengers and decomposers (Metz et al. 2020a,b; Stahler et al. 2020). Higher bison numbers during the IBMP period likely resulted in a greater potential for predation and scavenging. Some of these animals consume *Brucella* bacteria during these activities, but this does not result in sickness, and they cannot spread brucellosis (Cheville et al. 1998, National Academies of Sciences, Engineering, and Medicine 2017). Bison also may compete with other ungulates for food and other resources and indirectly affect them by their grazing intensities and effects on grasslands (Singer and Norland 1994, Coughenour 2005). However, intensely grazed areas make up a small portion of available habitat for bison and other ungulates in YNP and most summer ranges and all winter ranges generally experience low to moderate grazing during the summer growing season (Geremia and Hamilton 2019, 2022). Thus, it is unlikely grazing by bison would substantially affect the seasonal movement patterns or demographics of other ungulates, such as bighorn sheep, deer, elk, and pronghorn. Numbers of ungulates in YNP have remained high for numerous decades, with many thousands of animals attaining adequate forage to sustain body condition, reproduction, and survival (Geremia and Hamilton 2019, 2022).

Genetic Diversity

Yellowstone bison are descendants from the indigenous bison that survived in the central portion of YNP during the late 1800s and bison introduced to northern YNP from private ranch herds (Pablo-Allard herd [derived from the Walking Coyote herd] in Montana and Goodnight herd in Texas) in the early 1900s (Stroupe et al. 2022, 2023). They have relatively high genetic diversity, in part, because of the introduction of bison into YNP from different genetic lineages which, at least initially, created genetic differences between bison living in the central and northern regions of the park (Halbert and Derr 2007, Hedrick 2009, White and Wallen 2012). Geneticists identified 10 different mitochondrial DNA haplotypes in Yellowstone bison and an overall haplotype diversity of 0.78, indicating a healthy, diverse population (Forgacs et al. 2016). Yellowstone bison should retain this diversity for centuries if numbers average at least 3,000 to 3,500 bison, there is intermixing and gene flow between bison from the two primary breeding herds (central, northern), and removals are mainly juveniles (Pérez-Figueroa et al. 2012). Studies indicate a high portion of adults produce offspring during their lifetimes (Herman et al. 2014). Between two and five groups of related alleles based on neutral markers exist across the park, and allelic diversity, allele frequencies, and inbreeding levels remained similar over more than two decades based on 44 microsatellites across the bison genome (Geremia 2022). In addition, analyses of mitochondrial DNA indicate descendants of bison from the native and introduced lineages remain in the population in both the central and northern regions of the park (Forgacs et al. 2016, Stroupe et al. 2023).

Since the mid-1980s, thousands of Yellowstone bison have congregated in two primary areas for breeding; the Hayden valley in the central region of the park, and the Lamar Valley in the north (Wallen and White 2015). In a study evaluating samples from Yellowstone bison collected near western and northern boundaries of the park during winter between 1997 and 2003, geneticists from Texas A&M University identified two genetically distinct subpopulations using microsatellite genotype diversity and allelic distributions (Halbert et al. 2012). These differences were likely created by several events, including the population bottleneck caused by nearly extirpating Yellowstone bison in the late 19th century, the creation of another breeding herd in central YNP (Hayden Valley) from bison of unrelated breeding ancestry, and strong female philopatry to breeding areas, with most females returning to the same area each year, until the 1980s or 1990s (Wallen and White 2015). However, the differences in genetic make-ups were still a bit surprising given the apparent mixing of descendants from the native and introduced lineages in northern YNP for almost a century (Toll 1929, Meagher 1973, White and Wallen 2012). Bison spending winter in the Pelican (indigenous) and Lamar (introduced) valleys used the same areas during summer and the rut beginning in the 1920s and, in the mid-1930s, the NPS relocated descendants from the introduced Lamar lineage in northern YNP to the Hayden Valley and Madison headwaters area (Firehole River) in central YNP (Wallen and White 2015). Bison from this so-called Mary Mountain herd began mixing and breeding with bison from the Pelican Valley with the native lineage during the 1980s (Meagher et al. 2002).

From 2005 to 2020 there were substantial movements of bison between central and northern YNP that further mixed descendants of the introduced and native lineages throughout the central and northern regions of the park (see Chapter 4). Two-thirds of adult females fitted with radio-collars in central YNP during 2004 to 2017 moved in groups with hundreds of other female and young bison to northern YNP during winter. About one-half of these collared females remained in northern YNP at least through the breeding season the following summer (Wallen and White 2015). In addition, a subsequent study by geneticists from Texas A&M University in 2011-2012 analyzed 25 mitochondrial genomes of Yellowstone bison and compared them to 20 other bison from diverse populations (Forgacs et al. 2016). Analyses detected two distinct mitochondrial haplotype clades (descendants from a common ancestor) within the Yellowstone bison population representing the indigenous maternal lineage that survived the mass slaughter of bison in the late 1800s and the lineage introduced from the Pablo-Allard herd in the early 1900s. Based on mitochondrial haplotypes, the introduced and indigenous lineages were found in animals using both northern and central Yellowstone (Forgacs et al. 2016).

Given these findings, biologists at YNP collaborated with geneticists from Texas A&M University on a more comprehensive and definitive study. Biologists collected tissue biopsy samples from 282 Yellowstone bison during the summer of 2019 and winter of 2021. They sampled the two major summer breeding populations (central, northern) where one would expect to see genetic differentiation in ongoing population subdivision, and the two major winter ranges (northern, western) where migration patterns of both breeding herds can overlap (Stroupe et al. 2023). Geneticists at Texas A&M University evaluated these samples using a set of 24 microsatellite loci, previously characterized in Yellowstone bison (Halbert et al. 2012), as well as a newly developed set of highly informative, bison-specific single nucleotide polymorphisms (SNPs). There was no evidence supporting the hypothesis that Yellowstone bison are currently comprised of genetically distinct and independently breeding subpopulations (Stroupe et al. 2023). The analyses did not reveal substantial differentiation between bison sampled in the northern and central ranges during the summer breeding season and showed clear support for considering Yellowstone bison as one interbreeding population with two primary breeding herds.

Yellowstone bison are one of a few populations that meet the viability guidelines recommended by scientists (Freese et al. 2007, Sanderson et al. 2008, Hedrick 2009, Dratch and Gogan 2010, Gross et al. 2010). Geneticist Dr. Philip Hedrick at the University of Arizona indicated "[i]ndividual herds or clusters [of bison] should have an effective population size of 1000 (census number of 2000-3000) to avoid inbreeding depression and maintain genetic variation. If it is not possible to have this primary herd in 1 location, then it could be in 2 or 3 locations with significant genetic exchange between them. Note that this is larger than any of the plains bison herds except for Yellowstone NP [National Park] and any of the wood bison herds except for Wood Buffalo NP and Mackenzie Bison Sanctuary in Canada" (Hedrick 2009:419). Biologists counted almost 5,940 bison in YNP near the end of the rut in late August 2022, including about 4,500 in the northern portion and about 1,440 in the central portion with a relatively balanced sex ratio to support mate competition (Geremia 2022). More than 1,000 bison congregate in both the central and northern regions of YNP during the breeding season, where hundreds of mature males compete for breeding opportunities. Also, male bison are much more mobile on the landscape than females and it is possible they attend multiple breeding areas during the same season. Monitoring of radio-collared bison suggests Yellowstone bison are a single intermixing population, with substantial movements, breeding, and gene flow between bison originating from central and northern YNP during recent decades (White and Wallen 2012, Wallen and White 2015). In addition, the founding maternal lineages of the population occur in both breeding areas (Forgacs et al. 2016, Stroupe et al. 2023). Thus, Yellowstone bison meet Dr. Hedrick's criteria for sustaining an effective population size.

Yellowstone bison went through a severe genetic bottleneck in the late 1800s and became isolated from other populations, which is still the case (see Chapters 1 and 2). Counts during 1896 to 1912 remained between 25 and 50 bison, indicating a two-generation bottleneck for the remnant indigenous herd (Hedrick 2009). Eighteen females and three males were introduced into a fenced area near Mammoth, Wyoming, in 1902 and later moved to the Buffalo Ranch in the Lamar Valley. The effective number of founders for this herd was estimated at about 7 bison (Hedrick 2009). At least one of these introduced bison likely was a hybrid from a bison-cattle cross because introgression of cattle genes was recently detected in Yellowstone bison at very low levels (less than 0.5%). However, there is no evidence cattle genetic information has been selected for in Yellowstone bison (Stroupe et al. 2022).

A population reduced to, or started from, a few animals contains less genetic variation than the original, larger population, which is known as the founder effect (Wallen and White 2015). Thereafter, chance losses of genetic variation (genetic drift) may continue because of isolation and a lack of gene flow from other populations, which leads to inbreeding and reduces the abilities of animals to adapt to changing environmental conditions (Wallen and White 2015). Fortunately, there is no evidence of genetic drift or inbreeding depression in Yellowstone bison, nor demographic indicators such as low birth and high juvenile mortality rates (Halbert and Derr 2008). Yellowstone bison have a relatively long generation time of about 9 years, which is how rapidly individuals produce surviving offspring that reach sexual maturity and reproduce. This has likely helped them lengthen the retention of genetic diversity and allow individuals to be exposed to new mutations, some of which may be beneficial (Fuller et al. 2007b, Halbert et al. 2012, Stroupe et al. 2023).

Population substructure, with moderate dispersal rates between semi-distinct breeding herds, can reduce the loss of genetic diversity in an isolated population such as Yellowstone bison (Wallen and White 2015). However, culls of more than 1,000 bison in the winters 2006 and 2008 differentially affected bison from the central region by removing more females and dampening productivity (White et al. 2011). These non-random culls also raised concerns that continuing such management could differentially influence the genetic diversity of bison living in the central and northern regions of the park and change their genetic constitution (Halbert et al. 2012). Other geneticists indicated large removals could reduce generation time and competition among males for breeding opportunities (Pérez-Figueroa et al. 2012). As a result, NPS biologists recommended several adaptive management adjustments to enhance the conservation of Yellowstone bison, including the avoidance of frequent large culls greater than 1,000 animals (White et al. 2011, 2015c). This recommendation was modified as bison numbers increased with an annual objective of removing fewer than 1,500 bison, or 25% of the population, and focusing on the northern breeding herd which has grown substantially since 2005. Biologists also recommended maintaining more than 1,000 bison in the central and northern breeding areas (as recommended by Hedrick 2009) to help protect any existing unique diversity or rare alleles (genes) within each area (Geremia 2022).

Continuing current management in this manner should not reduce genetic diversity or change the genetic constitution of the population. The NPS is continuing to collaborate with geneticists to develop tools, conduct research, monitor the demographic and genetic status of bison in the central and northern portions of YNP, and recommend adaptive management adjustments as necessary. It would be impossible to recreate genetically distinct herds of the indigenous and introduced genetic lineages given the existing mixing. It also would be undesirable to prevent bison from moving between the central and northern portions of the park. Park biologists have recommended allowing ecological processes, such as natural selection, migration, and dispersal, to prevail and influence future population and genetic substructure, rather than actively managing to try and maintain or restore a genetic substructure initially created by human relocations of bison in the early 1900s (White and Wallen 2012, Wallen and White 2015).

Current Situation

Today, there are about 470,000 plains bison in North America and the species is no longer susceptible to demographic extinction (Boyd 2003, Boyd et al. 2010a). However, only about 30,000 of these bison are in herds managed primarily for conservation (Freese et al. 2007). Instead, most bison are selectively bred and fed for meat production, mixed with cattle genes, protected from natural predators, and managed in fenced pastures (Sanderson et al. 2008). Thus, most bison no longer have the significant influence they once did on grasslands and other ecosystems, including shaping the landscape by creating a mosaic of grazing intensities, recycling and redistributing nutrients, competing with other ungulates, making wallows and small wetlands, and converting grass to animal biomass for people, predators, scavengers, and decomposers (Knapp et al. 1999, Truett et al. 2001, Gates et al. 2010). In addition, all wild wood bison populations are wood-plains hybrids (Hedrick 2009). As a result, bison remain ecologically extinct across most of North America and their conservation would be enhanced by establishing additional wild, wide-ranging populations exposed to natural selection (Freese et al. 2007, Gates et al. 2010, White et al. 2015b).

Less than 1% of the park's 2.2 million acres are developed for facilities, parking areas, roads, and visitor services (Sholly 2022). While these areas are now used by about 4 million visitors each year, the rest of the park is far less impacted; as a result, wildlife move freely with little human disturbance (White 2016). Yellowstone bison are the largest conservation population of plains bison in North America and unique in that they have existed in a wild state since prehistoric times (Plumb and Sucec 2006). These bison move across a vast landscape where they are exposed to natural selection through competition for food and breeding opportunities, predation, and survival under challenging environmental conditions. As a result, they have adaptive capabilities that are continually honed compared to bison kept in fenced pastures with no predators and where older bulls are removed to simplify management (Freese et al. 2007, Gates et al. 2010, Wallen and White 2015). In addition, Yellowstone bison retain a high level of allelic richness and gene diversity and are sufficiently unique to contribute significantly to the overall genetic diversity of plains bison (Douglas et al. 2011, Stroupe et al. 2022). Furthermore, Yellowstone bison are the only conservation population of plains bison that exceeds the minimum size recommended for retaining more than 95% of genetic diversity for centuries without the need for introducing immigrants from other populations (Gross et al. 2006, Freese et al. 2007, Hedrick 2009, Pérez-Figueroa et al. 2010). In combination, these findings indicate Yellowstone bison comprise a healthy, diverse population with a relatively high level of allelic richness and gene diversity that should be retained into the future (Forgacs et al. 2016).

Many thousands of bison are necessary to fully express their ecological role and influence ecosystems through bottom-up processes such as redistributing nutrients, changing the duration and extent of plant growth, creating habitat for birds and small mammals, providing prey for predators and carcasses for scavengers and decomposers, and competing with other ungulates (Freese et al. 2007, Sanderson et al. 2008, Plumb et al. 2009). In addition, higher numbers of bison increase their function as a meaningful component of the food web, influencing energy and nutrient transfer through the ecosystem (Geremia and Hamilton 2019, 2022). The NPS has increased the role of bison as ecosystem engineers and maintained a variety of functional plant groups in grassland communities supported by healthy soils and functioning water, energy, and nutrient cycles (White et al. 2022b).

Though Yellowstone bison have been subjected to relatively intense culling to minimize the risk of brucellosis transmission to cattle, there is no evidence that culling to date has threatened the long-term genetic viability or persistence of the population (White et al. 2011, Geremia 2022). There likely will be a need for some type of population control into the future, given political and social constraints in areas surrounding YNP. Thus, the ecological future of plains bison could be significantly enhanced by resolving issues of disease and political intolerance for Yellowstone bison so that they could be used to synergize the recovery of the species and the restoration of grassland biodiversity across central and western North America (Freese et al. 2007, Sanderson et al. 2008, Gates et al. 2010, Nishi 2010). Such resolution should be attainable because diverse constituencies that cross many social and economic layers of society support the conservation of Yellowstone bison and relocation of surplus bison to suitable restoration areas in North America (White et al. 2015c).

Chapter 8—Cultural Importance

Lakota Sioux ceremony near Stephens Creek in Yellowstone National Park.
Photograph by Jim Peaco, National Park Service, 1997.

Introduction

Several American Indian tribes consider bison their ancestors who brought them onto this earth and provided them with necessities for life, including food, clothing, and shelter (Plumb and Sucec 2006). They feel a responsibility to care for their relatives and, as a result, bison are a prominent part of their ceremonies, ecological knowledge, and oral traditions (Potter et al. 2010). Yellowstone bison have special significance to many of these tribes because they are direct descendants from the ancient populations of bison (Plumb and Sucec 2006). Bison were an essential component in the lives of many indigenous tribes in western North America, and involuntarily played an important role in the colonization of the continent by European Americans (Stark et al. 2022). Market hunting for bison hides resulted in the near extinction of bison and the decimation of the tribes which depended on them (see Chapter 2; Nabokov and Loendorf 2002, Schullery and Whittlesey 2006).

The Yellowstone area has provided a home for indigenous people and herds of bison for more than 10,000 years (Nabokov and Loendorf 2002, Cannon et al. 2020). More than two dozen tribes have connections with the Yellowstone area due to its location where the Columbia Plateau, Great Basin, Great Plains, and Rocky Mountains merge (Sholly 2022). Members of the Crow and Shoshone tribes lived within and near the area encompassed by present-day YNP. The Mountain Crow resided in the northeastern portion of the Yellowstone area and hunted bison, elk, and other wildlife (Smith and

Greenwald 2006a). Some Mountain Shoshone lived in the Yellowstone area year-round and hunted ungulates and other animals for food and clothing (Krahe et al. 2006, Smith and Greenwald 2006b). Other tribes, such as the Bannock, Blackfeet, Eastern and Northern Shoshone, Nez Perce, Northern Arapaho, Northern Cheyenne, and Salish and Kootenai, made seasonal trips to and through the Yellowstone area (Nabokov and Loendorf 2002). These trips were more frequent as bison became scarce in the surrounding plains following colonization and settlement (Franke 2005, Krahe et al. 2006).

The influx of colonists during the mid- to late-1800s led to strife with indigenous residents, including conflicts with the Nez Perce, Bannock, and Shoshone during the late 1870s (Norris 1877, Franke 2005). The federal government established treaties with Indian tribes that acquired land for miners and settlers and provided peace and safe passage for non-Indians through the Montana and Wyoming territories (Nabokov and Loendorf 2002). The Constitution of the U.S., which is the supreme law of the land (Article VI, § 2), allows the President to make treaties, which are essentially contracts between sovereign nations, with the consent of the Senate (Article II, § 2; *Goldwater v. Carter*, 444 US 996 (1979)). The Constitution defines treaties as equivalent to laws passed by Congress (Article VI, § 2; *Foster v. Neilson*, 27 US (2 Pet.) 253, 313-314 (1829)). Since American Indian tribes are sovereign nations, the treaties established with them and ratified by the Senate are considered the law of the land. Furthermore, the treaties are to be interpreted as the Indians would have understood them, with uncertainties resolved in their favor (*Minnesota v. Mille Lacs Band of Chippewa Indians* 526 US 172, 119 S. Ct. 1187 (1999)). Congress has the authority to abrogate (terminate) these treaties, but "it must clearly express its intent to do so" and "[t]here must be clear evidence that Congress considered the conflict between its intended action on the one hand and Indian treaty rights on the other and chose to resolve that conflict by abrogating the treaty" (*Minnesota v. Mille Lacs*, 526 US 202-205, *Herrera v. Wyoming*, 139 S. Ct. 1686 (2019)).

Treaty Hunts of Bison

Many tribes that lived in or seasonally used the Yellowstone area agreed to one or more treaties with the federal government during 1851 to 1880, including the Arapaho, Assiniboine, Bannock, Blackfeet (Blackfoot, Blood, Gros Ventre, Piegan), Cheyenne, Crow, Flathead (Kootenai, Pend d'Oreille, Salish), Nez Perce, Shoshone, Umatilla, and Yakama (Nabokov and Loendorf 2002). The tribes often ceded portions of their homeland to the federal government and agreed to live on smaller reservations in return for small payments and annual annuities and agreements to maintain friendly relations with other tribes and non-Indians (Nabokov and Loendorf 2002). Federal agents relocated the Mountain Shoshone bands living inside YNP to reservations in the Idaho and Wyoming territories (Norris 1877, 1881a,b). In 1880, Congress purchased the western portion of the 1868 Crow Reservation that overlapped with the area set aside as YNP and ratified this agreement in 1882 (Ch. 74, 22 Stat. 42), thereby removing all reservation lands from the park (Smith and Greenwald 2006a, Stark et al. 2022).

Under most treaties, the tribes reserved rights to hunt on lands ceded to the federal government that were unoccupied, meaning free of residence or settlement by non-Indians (*Herrera v. Wyoming*, 139 S. Ct. 1686). Some treaties stated these rights were to persist so long as game was found on these lands and there was peace between Indians and non-Indians (Nabokov and Loendorf 2002). However, reservation agents and soldiers attempted to keep indigenous people on reservations and discouraged them from hunting in the park or on other ceded lands (Norris 1881a,b; Harris 1889, Franke 2005, Krahe et al. 2006, Smith and Greenwald 2006a,b). Given these circumstances, tribes did not routinely exercise their reserved rights to hunt bison on unoccupied lands near YNP for more than a century (Stark et al. 2022).

In 2006, the Confederated Salish and Kootenai Tribes of the Flathead Nation and the Nez Perce Tribe informed the State of Montana they intended to exercise their treaty hunting rights for bison on the CGNF. They were followed by the Shoshone-Bannock Tribes in 2009, Confederated Tribes of the

Umatilla Indian Reservation in 2010, Yakama Nation in 2017, Blackfeet Nation in 2018, Northern Arapaho Tribe in 2019, and the Crow Nation in 2021. The hunts are extremely important cultural and spiritual occasions for members of these tribes, reconnecting themselves and their children to their heritage, ancestors (including bison), and other family members (Robbins 2023). Surveyed residents in Gardiner and West Yellowstone, Montana, north and west of YNP, support hunting as an alternative to shipping bison to slaughter, but many do not support how the hunts are sometimes operated (Metcalf et al. 2016). Treaty hunts near the boundary of YNP often do not resemble the fair chase hunts of other big game, but rather subsistence hunts to procure large amounts of meat. These hunts are perceived as unethical by some people because bison appear relatively naïve to hunting and changes in technology have provided for more efficient travel (vehicles), coordination (cell phones), gathering (rifles, winches), and long-term storage (freezers; Wallen et al. 2015c). In addition, most of the hunts occur in very small areas of unoccupied land. The tribes would rather hunt bison across the natural landscape like their ancestors, but the valley winter ranges are now mostly developed and occupied by people (Robbins 2023).

As the numbers of tribal hunters on national forest lands near the park boundary increased, conflicts arose with nearby residents because of shooting near roads and houses, gut piles left on the landscape, shooting of elk and other ungulates, and occasional incidents of shooting toward other hunters, houses, and cars (Neighbors Against Bison Slaughter and Bonnie Lynn v. the National Park Service et al. 2019). The NPS does not have regulatory authority or jurisdiction over these hunts which occur outside YNP and, as a result, cannot control when, where, and how these hunter harvests occur, or the number of bison harvested by tribal or state hunters (Sholly 2020). Likewise, hunts conducted under permits from MFWP or tribes exercising their treaty rights do not require authorization from the USFS (Erickson 2019). The CGNF has taken actions to improve public safety by moving shooting and carcasses farther away from residences. These actions included closing areas near residences and roads to hunting and requiring hunters to place unused parts of carcasses at least 150 yards (137 meters) from roads and homes. These actions should reduce the likelihood of injuries to hunters, residents, or visitors traveling on Old Yellowstone Trail South Road. However, shooting and bison offal remain a concern for property owners (Bear Creek Council 2019).

There was a large migration of bison to the northern boundary of YNP during the severe and prolonged winter of 2022-2023, with tribal hunters harvesting about 1,100 bison; approximately 20% of the bison population (Geremia 2023). Assertions that federal and state agencies coerced or manipulated tribes into harvesting large numbers of bison near the park boundary are misguided because each tribe exercises its own treaty rights on unoccupied lands, including setting their own regulations and seasons and issuing their own permits (French 2023, Planas 2023). However, there is only a limited area of unoccupied lands on which tribal members can easily hunt bison north of the park during winter, which inadvertently creates competition for a limited number of migratory bison that become available at unpredictable times (Buffalo Field Campaign 2023). This situation has led to discord when various agencies and tribes begin to act in their own best interests rather than working together through holistic management. In 2017, the Salish and Kootenai, Umatilla, Nez Perce, and Yakama tribes attempted to remedy this situation by negotiating and signing a memorandum of agreement to implement common hunt protocols, safety regulations, and enforcement to ensure the safety of hunters, wardens, and the surrounding community (Confederated Salish and Kootenai Tribes et al. 2017). However, not all treaty hunting tribes agreed to participate and, as a result, the holistic management of tribal hunts was limited.

A unified harvest strategy with standardized regulations for public and tribal hunters would vastly improve safety and enforcement of violations. It also could increase hunting opportunities by dispersing bison and hunters across the landscape, reducing concentrations near residences and roads, and implementing agreed-upon removal strategies (White et al. 2017b). Reaching such an agreement may require convening high-level representatives from each of the hunting tribes and the federal and state agencies. The precise framework of this partnership could be established collaboratively by these representatives, including expectations, responsibilities, and protocols for negotiating and adapting the agreement. Given the complexity of bison management and the diversity of opinions on this topic, the process will be difficult, met with resistance by some parties, and require strong, determined leadership (White et al. 2017b, Stark et al. 2022). However, this effort would further meaningful and valuable discussion to ensure the effective conservation and management of Yellowstone bison, including the integration of management practices (captures, hunting) to reduce conflicts, sharing of knowledge and expertise to reach a common understanding, and relocation of bison for cultural and ecosystem restoration purposes.

The late-winter movement patterns of bison and firing lines of hunters near the park boundary limit the effectiveness of using hunting in Montana to manage the bison population and distribution during many winters. Thus, some people have proposed hunting bison inside YNP by revising regulations or issuing permits to tribal members (Harris 2008, Wenk 2012, Nickoloff 2021, Planas 2023). This proposal raises complicated and unresolved legal questions regarding treaty rights because Congress prohibited all hunting in YNP with the 1894 Lacey Act (16 USC 26). Congress stated "all hunting, or the killing, wounding or capturing at any time of any bird or wild animal, except dangerous animals, when it is necessary to prevent them from destroying human life or inflicting an injury, is prohibited within the limits of said park." The Lacey Act culminated a deliberate intent by Congress to terminate all hunting in YNP, including by Indian tribes. Congress considered the conflict regarding hunting and poaching in the park and clearly intended to terminate all hunting by (1) establishing the park, in part, to protect and preserve the last remaining herd of buffalo from poaching, (2) relocating Indians living in the park to reservations and discouraging their use of the park, (3) purchasing a portion of the Crow reservation overlapping the newly established park, in part, to exclude tribal use, and (4) prohibiting all hunting at any time within the existing or future boundaries of the park (16 USC 26; see Chapter 2). In 1984, after careful consideration of congressional intent with respect to hunting in national parks, the NPS promulgated a rule that allows public hunting in national park areas only where "specifically mandated by Federal statutory law" (36 Code of Federal Regulations 2.2). However, many people point out the off-reservation hunting rights guaranteed in many treaties were never specifically terminated by Congress and others suggest the 1923 statute from Congress allowing the disposal of surplus" buffalo (16 USC 36; 54 USC 100101, 100752) gives the Secretary of the Interior authority to support tribal hunting in the park. As a result, any formal proposals to begin hunting (or permitted shooting) of bison in YNP would likely require new legal, legislative, and policy frameworks and be extremely contentious, politically challenging, unpopular with many visitors and, almost certainly, result in protracted litigation (Wenk 2012, White et al. 2015b, 2017; Stark et al. 2022).

Co-stewardship of Bison

The NPS has a unique relationship with tribes due to their shared commitment to the stewardship of parks and the resources therein (USDI, NPS 2006a). The NPS *Management Policies 2006* indicate "[a]s the ancestral homelands of many tribes, parks protect resources, sites, and vistas that are highly significant for the tribes. Therefore, the Service will pursue an open, collaborative relationship with tribes to help tribes maintain their cultural and spiritual practices and enhance the Park Service's understanding of the history and significance of sites and resources in the parks" (USDI, NPS 2006a:19). The NPS consults with 27 tribal governments associated with YNP through their aboriginal rights and historical use of the area (Wallen et al. 2015c). Some of these tribes want more involvement in the management of Yellowstone bison, including the consideration of tribal treaty and reserved rights early in the decision-making process. They also want respectful treatment of bison, including allowing them to roam freely without fencing or hazing like other wildlife. The tribes would like more opportunities for treaty hunting and more brucellosis-free bison transferred to tribal lands. In addition, they want tribal interns involved in bison management programs and the opportunity to interact with visitors in YNP about their culture and history (Wallen et al. 2015c).

The Secretaries of Agriculture and the Interior issued a *Joint Secretarial Order on Fulfilling the Trust Responsibility to Indian Tribes in the Stewardship of Federal Lands and Waters* to ensure all decisions relating to the preservation and management of lands, waters, and wildlife under their jurisdiction include considerations to safeguard the interests of tribes (USDI and USDA 2021). The NPS has continued fulfilling its trust responsibilities to tribes associated with YNP by sustaining a large population of bison that supports hunter harvests outside the park and restoring more brucellosis-free bison to tribal lands. Park staff work with tribal officials whenever plans or activities may directly or indirectly affect tribal interests, practices, and/or traditional use areas such as sacred sites. They engage them in meaningful consultation during planning, consider their expertise and indigenous knowledge, and consider tribal recommendations.

In addition, the NPS Director issued a policy memorandum describing how the agency would ensure tribal nations play an integral role in decision-making related to the management of federal lands and waters through co-stewardship (USDI, NPS 2022). Co-stewardship refers to collaborative partnerships between land managers and Indian tribes related to shared interests in managing, conserving, and preserving natural and cultural resources under the primary responsibility of Federal land and water managers (USDI, NPS 2022). It includes the sharing of expertise and information and combining capabilities to improve resource management, advance shared interests, and ensure tribal involvement when plans or activities may affect their interests, practices, or traditional use areas (USDI, NPS 2022).

Under the IBMP, the NPS and other federal, state, and tribal members have taken many actions to incorporate the traditional knowledge and expertise of tribes into planning and resource management activities to facilitate the co-stewardship of bison. The IBMP partners have allowed the number of bison in the population to increase, in part, to facilitate migration and hunting opportunities (IBMP Agencies 2016). They support tribal rights to conduct hunts of bison migrating from YNP onto unoccupied national forest lands in Montana pursuant to treaties with the federal government (IBMP Agencies 2016). They involved tribes as partners in the management of Yellowstone bison, including the development of adaptive management and annual operating plans that increased spatial and temporal tolerance for bison migrating north and west of the park, in part, to facilitate tribal access a traditional resource (IBMP Agencies 2016, IBMP Partners 2022). In addition, they provided tribes with captured bison for shipment to meat processing facilities and subsequent distribution of meat, hides, and other resources to their members, and coordinated with tribes that hunt bison on unoccupied lands of the CGNF adjacent to the park to reduce the effects of capture operations on hunting opportunities (IBMP Agencies 2016, IBMP Partners 2022). Furthermore, they implemented and expanded a quarantine program to identify brucellosis-free bison and transfer them to tribes for restoration on Indian lands. They evaluated the testing of bison in this BCTP to improve effectiveness and shorten timelines and involved tribal interns and trained other personnel in bison management (IBMP Agencies 2016, USDI, NPS 2018, 2023).

In January 2023, the Secretary of the Interior issued an order entitled *Restoration of American Bison and the Prairie Grasslands* to restore wild and healthy populations of bison through collaboration with other federal agencies, states, tribes, and landowners. The order directs the NPS to increase the quarantine capacity for Yellowstone bison to further increase shared stewardship and the number of live bison transferred to tribes, which YNP would continue to do. This order included a *Bison Conservation Initiative* committed to five overarching goals: 1) conserving bison as healthy wildlife; 2) restoring gene flow among conservation herds; 3) sharing stewardship with states, tribes, and other stakeholders; 4) establishing and maintaining large wide-ranging bison herds on appropriate large landscapes; and 5) restoring cultural connections to honor and promote the unique status of bison as an American icon. The Buffalo Treaty Nations (see below) communicated their support for the initiative to the Secretary of the

Interior, indicating it was an important step toward better health, ecological and cultural recovery, and continent-wide reconciliation. They agreed to collaborate with the Department and others through shared stewardship to bring this vision into reality.

Restoring Yellowstone Bison to Tribal Lands

About 28 Indian tribes signed *The Buffalo: A Treaty of Cooperation, Renewal and Restoration* to honor and recognize their relatives, the bison, as wild free-ranging animals and an essential partner in the natural world. The 2014 treaty describes their intertwined and interdependent relationship with bison and conveys their collective intention to provide a safe space and environment in North America so bison can once again lead them in nurturing the land, plants, and other animals. The signatories of the treaty committed to restoring bison to their rightful place in their respective cultures and territories so future generations can realize the bison ways culturally, materially, and spiritually. This significant action to preserve and restore their sacred web of relationships with the natural world also provided the USDI with an opportunity to partner more effectively with tribes to address interests of mutual benefit, such as restoring sustainable populations of bison to tribal and public lands, conserving habitat for bison and other wildlife, and supporting treaty rights. In 2016, the Buffalo Treaty Nations provided the Secretary of the Interior with a resolution supporting the use of quarantine to identify brucellosis-free bison for relocation to the Fort Peck Indian Reservation in northeastern Montana and, eventually, other tribal lands.

In 2018, the NPS, APHIS, and MDOL began a quarantine program (now called the BCTP) to identify brucellosis-free Yellowstone bison and transfer them to the Fort Peck Indian Reservation. Quarantine involves keeping groups of bison in isolated pens and testing them repeatedly for brucellosis exposure until all positive animals are removed and the remainder test negative for two consecutive months. These bison then undergo additional testing based on their age and sex following protocols outlined in APHIS' 2003 *Uniform Methods and Rules* (USDA, APHIS 2003). Since 2019, the NPS and APHIS have sent about 300 brucellosis-free Yellowstone bison to the Assiniboine and Sioux Tribes at Fort Peck for one year of additional testing and eventual release. The Fort Peck tribes have agreed to transfer approximately 70% of the bison that complete testing to the ITBC for restoration on tribal lands elsewhere. The ITBC has about 82 member tribes that collectively manage more than 20,000 bison in 65 herds (Robbins 2023). Several tribes have significant lands that could sustain large bison herds and the ITBC is working with them to achieve this goal. The ITBC has transferred more than 170 bison of Yellowstone-origin from Fort Peck to at least 23 tribes across 12 states. In 2021 and 2022, YNP doubled the capacity of this program through a partnership with Yellowstone Forever, the Greater Yellowstone Coalition, and Defenders of Wildlife to lower the number of animals sent to slaughter and increase the restoration of bison to tribal lands (USDI, NPS 2018, 2023).

Conclusions

Many tribes have a deep relationship with Yellowstone bison because they are wild descendants of the huge herds of bison that once roamed across North America and provided their ancestors with food and other resources for centuries (Plumb and Sucec 2006). These tribes see the differential treatment of Yellowstone bison, including confinement, testing, and slaughter, compared to elk that also have brucellosis as analogous to the social injustices experienced by indigenous people following colonization (Plumb and Sucec 2006). As a result, Yellowstone bison are important for these tribes to recover and restore their long-lasting cultural and spiritual relationships with bison (Potter et al. 2010).

American Indian tribes also have sovereign interests in restoring tribal control over their own food production and security and decreasing reliance on external sources (Potter et al. 2010). Thus, the transfer of brucellosis-free Yellowstone bison to tribal lands has a beneficial impact on federal-tribal trust relationships. Tribes use transferred bison to establish or supplement tribal herds for conservation, hunting, nutrition, and cultural purposes. The frequent occurrence of diabetes on reservations has motivated a return to a more-traditional, bison-based diet in recent years (Adams and Dood 2011). Tribes benefit by receiving meat from bison completing the BCTP, or those harvested or shipped to slaughter, that are made available to their families or other tribal members, including seniors, diabetics, Head Start centers, school lunch programs, homeless shelters, and cultural and traditional ceremonies (Wallen et al. 2015c). The NPS is continuing to transfer more brucellosis-free bison to augment or establish populations of plains bison on tribal lands in North America to restore these cultural, ecological, and spiritual relationships. These actions will facilitate bison recovery; improve hunting opportunities; enhance local, regional, and tribal economies; and enrich the experiences of tribal members, residents, and visitors (White et al. 2015b,c).

Brucellosis-free Yellowstone bison released from trailers on the Fort Peck Indian Reservation.
Photograph by Jacob W. Frank, National Park Service, 2019.

Chapter 9—Current Management

Goals and Objectives

Park biologists established several demographic, ecological, and genetic objectives to guide the conservation and management of Yellowstone bison (White et al. 2015c, IBMP Agencies 2016, Geremia 2022). The first demographic objective is to *Sustain a Viable, Wild Population*. The term 'viable' or 'viability' refers to a population persisting without human interference for the foreseeable future (Gates and Ellison 2010). A population viability analysis indicated Yellowstone bison should retain about 95% of existing allelic (genetic) diversity for neutral nuclear microsatellites ('genes') for centuries with total abundance averaging at least 3,000 to 3,500 bison, provided intermixing and gene flow continue between bison in the two primary breeding herds (Pérez-Figueroa et al. 2012). However, more diversity could be lost if there is high variance in female reproductive success or removals are not primarily juvenile bison (Pérez-Figueroa et al. 2012, Geremia 2022). The NPS is continuing to assess genetic information and will revise these population viability analyses, adjusting minimum numbers as dictated by the best available science. Per statute and policy, however, the NPS does not manage for minimum numbers of wildlife but, rather, to sustain populations in their natural condition, which was defined as "the condition of resources that would occur in the absence of human dominance over the landscape" (USDI, NPS 2006a; 16 USC 21 et seq., 17 Stat. 32; 54 USC 100101a,b). Thus, to the extent feasible, the NPS allows bison and other wildlife to move freely and unpursued within the interior of YNP, with their behaviors, movements, reproductive success, and survival primarily affected by their decisions and natural selection (White et al. 2013, White 2016). The NPS "has discretion to manage Yellowstone bison at levels that can be accommodated on the available habitat" (*Western Watersheds Project et al. v. Secretary of the Interior Salazar et al*., 766 F.Supp.2d 1095 (2009), affirmed No. 11-35135 (9th Cir. 2012:3)).

A second demographic objective is to *Maintain More than 1,000 Bison in the Central and Northern Breeding Herds*. Bison breed in the northern or central geographic regions of the park with some interchange of animals between breeding areas among years (Wallen and White 2015). The founding maternal lineages of the population are found in both breeding areas (Forgacs et al. 2016). As mentioned previously, Hedrick (2009:419) indicated "[i]ndividual herds or clusters [of plains bison] should have an effective population size of 1000 (census number of 2000–3000) to avoid inbreeding depression and maintain genetic variation. If it is not possible to have this primary herd in 1 location, then it could be in 2 or 3 locations with significant genetic exchange between them." Thus, biologists want to maintain more than 1,000 bison in each breeding area to help protect any existing unique diversity or rare alleles (genes) within each area. This objective also allows bison to be a meaningful component of the food web influencing energy and nutrient transfer across a broad geographic area of the park, as described under the ecological objectives (Wallen et al. 2015b, Geremia et al. 2019). The IUCN guidelines for the conservation of wild bison recommend avoiding the removal of more than 30% of the population and the disproportionate removal of female groups (Gross et al. 2010). Thus, managers track the numbers of Yellowstone bison removed by all tribes and agencies and try to avoid removing more than 25% of the post-calving population in a single winter or reducing the late-winter population below 3,000 bison. Removing less than 25% of the population reduces the chances of altering population composition and reducing genetic diversity (Geremia 2022).

A third demographic objective is to *Maintain a Balanced Sex Ratio*. The IUCN recommends maintaining a population with neither sex comprising more than 60% to facilitate competition for mates (Gross et al. 2010). Thus, managers of Yellowstone bison try to maintain a balanced sex ratio of about 50% males and 50% females to support mate competition and allow natural selection, including predation and starvation, to vary reproductive success and survival among years and sustain genetic diversity (Gross et al. 2010, Pérez-Figueroa et al. 2012, White 2016, Geremia 2022). A fourth demographic objective is to *Maintain an Age Structure of About 70% Adults and 30% Younger Animals*. Managers of Yellowstone bison try to maintain this age structure, which is based on the expected population composition given age-specific birth and survival rates (Geremia et al. 2015c, Hobbs et al. 2015, Geremia 2022). The IUCN recommends trying to mimic natural mortality patterns of higher mortality for younger and older bison. The removal of young animals prior to breeding increases the generation (replacement) interval and lengthens the retention of genetic diversity (Gross et al 2010).

A specific genetic objective is to *Maintain Gene Flow Between Primary Breeding Herds and Preserve Existing Genetic Diversity*. Yellowstone bison are currently a single intermixing population with breeding and gene flow between bison originating in central and northern YNP (White and Wallen 2012, Stroupe et al. 2023). To the extent possible, managers allow ecological processes, such as natural selection, migration, and dispersal, to prevail and influence population and genetic substructure (White and Wallen 2012, Wallen and White 2015). Biologists would like to maintain existing allelic richness and diversity based on neutral nuclear markers (Geremia 2022).

The first ecological objective is to *Sustain the Role of Bison as Ecosystem Engineers*. To the extent feasible, managers allow bison to move unfettered in the interior of YNP so they can fulfill their ecological role. When bison roam without human constraints, they begin to engineer the landscape as described by Geremia et al. (2019, 2022). A second ecological objective is to *Maintain Functional Grasslands*. Biologists are attempting to maintain functional vegetation communities that 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 (Geremia and Hamilton 2019, 2022). Many communities include invasive plants due to their previous spread (Renkin 2022, Wacker 2022). Bison 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, 2022).

A third ecological objective is to *Sustain Bison as a Meaningful Component of the Food Web Influencing Energy and Nutrient Transfer through the Ecosystem*. To the extent feasible, bison are managed with minimal intervention in the interior of YNP, so they continue to provide a key food source for species ranging from wolves to magpies to beetles and bacteria in the soil that redistribute nutrients across the landscape (Wallen et al. 2015b). Bison carcasses contribute to nutrient surges that greatly enhance the productivity of nearby plants. Carcasses of bison dying from injuries or malnutrition provide about 25% of the meat wolves eat during winter (Metz et al. 2020a,b).

Social objectives include *Promoting an Environment in YNP Where Wildlife Remain Uncontrolled and Visitors Can be Impressed and Inspired by Their Uninhibited Behaviors*. As a park historian emphasized, the greatest value of YNP may be the "authenticity of its wildness—the opportunity for us to be awed and learn from nature making its own decisions" (Schullery 2010, White et al. 2013, White 2016). The IBMP agencies also *Manage Brucellosis Transmission Risk to Cattle*. Park staff work with Montana, APHIS, CGNF, and private landowners to manage brucellosis transmission risk from bison to livestock by preventing mingling through hazing, hunting outside the park, fencing, removing attractants, and improving forage on public lands. Montana uses these same techniques to manage risk from elk populations in the Madison and Paradise valleys also chronically infected with brucellosis (National Academies of Sciences, Engineering, and Medicine 2017, Rayl et al. 2019). Another objective is to *Protect Human Safety and Property*. Park staff work with Montana, CGNF, tribes, and private landowners to reduce and alleviate conflicts with livestock, people, and property using hazing, captures, and other tools when necessary (IBMP Agencies 2016, Geremia 2022).

Adaptive Management

The NPS defines adaptive management as "a system of management practices based on clearly identified outcomes and monitoring to determine whether management actions are meeting desired outcomes; and if not, facilitating management changes that will best ensure that outcomes are met or re-evaluated" (43 Code of Federal Regulations 46.30). More simply, adaptive management "refers to the process of learning by doing and then adapting or adjusting" (USDI, NPS 2016). It recognizes imperfect knowledge and the uncertainties in natural systems and allows managers to adapt to changing conditions and new information (learning) to progress toward objectives (Williams et al. 2007).

The agencies and tribes involved with the IBMP have used this process to inform decision-making and adjust bison management. Park biologists evaluate current conditions, identify undesired trends, implement management actions, monitor progress toward desired conditions, and adjust actions to improve progress. Managers have met with partners to explore options outside the park, including streamlining testing protocols for quarantine as part of the BCTP and the construction of additional quarantine facilities in the Designated Surveillance Area for brucellosis (Springer Browne et al. 2023). The management of Yellowstone bison requires frequent adaptive adjustments and evaluations of progress in achieving objectives as circumstances change and new information is acquired (Hobbs et al. 2015). Biologists in YNP recommended implementing management actions for 3 to 5 years, followed by assessments of progress, current knowledge and conditions, and updated model forecasts, to provide managers with sufficient information to decide how to proceed (Hobbs et al. 2015).

IBMP Partner Responsibilities

In recent years, a few people have maintained the IBMP violates Article II, Section 3, of the U.S. Constitution which prohibits federal agencies from delegating their authorities to nonfederal bodies. They maintain the NPS and USFS have illegally ceded their authority over bison management to the IBMP and must either establish a committee under the Federal Advisory Committee Act (FACA) or issue separate or joint (federal) decision documents after every IBMP decision. However, a FACA committee is not required when participants in a collaborative group are solely federal, state, tribal, or local government employees operating in their official capacities, which is the structure of the IBMP partnership. The Superintendent of YNP, through the Secretary of the Interior and Director of the NPS, has the authority to enter into agreements and discussions with other federal, state, and tribal agencies, but cannot wholly delegate their responsibilities to other entities not bound by the NPS Organic Act (*National Park & Conservation Association v. Stanton*, 54 F. Supp. 2d 7, 18 (D.D.C. 1999)). As a result, the Secretary of the Interior and responsible NPS managers collaborate with other federal and state agencies and tribes and tribal organizations but retain final reviewing and decision-making authorities about the management of bison within YNP. The Partner Protocols for the IBMP clearly indicate "[p]artners recognize that they each retain their own independent goals and responsibilities. They are not required to relinquish or subjugate those individual mandates to be part of the Partner group." Instead, the partners "work as a collaborative, problem-solving body seeking to produce consensus management actions that address, to the greatest extent possible, the needs and interests of all participants" (IBMP Partners 2016).

Under the IBMP, federal and state partners have issued separate decision documents for implementing bison management within their respective jurisdictions. In 2014, the NPS issued a Record of Decision pursuant to the National Environmental Policy Act which concluded the implementation of park-wide remote vaccination would not achieve desired results and could have unintended negative effects to bison and visitor experience. In 2015, the State of Montana issued a Decision Notice pursuant to the Montana Environmental Policy Act to increase tolerance for more bison across a larger management area in the state, including year-round in some areas (Bullock 2015). In 2018, the NPS issued a Finding of No Significant Impact to conduct quarantine with Yellowstone bison in YNP and on the Fort Peck Indian

Reservation (USDI, NPS 2018). In 2022, the Custer Gallatin National Forest issued a Record of Decision on a new Land Management Plan. The selected alternative includes components supporting habitat improvement projects to create or connect suitable bison habitat with enough bison present and distributed year-round to provide a self-sustaining population on the national forest in conjunction with bison herds in YNP (USDA, USFS 2022).

Under the IBMP, the NPS implements bison management actions inside YNP and has legal responsibilities to protect tribal treaty rights, lands, assets, and resources (IBMP Agencies 2016). The YNP Protection Act of 1872 requires the Secretary of the Interior to preserve "from injury or spoilation" the "timber, mineral deposits, natural curiosities and wonders" of the park and to ensure "their retention in their natural condition" (16 USC 21 *et seq*., 17 Stat. 32). The NPS Organic Act of 1916 directs park managers to "conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations" (54 USC 100101a,b). As mentioned previously, contemporary management policies clarified managers should preserve "components and processes in their natural condition" which is defined as "the condition of resources that would occur in the absence of human dominance over the landscape" (USDI, NPS 2006a:36, 42).

Some people contend the National Park Service has jurisdiction and legal authority over Yellowstone bison and their management wherever they roam, including outside the park and, as a result, can ignore management zones in the State of Montana and regulate bison distribution and hunting in that jurisdiction. These assertions are based on the Supremacy Clause in the Constitution, federal treaties with American Indian tribes that guarantee off-reservation hunting rights, and 16 U.S.C. 36, *Disposition of Surplus Elk, Buffalo, Bear, Beaver, and Predatory Animals* which states "[t]he Secretary of the Interior is authorized, in his discretion and under regulations to be prescribed by him, to give surplus elk, buffalo, bear, beaver, and predatory animals inhabiting Yellowstone National Park to Federal, State, county, and municipal authorities for preserves, zoos, zoological gardens, and parks. He may sell or otherwise dispose of the surplus buffalo of the Yellowstone National Park herd, and all moneys received from the sale of any such surplus buffalo shall be deposited in the Treasury of the United States as miscellaneous receipts" (16 USC 36; 54 USC 100101, 100752). However, Congress passed this statute in 1923 due to concerns about brucellosis transmission and overgrazing by ungulates; it was never intended to be applied to animals that migrated or dispersed outside the park and into the jurisdictions of surrounding states—as indicated by the phrase "animals inhabiting Yellowstone National Park." Thus, to argue the NPS has authority or jurisdiction over wildlife (including harvests) once they leave the park, based on the contention that this statute does not provide geographic limits, is misrepresenting its intent.

In Montana, the Fish, Wildlife & Parks Commission typically sets policies for the protection, management, and public use of wildlife (MCA 87-1-201). However, in 1994 the Legislature assigned the management of Yellowstone bison to the MDOL due to the population's chronic exposure to brucellosis. The Department can remove Yellowstone bison moving into Montana if they jeopardize programs to control livestock diseases (MCA 81-2-120). Pursuant to a plan approved by the Montana Governor, the MDOL contains bison in areas near YNP and keeps them separate from livestock. Staff from MFWP cooperate in this management paradigm, focusing on public hunting and preventing damage to property (MCA 87-1-216, MCA 87-2-730). The MDOL authorizes the dates of the public hunt, which is then administered by MFWP (MCA 87-2-730).

The USFS manages National Forest System lands as habitat for native species, which includes bison, in collaboration with other federal, state, and tribal partners. The USFS manages national forests pursuant to a multiple-use mandate, whereby renewable resources are used to best meet the needs of the American people (16 USC 528, 1604). Comprehensive forest plans are prepared to sustain wildlife populations and their habitats, with the management of wildlife often primarily conducted by the respective states (16

USC 528, 1604). If necessary, the USFS can preempt or supersede state laws and policy to meet their statutory and trust obligations regarding issues such as public safety and natural resource protection after consultation with the states (43 USC 1732).

The mission of APHIS is to protect the health, quality, and productivity of American agricultural resources. The Secretary of Agriculture establishes regulations to prevent the interstate or international spread of livestock diseases, including the quarantine of animals. Under the Animal Health Protection Act (7 USC 8301 et seq.), the Veterinary Services section of APHIS administers the National Brucellosis Eradication Program in cooperation with the states. The 2003 Uniform Methods and Rules for Brucellosis Eradication describe standards for surveillance, testing, and interstate transport of livestock and domestic bison (USDA, APHIS 2003). They also contain a protocol for the quarantine of bison from Grand Teton and Yellowstone national parks to determine if animals are brucellosis free.

American Indian tribes retained aboriginal rights over lands within their aboriginal territories and exercise rights reserved by treaties with the U.S. government. Each tribe exists as a sovereign nation with self-governing authority and an emphasis on preservation of cultures and traditional ways of life. Tribal sovereignty is recognized in the U.S. Constitution and protected by U.S. Supreme Court decisions. The Salish and Kootenai, Nez Perce, Shoshone-Bannock, Umatilla, Yakama, Blackfeet, Northern Arapaho, and Crow tribes have reserved treaty hunting rights, including on unoccupied lands within Montana. The ITBC is a federally-chartered Indian organization pursuant to the Indian Reorganization Act and includes about 82 member tribes working to reestablish buffalo on Indian lands.

Under the IBMP, the NPS has lead responsibility for implementing bison management actions inside YNP while the State of Montana has lead responsibility outside the park (IBMP Members 2022). Thus, the NPS does not have regulatory authority or jurisdiction over hunts or other management actions that occur outside YNP (Sholly 2020), and hunts conducted on national forests under permits from MFWP or tribes exercising their treaty rights do not require authorization from the USFS (Erickson 2019). In addition, the State of Montana does not have the authority to decide which tribes have rights to hunt bison through treaties with the federal government. Rather, state officials have recognized tribes with rights to harvest bison after reviewing relevant treaty language and accounts of their historic use of the area (see Dockter 2017). A tribes' declaration that "it has used and occupied an area since time immemorial is sufficient proof of aboriginal title, … by virtue of possession of the land and their inherent tribal sovereignty" (*Narragansett Tribe of Indians v. Southern Rhode Island Land Development Corporation*, 418 F. Supp. 798, 806-807 n.7 (D.R.I. 1976); Stark et al. 2022:412-413). More discussion is needed between the federal departments of Agriculture, Interior, and Justice to identify responsible federal agencies and their authorities because these questions are important for improving management and pertinent to ongoing litigation (Neighbors Against Bison Slaughter versus the NPS in the U.S. District Court for the District of Montana, Billings Division, CV 19-128-BLG-SPW).

Coordination and Surveys

Under the IBMP, operating plans are used to set out "specific expectations and areas of responsibility for personnel from each of the cooperating agencies" (USDI, NPS and USDA, USFS and APHIS 2000b:42). The NPS meets with IBMP partners each spring to evaluate operations from the prior winter, identify problems, and propose solutions. Representatives from tribes that hunt Yellowstone bison outside the park meet with representatives from Montana and the CGNF to discuss issues and concerns from previous hunts, safety concerns such as no shooting zones, access, and enforcement, and to share hunter harvest data. Park staff attend these meetings to provide information on the status of the bison population and discuss management objectives for the overall population and each breeding herd (central, northern). Each summer, NPS biologists conduct counts and classifications of bison using an airplane and ground surveys. They update an integrated population model with current data to evaluate trends in the central and northern breeding herds and identify a management strategy that meets demographic, genetic, ecological, and social objectives (Geremia 2022). Biologists provide this summary, with recommendations for conservation and management, to the superintendent of YNP and then, each autumn, convey this information to the other IBMP members and hunting tribes for their consideration (Geremia 2022).

The actual number of bison removed from the population each winter depends on the number of animals migrating to the park boundary, capacity for the quarantine and live transfer of brucellosis-free animals, hunter success outside the park, and level of conflicts outside the park (Geremia 2022). As winter progresses, the NPS conducts aerial and ground surveys to predict numbers of bison moving to the park boundary and support decision-making for management activities. The NPS participates in weekly calls to inform other IBMP members and treaty hunting tribes about the timing and extent of bison migrations toward the boundary of YNP and coordinate with them regarding capture activities for the BCTP and slaughter to reduce effects on hunting opportunities outside the park. However, the NPS does not have authority or jurisdiction over when, where, and how hunter harvests of wildlife occur outside the park.

Bison Distribution

Bison can use all wilderness and other undeveloped areas in YNP and leave the park into established management areas north and west of the park in Montana where state agencies in cooperation with the national forest supervisor and private landowners determine levels of tolerance for bison. Bison of both sexes can use the Eagle and Bear creek areas and portions of the Absaroka-Beartooth wilderness north of YNP year-round (Figure 3). State personnel haze female and young bison from the northern management area back to YNP by May 1, but male bison can remain in this area year-round. In addition, bison of both sexes can use the Hebgen Basin west of YNP year-round, including Horse Butte and north along Highway 191 to the Cabin Creek Recreation and Wildlife Management Area, Monument Mountain Unit of the Lee Metcalf Wilderness, and the Taylor Fork drainage (Figure 4). State personnel limit numbers of bison in the western management area to 250 from July through September, 450 from October through February, and 600 from March through June. From November 15 through April 15, up to 30 female bison (or a mixed group of 30 males and females) can use the Madison Arm. After April 15, up to 30 female/mixed group bison can be east of the Madison Arm Resort. After May 15, no females or mixed groups of bison can use the Madison Arm, and state personnel haze them to nearby areas or remove them (IBMP Agencies 2016).

Methods of Management

Bison move freely within the park year-round and a variable number migrate to the boundary during winter. Bison are allowed to move into management areas north and west of the park, where they are managed by Montana and the USFS. Several American Indian tribes exercise their rights to hunt bison on unoccupied lands in Montana near the park boundary. If desirable, bison are captured in the Stephens Creek Administrative Area near the north boundary of YNP to reduce numbers and limit migration into Montana. Managers implement hazing to protect people and property and prevent bison from leaving management areas in Montana and mingling with cattle.

<u>Public and Tribal Hunting</u>—Since 2012, the IBMP partners have prioritized harvests as a primary removal method for bison to reduce shipments to slaughter (IBMP Agencies 2016). Congress prohibited hunting in YNP in 1894 (16 USC 26), and this prohibition includes the boundary lands area in northern YNP between Gardiner, Montana, and the northern boundary of the park at Reese Creek. Thus, bison hunting in Montana occurs outside the northern (Gardiner basin) and western (Hebgen basin) boundaries of YNP. An annual 90-day public bison hunt administered by MFWP occurs from November 15 to February 15 on lands adjacent to the park. In addition, tribal hunts outside the park generally occur from

December through March, with each tribe determining its own regulations and seasons. Eight tribes have exercised their treaty rights and harvests vary from year-to-year depending on how many bison move to the park boundary in response to forage production, snow depths, and forage availability in the higher mountains (Geremia 2022).

The NPS supports the treaty hunting rights of tribes by sustaining a wild population of bison capable of migrating and dispersing outside YNP onto adjacent USFS-managed lands so tribes can access this traditional food, cultural, material, and spiritual source. Park staff participate in hunt-capture coordination efforts to reduce the effects of capture operations in YNP on hunting opportunities. They also provide requesting tribes with captured bison for processing and the distribution of meat, hides, and other resources to their members. The NPS has indicated it will work with the tribes and CGNF to connect suitable habitat and provide a self-sustaining bison population on the national forest in conjunction with bison herds in YNP (USDA, USFS 2022). In addition, staff engage with tribes associated with Yellowstone bison, the CGNF, MFWP, residents, and non-governmental organizations to explore ways to increase the efficiency and safety of hunting outside the park.

<u>Captures</u>—When deemed necessary, the NPS captures bison at a facility in the Stephens Creek Administrative Area of northern YNP for quarantine to transfer live animals to tribal lands, provide carcasses of culled bison to requesting tribes for nutrition, lower the number of bison exiting the park, and reduce population growth. The NPS does not capture bison in the interior of the park because it would "detract from the wild free-ranging qualities of the bison population" and "could have a major adverse impact on the distribution of bison" (USDI, NPS and USDA, USFS and APHIS 2000a:415). It also would adversely affect the movements of other wild animals and negatively affect visitor experiences. Capturing bison in the interior of the park during October to March is impractical because it would require plowing roads to facilitate effective operations at various locations and allow for the transportation of bison from the park to quarantine, research, or slaughter facilities. The NPS developed a long-term regulation for winter recreation during 2013 that rejected plowing roads for wheeled vehicles in favor of an alternative that allows over-snow vehicles on interior park roads (USDI, NPS 2013). In addition, capturing bison in the spring after calving during June to August would disturb mother-calf pairs and affect their nutrition during lactation due to stress and energetic costs. If later or impeded migrations due to climate warming, hunting, or other factors severely limit the effectiveness of managing bison abundance near the boundary, park managers may consider capturing bison further inside the park. However, such actions would require a substantial increase in staff, time, and funding to capture, process, and distribute bison, as well as to ensure the safety of visitors and staff by restricting access to areas of the park for extended periods.

The Stephens Creek Administrative Area is closed to public access year-round. During capture, processing, and shipping operations, the NPS enacts a temporary area closure that extends about 0.6 miles (1 kilometer) from the area and is about 3.5 miles (5.6 kilometers) long. The duration of the closure is determined by bison migration to the park boundary and operational needs. This temporary closure is implemented for public, staff, and bison safety and to ensure management operations are unimpeded. Once capture and/or herding actions begin, operations are often sporadic, dynamic, and unscheduled, leaving no time to ensure members of the public are absent from the operational area. Capture and herding events could involve many dozens of bison. The unanticipated presence of people in the area could disrupt operations and panic the bison, placing the public, staff, horses, and bison at risk of injury.

The number of bison removed from the population each winter depends on the number of animals migrating to the park boundary, capacity for the live transfer of animals, hunter success outside the park, and level of conflicts outside the park (Geremia 2022). The NPS captures bison before April, when females are later in gestation. Bison generally migrate to the northern boundary area over a period of 4 to 6 weeks. Larger captures generally occur during more severe winters or persistent droughts when larger, earlier, and prolonged migrations occur (Geremia et al. 2011, 2014, 2015b). If the NPS decides to cull bison to limit abundance, personnel primarily capture migrating groups of females and young that move to the boundary more frequently than adult males. The general philosophy for capture and processing is to apply as little pressure and stress as necessary to move bison into and through the facility. Bison are enticed (hay) or hazed into fenced pens using low-stress techniques such as people walking or on horseback slowly moving behind them to influence their direction (Geremia 2021, Hibbard 2021). Thereafter, NPS personnel contact tribal and agency partners to schedule transport to the BCTP, slaughter, or research facilities. Based on these discussions, bison are sorted into appropriately sized groups in various holding areas so they can be moved into quarantine pastures adjacent to the Stephens Creek Administrative Area or loaded onto trailers for shipment to other quarantine, slaughter, or research facilities outside the park.

If space is available, some bison testing negative for brucellosis exposure are placed in the BCTP to increase the number of live brucellosis-free animals relocated to the Fort Peck Indian Reservation and eventually other tribal lands. Up to about 100 to 300 bison could be entered into the BCTP during most winters, which would require the capture of about 300 to 750 bison, many of which would not be eligible due to previous exposure to *Brucella* bacteria (Geremia 2022). After the capacity of the BCTP is filled, park staff either release other animals or give them to the tribes for slaughter. Other bison are allowed to move past the facility throughout the winter to support hunting opportunities outside the park. If the winter is severe and a mass migration to the northern park boundary could hinder the capacity of managers to keep bison and cattle separate, additional bison may be captured (Geremia 2022). These bison can be held in the Stephens Creek Administrative Area facility for later release in spring when conditions are suitable for bison to migrate to higher-elevation summer ranges in YNP. In 2011 and 2023, the NPS held roughly 800 bison in captivity and fed them hay for several weeks to prevent mass migrations north of the park. These bison were released during spring, but confinement and feeding conflict with the management of bison as wildlife and could lead to food-conditioning, disease transmission during confinement, and disruption of traditional migratory patterns (Gross et al. 2010).

<u>Bison Conservation Transfer Program</u>—This program was established in 2018 to reduce shipments of bison to slaughter and provide live bison to American Indian tribes. Captured bison initially testing negative for brucellosis exposure are put through a multiple-year testing protocol and eventually deemed brucellosis-free. They are then transferred to the Fort Peck Indian Reservation for an additional year of testing. Thereafter, bison can be moved anywhere for conservation, cultural, and spiritual purposes. Since 2019, about 300 bison have been sent to Fort Peck; another 282 were placed in the program last winter. The ITBC has transferred about 170 Yellowstone-origin bison to 23 tribes in 12 states.

Quarantine is conducted in fenced facilities in and adjacent to the Stephens Creek Administrative Area in YNP, north of the park in Corwin Springs, Montana (two properties leased by APHIS), and at the Fort Peck Indian Reservation (USDI, NPS 2018). In 2022, the NPS doubled the capacity of the quarantine pastures near the Stephens Creek Administrative Area in YNP to about 200 to 250 bison. Prior to winter, the NPS coordinates with the tribes and ITBC regarding the composition of bison they would like taken into quarantine, such as all males or family groups. Park staff capture and test bison for brucellosis exposure using trap-side tests specified by APHIS and Montana health officials. Animals that initially test negative are placed into the quarantine facility in groups based on age and sex. Their blood sera are sent to diagnostic laboratories for comprehensive testing to confirm the initial results. Captured bison not eligible for the BCTP may be released so they are available for tribal hunters outside the park or shipped to slaughter if there is a need to reduce numbers substantially.

Bison placed in quarantine are then tested according to USDA rules for brucellosis eradication as specified by APHIS' *Uniform Method and Rules for Brucellosis Eradication* (USDA, APHIS 2003). For groups of males to complete the quarantine process, the entire group of bison in a pen must test negative with the result confirmed 30 days later (phase I), which generally takes about 180 to 210 days. Thereafter, the entire group must test negative again 6 and 12 months later (phase II). After all males in the group reach 3 years of age, the group is certified as brucellosis-free and transferred to an assurance testing facility on the Fort Peck Indian Reservation. The group is then retested at 6 and 12 months (phase III), after which they can be released or transferred to other areas.

For groups of non-pregnant females to complete the quarantine process, the entire group must test negative with the result confirmed 30 days later (phase I), which generally takes about 180 to 210 days. Thereafter, the females are bred with a brucellosis-free male and must test negative via the culture of a uterine swab collected within 5 days of parturition. The entire group must test negative 30 to 90 days after each female gives birth and at least 6 months after the last female calved (phase II). The group is then certified as brucellosis-free and transferred to an assurance testing facility for retesting at 6 and 12 months (phase III), after which they can be released or transferred to other areas. In summary, a test group of males requires about 20 months within a holding pen to complete the quarantine process, while a group of females requires about 34 months (USDA, APHIS 2003).

Since 2005, APHIS and the NPS have placed more than 600 Yellowstone bison in quarantine. In 2022, APHIS and the NPS analyzed existing quarantine data to determine the number of days a group of bison needed to be held and tested in quarantine to ensure a negligible risk of one animal having brucellosis. A time-to-event model using this data predicted 95% of bison with brucellosis would seroconvert (test positive) within 210 days, 99% by 250 days, and 99.9% by 294 days. In other words, only 1 in 1,000 bison (0.0014 probability) with brucellosis bacteria would not be detected by 300 days and fewer than 4 in 10,000 bison would not be detected by 330 days. The results were similar for males and females. These findings suggest regulators could reduce testing timelines to allow animals to complete quarantine within one year with negligible risk of brucellosis transmission. Reducing the quarantine requirements (phases I and II) of bison to less than one year, while still using assurance testing (phase III) as an added safety measure, could nearly triple program capacity to graduating about eight groups totaling about 225 bison to assurance testing annually (USDA, APHIS 2022; Springer Browne et al. 2023). The NPS is continuing to work with APHIS and Montana to shorten quarantine testing timelines, as feasible, which could involve modifying or eliminating the current three-phased testing approach (Springer Browne et al. 2023).

Shipments of Bison to Slaughter—If space is not available in the BCTP, bison can be transferred to tribal representatives at the capture facility for delivery to slaughter plants and subsequent distribution of meat, hides, and other resources to their members. Local representatives from APHIS certify the numbers, sexes, and age categories of bison loaded and secured in each trailer using Veterinary Services Form 1-27. The haulers then chain and lock the trailer doors, and personnel from APHIS put an official seal on the lock and chain and provide the hauler with a list of each bison on board the trailer. The trailers leave the Stephens Creek Administrative Area with law enforcement escorts and proceed directly to quarantine, slaughter, or research facilities. Shipments of bison to slaughter were the primary method used to reduce numbers until 2012. However, this method is stressful to the bison and unpopular with staff and the public. Thus, the NPS wants to minimize the use of this method and lower numbers of bison were shipped to slaughter during the past three years (IBMP Agencies 2016)

Hazing—Staff haze bison in YNP when necessary for safety reasons, to protect property, or to move bison into the capture facility in the Stephens Creek Administrative Area, primarily from February to April. Hazing in YNP is conducted by people walking, on horseback, or in vehicles. Before initiating hazing, personnel assess the condition, size, and temperament of the herd, as well as the terrain where the herd is located, potential paths along which to move the bison, and potential hazards along the path of hazing. Weather conditions are considered because snow, ice, and mud negatively affect the footing of bison, horses, and people. Bison may not be amenable to moving very far, if at all, if they are already acting aggressive, such as bucking or butting, in poor condition, or have newborn calves. Furthermore, bison may resist moving after being hazed several times. Smaller groups of bison generally are easier to move safely and efficiently than larger groups, which tend to fragment into several smaller groups as they move (Wallen and Keator 2012).

The general philosophy for hazing is to apply as little pressure as necessary to move bison in the desired direction. Hazing is initiated by approaching a group of bison at an angle (zig-zag pattern) from behind the direction of intended travel. Bison may initially trot in response to hazing but should calm down and move along in a somewhat slow, orderly manner if minimal pressure is applied. Hazing distances are minimized to avoid undue stress to the bison, especially mothers with recently born calves. Also, if bison in the group become aggressive or resistant to hazing, staff temporarily halt the operation and allow the bison to feed and rest. The snow cover and conditions in the area to which the bison are hazed is important. If bison are hazed to an area with deep or hard packed snow, or with many bison already present, it is unlikely they will remain because forage would be inaccessible (Wallen and Keator 2012).

If bison approach set boundaries in management areas in Montana, the State Veterinarian evaluates the circumstances, including numbers of bison, their behavior, weather, snowpack, and time of year, to determine what management actions are necessary to prevent bison from moving from the management area (IBMP Agencies 2016). Hazing by state and other officials outside the park in Montana is at the discretion of the state in cooperation with the national forest supervisor and private landowners to prevent the mixing of bison and cattle, to move bison away from private lands where they are not wanted, or to move bison away from homes and highways where they create safety or property issues. Hazing in Montana is conducted by people walking or on horseback, all-terrain vehicles, in trucks, or in helicopters. The NPS may assist state personnel with hazing bison in Montana by walking or on horseback, if requested and appropriate. Personnel from MFWP work with landowners who have safety and property damage concerns, as well as those who favor increased tolerance for bison, to allow bison to use suitable habitat while reducing conflicts.

Current Situation

Prior to the IBMP, bison that migrated into Montana were shot, slaughtered, or hazed back into the park by Montana personnel where some bison died of starvation or other natural causes (USDI, NPS, and USDA, USFS and APHIS 2000a). This approach involved more hands-on management by Montana, including funding and staff, to mitigate possible land use conflicts. In contrast, the management of bison under the IBMP has included more intrusive actions in the park, such as captures and shipments to slaughter, to constrain their abundance and distribution. Thus, the ecological processes of bison migration and dispersal are restricted at or near the park boundary due to concerns about brucellosis transmission to cattle. In contrast, elk with the disease are allowed to move freely into Montana and managed far less intrusively even though they have transmitted brucellosis to cattle numerous times while no transmissions to cattle have been attributed to bison (White et al. 2015a).

Although managers have successfully restored a viable population of bison within YNP and nearby areas, there are still important issues needing additional coordination, clarification, and resolution. There is always some uncertainty about management and tolerance in Montana because the NPS does not control what happens outside its' boundary, including adjacent land use practices and management policies. There are recurrent disputes with the State about bison numbers and disagreements about the effects of bison grazing (White et al. 2017b). The transmission of brucellosis to cattle from elk continues to be an intractable problem and there is a need to continue improving the safety and effectiveness of tribal bison hunts. As a result, there is ongoing litigation and several petitions to list bison as an endangered or threatened species. In addition, it is uncertain if periodically sending bison to quarantine will serve as a long-term tool for regulating the size of the Yellowstone population (in combination with hunting) or be effective in establishing other wild populations. Currently all bison sent to tribal lands are still in confinement (fenced), though many are within large areas and several tribes are working to establish wild, unfenced populations on their lands.

For continued recovery, Yellowstone bison need access to habitat outside YNP like other wildlife species, such as elk, including on public lands such as national forests (White et al. 2015b). Managers at YNP cannot preserve a viable population of bison on their own because when bison leave the park they are no longer under the agency's jurisdiction. Instead, their management becomes the prerogative of Montana in collaboration with the USFS on National Forest System lands. The NPS has worked with these agencies using adaptive management to increase tolerance for bison in their jurisdictions, including year-round in some areas (Bullock 2015). However, there is not much room to expand the management areas for bison further outside the park given the prevalence of agriculture, cattle, and rural residential development in the Paradise and Madison valleys. Expansion would likely require the eradication of brucellosis in bison but, even then, tolerance would likely be limited due to concerns about competition for grass, property damage, and other social issues (Plumb et al. 2009, Adams and Dood 2011, Hobbs et al. 2015, White et al. 2015a-c; MFWP 2019).

Public opinion is shifting toward more tolerance for bison in the region and managers have shown they can sustain more bison and allow them to move more freely onto suitable public lands. In recent decades, the areas north and west of YNP have become more demographically and economically diverse, with recreation, tourism, and amenity living competing with agriculture and natural resource extraction economies (Haggerty and Travis 2006, Hansen and Phillips 2018). As a result, more residents now consider the environment and wildlife viewing to be primary assets and values. Surveys indicate about two-thirds of Montanans want bison to be managed similar to other wildlife and restored to suitable public and tribal lands (National Wildlife Federation 2011, Tulchin Research 2015). In addition, MFWP concluded the restoration of bison on public, tribal, or private lands with willing landowners was appropriate on large landscapes where conflicts with livestock would be minimal (MFWP 2019, 2020). Montana has increased its tolerance for bison adjacent to YNP to facilitate conservation and hunting, including year-round in some areas (Bullock 2015). The CGNF recently issued a Land Management Plan that allows for expanded tolerance of bison on the national forest, including a desired condition to have a self-sustaining population of bison on the forest year-round (USDA, USFS 2022). Allowing bison to occupy more public lands would create new opportunities for hunting, bolster tourism, and enhance conservation. However, some state and local officials and private landowners do not support more tolerance for bison on public lands farther from the park (White et al. 2015c, State of Montana Newsroom 2021, Gianforte 2023). In addition, the continuing development of open space on private lands around the park degrades and fragments habitat and movement corridors for wild animals, including bison.

The number of people in the GYE has doubled to about 473,000 since 1970, and the number of homes has tripled, with about 31% of the area developed or used for agriculture (Hansen and Phillips 2018). Habitat destruction and fragmentation have mostly affected valley bottoms and floodplains with higher plant productivity and more moderate winter conditions. These valleys were the primary winter ranges for bison migrating out of mountainous areas, such as YNP. Agriculture, primarily livestock production, can degrade bison habitat by radically modifying native plant communities, displacing or prohibiting bison use of private lands, and reducing forage available for bison due to livestock grazing. Thus, conflicts with agriculture have constrained the restoration of wild, free-ranging bison populations and may continue to do so given real and perceived conflicts (Plumb and Sucec 2006, White et al. 2015c). However, agriculture also has maintained open spaces, some of which could be used as habitat by bison and other wildlife in the future rather than urban/exurban development (Hansen and DeFries 2007). The bison population in the Henry Mountains of Utah represents an example of successful management of a relatively small wild bison herd in a mixed ownership, agricultural setting (Adams and Dood 2011).

Conditions in the GYE present an opportunity to manage bison like other wildlife in some areas outside national parks and refuges. Tourism and recreational activities have a large and growing influence on the economy, and most 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 proximity on the landscape and within view from paved roadways. About 80% of visitors surveyed during 2016 rated bison as one of the most important resources in the park, equivalent to Old Faithful Geyser (Resource Systems Group 2017). During a similar survey in 2018, 91% of visitors listed wildlife viewing as extremely important or very important to their visit (USDI, NPS 2019). In addition, tourism is a major driver of the economy in the GYE with visitors to national parks and other public lands providing substantial economic stimulus to surrounding communities. In 2021, visitors to YNP spent approximately $630 million in gateway towns near park entrances and this revenue supported about 8,740 jobs, $294 million in labor income, $456 million in value-added, and $834 million in economic output (Cullinane Thomas et al. 2022).

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 (Plumb and Sucec 2006, Stark et al. 2022). As a result, efforts to respect the presence of bison as wildlife on the larger landscape will be welcomed by native peoples and most of the local, national, and international public. This vision is attainable because decades of management have shown 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, boost local and state economies, and hopefully, elicit regional and national pride in this tremendous conservation accomplishment. The time is right to recover bison, the iconic symbol of power and strength in our nation, as wildlife in appropriate locations of the GYE and elsewhere (Adams and Dood 2011, White et al. 2015c).

Chapter 10—Risks and Sustainability

Bull bison near Swan Lake in Yellowstone National Park.
Photograph by Jacob W. Frank, National Park Service, 2020.

The USFWS recently announced they would initiate a status review of Yellowstone bison based on information provided in three petitions received from 2014 to 2018 (USDI, USFWS 2022). A species status assessment begins with the compilation of information, including species' natural history, ecological needs, abundance, distribution, demographics, condition of habitats, and genetic diversity. The assessment then forecasts the viability of the species given various scenarios of future environmental conditions and conservation efforts (USDI, USFWS 2016). The species status assessment is not a decision document, but it does provide biological information, analyses, and predictions to support decisions pursuant to the Endangered Species Act of 1973, as amended (16 USC 1531 *et. seq*.). The species status assessment is scheduled for completion in 2026 (USDI, USFWS 2023).

This chapter provides relevant information for the status review of Yellowstone bison by the USFWS and a subsequent determination of whether these bison are a distinct population segment, whether they are threatened or endangered, and the extent of their resiliency, redundancy, and representation.

Distinct Population Segment

The petitions received by the USFWS suggest Yellowstone bison are a distinct population segment of plains bison, and that possibly, the central and northern breeding herds are distinct segments as well. A distinct population segment is a discrete and significant segment of a species that can be analyzed as if it were a species under the Endangered Species Act. The USFWS considers two elements when evaluating whether to designate a distinct population segment: 1) the discreteness of the population segment in relation to the remainder of the species; and 2) the significance of the population segment to the species (USDI, USFWS and U.S. Department of Commerce, National Oceanic and Atmospheric Administration 1996).

Discreteness

The Yellowstone bison population is markedly separated from other populations of plains bison and, as a result, there has been no gene flow into the population for numerous generations. Yellowstone bison have rarely dispersed to the nearest population in Grand Teton National Park (about 85 miles) and there are no known instances of bison from Grand Teton dispersing to YNP even though there are no physical barriers to such movements (Wallen and White 2015). Also, there are genetic differences between these populations because the Grand Teton population was founded partially from bison relocated from Theodore Roosevelt National Park, which has a different genetic lineage than Yellowstone bison (Dratch and Gogan 2010).

Significance

Yellowstone bison are significant because they represent a unique genetic lineage with a critical source of genetic material and heritable information for the recovery and evolution of plains bison (Halbert and Derr 2007, 2008; Hedrick 2009, Dratch and Gogan 2010, Forgacs et al. 2016). Descendants of the indigenous Yellowstone bison have persisted in a unique ecological setting for plains bison and developed adaptive capabilities honed by natural selection (Wallen and White 2015). Hence, the loss of the population would result in a significant gap in the range and adaptive behaviors of plains bison. Furthermore, Yellowstone bison have special significance to many American Indian tribes because they are considered the last living link to the indigenous herds of bison which once roamed across North America (Plumb and Sucec 2006, Wallen et al. 2015c). Yellowstone bison are one of a few unfenced, wild, wide-ranging populations of plains bison in existence today—and the only population large enough to be considered ecologically and genetically viable (Hedrick 2009, Gross et al. 2010). Thus, to many native people and scientists this population represents the only surviving natural occurrence of plains bison (Plumb and Sucec 2006, Freese et al. 2007, Sanderson et al. 2008, Hedrick 2009, Dratch and Gogan 2010, Gross et al. 2010).

Listing Factors

The petitions received by the USFWS requested Yellowstone bison be listed as threatened or endangered under the Endangered Species Act due to the curtailment of their historic range, lack of access to existing winter range, and loss of genetic diversity due to overutilization through culling and hunting because of the chronic presence of the disease brucellosis in the population (USDI, USFWS 2022). The USFWS can determine a species is threatened or endangered due to one or more of the following factors: A) present or threatened destruction, modification, or curtailment of its habitat or range; B) overutilization for commercial, recreational, scientific, or educational purposes; C) disease or predation; D) inadequacy of existing regulatory mechanisms; and E) other natural or manmade factors affecting its survival (16 USC 1533(a)(1)).

Factor A—Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range

Range Curtailment—Archaeological and historical records indicate plains bison were living in the area now encompassed by YNP and widespread through the larger ecosystem prior to colonization (Cannon et al. 2020, Whittlesey and Bone 2020). Historical observations suggest many bison in the area migrated seasonally between productive grasslands and meadows in the mountains during summer and lower elevation valleys and plains in outlying areas during winter (Whittlesey et al. 2018, Whittlesey and Bone 2020). However, the number of bison that spent time in the mountainous area now encompassed by YNP is unknown and sparse archaeological sampling and casual observations cannot be used to estimate population sizes, seasonal movements and migration routes, or periods of occupancy with certainty (Whittlesey et al. 2018, Cannon et al. 2020).

Park biologists and historians developed a rough approximation of the pre-settlement distribution of plains bison in the Yellowstone area (about 7,720 square miles or 20,000 square kilometers) based on written narratives from people traveling through the area but cautioned against interpreting this figure with any degree of accuracy or precision (Plumb et al. 2009:2378; Whittlesey et al. 2018). Regardless, the historic abundance and distribution of plains bison in the GYE was substantially reduced by 1900 due to the slaughter for hides during the 1870s and 1880s, with only about two dozen bison remaining inside YNP by 1900 (Meagher 1973, Whittlesey and Bone 2020). These indigenous bison and about two dozen bison introduced to northern YNP during the early 1900s spent winter in relatively small areas in the Pelican and Lamar valleys, respectively, and migrated to the Mirror Plateau and upper Lamar River drainages during summer (Meagher 1973). Protection and restoration actions over the next century allowed bison to increase in abundance and distribution, which now encompasses about one-half of the park and nearby areas of Montana north and west of the park (Plumb et al. 2009).

The current area used by plains bison in the GYE is roughly about 1,870 square miles (4,850 square kilometers) in Yellowstone and Grand Teton national parks and nearby management areas in Montana and Wyoming, respectively (White et al. 2015c). The bison population living in Grand Teton National Park (summer) and the National Elk Refuge (winter) in Wyoming was founded from Yellowstone bison in 1948 and supplemented with bison from Theodore Roosevelt National Park in 1964 (Aune et al. 2010). The bison in Theodore Roosevelt National Park were founded in 1956 with bison from Fort Niobrara National Wildlife Refuge in Nebraska and have somewhat sodifferent genetic lineage than Yellowstone bison (Halbert and Derr 2008, Hedrick 2009). Currently, there is no known intermixing of bison (gene flow) between Grand Teton and Yellowstone national parks (Wallen and White 2015).

Limited Distribution—Movements of bison beyond the boundary of YNP are limited to adjacent management areas in Montana (Figures 3 and 4) due to concerns about mingling with cattle and transmitting the bacterial disease brucellosis (USDI, NPS and USDA, USFS and APHIS 2000a,b; Bidwell 2010). The IBMP was adjusted several times during 2005 to 2016 to increase tolerance for bison migrating outside the park (IBMP Agencies 2016). Since 2011, hundreds to more than one thousand bison have migrated outside the park to habitat in the Hebgen and Gardiner basins of Montana during winter (Geremia et al. 2015a, Geremia 2022, 2023). There are additional public lands already protected in the GYE that could support wild bison in the future as conflicts are mediated and tolerance increases (White et al. 2015b, USDA, USFS 2022). To date, however, the impacts of conservation and management actions have been to recover a viable, wild population of migratory Yellowstone bison from near extirpation in the late 1800s and substantially increase their distribution in and near YNP, but not fully recover the species throughout the GYE or elsewhere due to a lack of tolerance for wild, unfenced bison outside of parks and preserves (White et al. 2015b). The Paradise and Madison valleys north and west of YNP support numerous livestock producers and rural residential development has increased rapidly during the past several decades; both of which are at times incompatible with the conservation of a free-ranging bison population (Haggerty and Travis 2006, Metcalf et al. 2016, Tilt 2020).

Livestock Grazing—Historic livestock grazing and ranching in areas within (Gardiner basin, Lamar Valley) and around (Madison and Paradise valleys) YNP has altered plant communities, soil characteristics, and other habitat elements (Rush 1932, Marlowe et al. 2016, Hansen and Phillips 2018). Bison are not allowed to occupy areas where cattle are grazing. The federal government and non-governmental groups have worked with lease holders of grazing allotments on public lands to remove livestock grazing from some portions of the GYE to reduce conflicts with grizzly bears, wolves, and other wildlife. These agreements have removed livestock grazing from almost 700,000 acres (283,280 hectares) of habitat in the ecosystem (Wuerthner 2017, National Wildlife Federation 2018, USDA, USFS 2022).

In 1990, the USFS acquired the 3,200-acre (1,295-hectare) OTO Ranch north of the park from the Rocky Mountain Elk Foundation for $3.5 million. The ranch is within a key migration corridor for ungulates and other wildlife seasonally moving to or from YNP. In addition, the Rocky Mountain Elk Foundation transferred 1,508 acres (610 hectares) of land on the Royal Teton Ranch north of the park to the USFS in 1999. The USDI provided $1.8 million for the acquisition of this conservation easement "to aid and assist in the preservation of the YNP [Yellowstone] bison and other wildlife by setting aside a portion of its lands, in perpetuity, thereby providing in the natural world, a safe haven for the bison." The easement also facilitated "the use, movement, or migration of the surface estate by bison, elk, bighorn sheep, pronghorns, grizzly bear, black bear or mule deer" and avoided the "destruction or impairment of the natural habitat" (Deed of Conservation Easement, Royal Teton Ranch, Devil's Slide Area, Security Title 99-114).

There also have been efforts to encourage landowners to voluntarily remove cattle from key areas adjacent to YNP where bison could comingle with them during the brucellosis transmission period. In 2003, grazing permit holders on the Horse Butte peninsula west of YNP agreed with the National Wildlife Federation and USFS to transfer their rights to the nearby Targhee National Forest where bison are not present. In 2008, MFWP signed a 30-year livestock grazing restriction and bison access agreement to remove livestock from the Royal Teton Ranch north of YNP. The NPS provided the federal government's $1.5 million share of the total $3 million cost. This voluntary acquisition of grazing rights enables bison to use additional habitat along the Yellowstone River up to 10 miles (16 kilometers) away from the park boundary. In 2019, the USFS completed a land exchange to acquire 583 acres (236 hectares) of the Slip and Slide Ranch, north of the park in a key migration corridor for ungulates and other wildlife. Combined with previous fee purchases and conservation easements, partnerships between federal and state agencies, private landowners, and non-governmental organizations such as the Rocky Mountain Elk Foundation have conserved about 13,000 acres (5,260 hectares) of habitat for bison and other wildlife in this area, reduced the number of livestock grazing adjacent to YNP, and improved connectivity for migrating bison between the park and the CGNF (USDA, USFS 2022).

Development—The natural condition for the native shrub-grass plant association and ungulate guild in northern YNP would be pre-settlement before substantial alteration by colonists and settlers. It is impossible to recreate these conditions given subsequent changes such as the slaughter of large mammals during the 1870s, removal of indigenous people, farming and ranching in and near the park, increasing visitation, and settlement (Meagher and Houston 1998, Cole and Yung 2010, White et al. 2013, Whittlesey et al. 2018). Development has substantially decreased suitable habitat for bison in the GYE (Hansen and Phillips 2018). However, more than 99% of YNP is preserved as wilderness (92%) and undeveloped land (7%; Sholly 2022). Also, there are almost 11 million acres (4.5 million hectares) of other protected federal lands, primarily national forests, surrounding the park in the GYE. The federal agencies have agreed not to increase development, livestock grazing, or roads from circa 1998 levels on about 5.9 million acres (2.4 million hectares) in this area to protect secure habitat for grizzly bears (USDI, USFWS 2017).

Invasive Plants—Invasions by more than 185 exotic plant species and a century of climate warming have changed the composition and production of several plant communities and soils in YNP which, in turn, likely has affected ungulate foraging to some extent (Yellowstone Center for Resources 2021, Renkin 2022, Wacker 2022). Invasive nonnative plants infest much of the Stephens Creek Administrative Area, where the bison capture facility is located. Native vegetation is sparse because of historical uses and, more recently, from the horse corrals, bison capture and quarantine facilities, equipment storage, barn and associated buildings, and nursery operations. Nonnative plants include crested wheatgrass, mustard, Kochia, Russian thistle, cheatgrass, and Canada thistle. The surrounding area consists of foothills with widespread nonnative plants and a mixture of native vegetation, including sagebrush, rabbitbrush, greasewood, juniper, cottonwoods, willow, Douglas fir, and a variety of forbs and grasses. There are also terraces near the Yellowstone River and Reese and Stephens creeks that ranchers cultivated before being included in YNP. Nonnative plants including crested wheatgrass and mustard dominate the vegetation in these areas (Yellowstone Center for Resources 2021, Renkin 2022, Wacker 2022).

In addition, some non-native plants were intentionally introduced to provide forage for bison and other ungulates, including in the Gardiner basin and Lamar Valley which were planted with hay for bison and other wildlife during the first half of the 20th century (White et al. 2022c). Today, bison intensely graze on grasses that have proliferated from abandoned hayfields in the Lamar Valley during summer. They create grazing lawns of dense, short-statured plants in some areas through intense and repeated grazing. This grazing strategy sustains highly nutritious food through summer by prolonging new plant growth and stimulating nutrient cycling and water-holding potential (Geremia et al. 2019). The deposition of feces and urine into the soil released plants from nitrogen limitation, and precipitation became the primary factor influencing plant growth (Frank et al. 2013 and references therein, Geremia and Hamilton 2019, 2022; Geremia et al. 2019). It may be impossible or cost prohibitive to remove many species of nonnative plants from YNP given their widespread distribution and proliferation in some areas (Yellowstone Center for Resources 2021, White et al. 2022b). Also, it may not be imperative or prudent to attempt to remove all nonnative plant species from areas where many are providing functional ecosystem services, such as healthy soils, water, energy, forage, and nutrients, like native species (Geremia and Hamilton 2019, 2022).

<u>Factor B—Overutilization for Commercial, Recreational, Scientific, or Educational Purposes</u>

The petitioners indicated culling negatively impacts the bison population by decreasing genetic viability, selecting for traits that decrease fitness, and altering the sex ratio. The petitions suggested genetic viability may be degraded through the disproportionate culling of migratory animals, which would favor less migratory bison, select for a mitochondrial gene defect that impairs aerobic capacity and disrupts cold tolerance (Pringle 2011), skew sex ratios, and disproportionately remove bison from central YNP (USDI, USFWS 2015). Bison sampled in the central and northern regions of YNP during 1997 to 2003 had significantly different distributions of alleles and genotypes based on microsatellite DNA markers and were genetically distinguishable based on 20 alleles only found in one of the two regions (Halbert et al. 2012). Based on these analyses, the petitioners concluded Yellowstone bison are comprised of at least two genetically distinct subpopulations that are being differentially affected by culling, which could decrease genetic viability (USDI, USFWS 2015).

Culling has Decreased Genetic Viability—Research does not support the contention of a recent loss of genetic viability in Yellowstone bison due to culling. The Yellowstone population contains two genetic lineages of bison that contribute to relatively high genetic diversity. Circa 1900, there were about two dozen indigenous bison remaining in the central (winter) and northeastern (summer) regions of YNP. As a result, managers created another breeding herd in the northern portion of the park (Lamar Valley) during 1902 to 1909 with 18 female bison from northwestern Montana, 3 male bison from Texas, and four indigenous calves (Meagher 1973). After several decades, the indigenous and reintroduced herds began mixing and interbreeding, which increased as bison numbers and movements increased (Meagher 1973, Meagher et al. 2002). In recent decades, as bison numbers increased further, many hundreds dispersed from central to northern YNP and subsequently bred and produced calves; thus, there was significant mixing, breeding, and gene flow between bison originating from these two regions (Fuller et al. 2007a, White and Wallen 2012, Wallen and White 2015).

Recent genetic analyses of mitochondrial haplotypes from bison sampled in central and northern YNP did not detect subpopulations but did detect two independent lineages from the indigenous bison originally in central YNP during winter and the female bison introduced into northern YNP from northwestern Montana in 1902 (Forgacs et al. 2016). These geneticists from Texas A&M University identified 10 different mitochondrial DNA haplotypes and an overall haplotype diversity of 0.78 in Yellowstone bison, indicating a healthy, genetically diverse population (Forgacs et al. 2016). Between two and five groups of related alleles based on neutral markers exist across the park, and allelic diversity, allele frequencies, and inbreeding levels have remained similar during the IBMP era based on 44 microsatellites across the bison genome (Geremia 2022). Yellowstone bison should retain this diversity for centuries if numbers average at least 3,000 to 3,500 bison, there is intermixing and gene flow between bison from the two primary breeding herds, and removals are mainly juveniles (Pérez-Figueroa et al. 2012).

Culling Decreases Migratory Tendencies—Culling bison at the boundary of YNP selectively removes migratory bison. The IBMP was designed to avoid management actions within the interior of the park to limit adverse effects to other cultural and natural resources and visitor experience (USDI, NPS and USDA, USFS, APHIS 2000; White et al. 2011). However, there is no evidence Yellowstone bison are losing their ability to migrate. Under the IBMP, hundreds to more than one thousand bison have migrated outside YNP and into Montana during winter, depending on bison density, forage production and availability, snow cover, and other factors (Geremia et al. 2011, 2014, 2015b). In recent decades, Yellowstone bison have migrated farther than at any time since the massive slaughter of bison in the middle to late 1800s, with tolerance for these bison in Montana increasing since 2011 (Bullock 2015, Geremia et al. 2015b, IBMP Agencies 2016). More than 4,100 bison migrated north of Mammoth, Wyoming, in YNP during the prolonged, severe winter of 2023, which was twice the previous high of about 2,000 bison in 2008 (Geremia 2023).

Mitochondrial Gene Defect—Pringle (2011) suggested some Yellowstone bison with haplotype 6 in their mitochondrial genome carry a double mutation that affects one gene for cytochrome b and another for ATP6. He suggested this inherited mutation was primarily found in bison in the central region of YNP and would adversely affect the production and transport of energy within cells and aerobic capacity (Pringle 2011). In contrast, geneticists from Texas A&M University suggested descendants of bison introduced to northern YNP in 1902 from the Pablo-Allard herd in northwestern Montana and, subsequently, the Mary Mountain area in central YNP in 1936, have the mutation identified by Pringle (2011; Forgacs et al. 2016). Regardless, if the double mutations in the bison were expressed and caused the detrimental effects hypothesized by Pringle (2011), over time there should have been a substantial reduction in the frequency of genetic haplotypes with these mutations due to strong negative selection (Forgacs et al. 2016). However, geneticists at Texas A&M University found the two independent genetic lineages from the indigenous bison and the bison introduced into YNP from northwestern Montana in 1902 were still present in both the central and northern regions of the park more than a century later. They concluded "[d]ue to the statistically non-significant change in haplotype frequencies in the Yellowstone population ($p = 0.412$) based on Fisher's exact test and the lack of any kind of reported lesion or disease that affect a large proportion of Yellowstone bison, we did not find evidence to support Pringle's hypothesis" (Forgacs et al. 2016). In other words, there does not appear to be any strong negative selective forces occurring in this population that influence mitochondrial haplotype frequencies.

Culling Alters Bison Sex Ratios—Culling tends to remove more female and young bison because they tend to migrate to lower elevations during winter and be captured more than adult males (White et al. 2011). Park biologists want to maintain a balanced sex ratio of about 50% males and 50% females to support mate competition and allow natural selection to affect population genetics (Pérez-Figueroa et al. 2012, Geremia 2022). They also try to maintain an age structure of about 70% adults and 30% juveniles, which is based on the expected population composition given age-specific birth and survival rates (Geremia et al. 2015b, Hobbs et al. 2015, Geremia 2022). Over the last five years, the sex ratio averaged 52% males and 48% females, which is near the objective, though males were overrepresented in the central herd (five-year average of 144:100) and slightly underrepresented in the northern herd (five-year average 98:100). The age structure of the population was also near the objective with about 28% juveniles and 72% adults over the past five years. Juveniles made up 24% of animals in the central herd (five-year average) compared to 29% in the northern breeding area (Geremia 2022).

Culling Disproportionately Removes More Bison from Central Yellowstone—Bison are intensively managed at times near the boundary of YNP, and culls of more than 1,000 bison in winters 2006 and 2008 may have differentially affected bison from the central region of the park by removing more females and dampening productivity (White et al. 2011, Halbert et al. 2012). However, recent monitoring suggests there was substantial mixing, breeding, and gene flow between descendants of bison from the indigenous and introduced lineages during the past two decades (White and Wallen 2012, Wallen and White 2015, Forgacs et al. 2016). The population has recovered rapidly from decreases in abundance due to culling or natural mortality (White et al. 2011, Geremia 2022). Geneticists from Texas A&M University (Forgacs et al. 2016) concluded "[t]he status of the Yellowstone bison population based on our findings of high [mitochondrial] haplotype diversity and lack of population subdivision appears to be genetically healthy, especially for a population with a history of intensive management that included periods of extreme reductions in size. In recent years, as the number of bison has grown exponentially and more bison leave the park during the winter, culling of animals to control their abundance and distribution has become necessary. Our finding that there is no subdivision based on mtDNA [mitochondrial DNA] support that Yellowstone bison can be managed - for mitochondrial haplotype diversity - as a single population with multiple breeding segments." Since 2017, park biologists have recommended population management removals focus on bison living in northern YNP, not the central breeding herd (Geremia 2022). About 1,550 bison were removed during winter 2022-2023, including about 1,500 bison near the northern boundary of YNP. Aerial distribution flights suggest most of these animals were from the northern breeding herd (Geremia 2023).

<u>Factor C—Disease or Predation</u>

The petitioners suggested diseases, such as hemorrhagic septicemia and malignant catarrhal fever, pose a direct threat to Yellowstone bison, while the impacts of brucellosis indirectly threaten bison due to limitations on bison distribution and population size to reduce transmission risk to cattle.

Disease Outbreaks—There were several outbreaks of hemorrhagic septicemia in the Lamar herd that killed 15% of the bison in 1911 and 9% in 1919 and 1923 but no subsequent outbreaks have occurred (Baggley 1934, Skinner et al. 1942, Plumb and Sucec 2006). In 2003, an outbreak of malignant catarrhal fever in southern Idaho killed 51% of the bison in a feedlot that had been exposed to domestic sheep for two weeks (Li et al. 2006). However, park biologists are not aware of any imminent threats to Yellowstone bison from hemorrhagic septicemia or malignant catarrhal fever. Biologists monitor animals placed in the BCTP (quarantine) for diseases of high health concern, including brucellosis, Johne's disease, and *Mycoplasma bovis*.

Culling to Suppress Brucellosis Prevalence—The IBMP has not focused on brucellosis suppression since at least 2014, when the NPS decided not to implement the remote vaccination of bison for brucellosis

(USDI, NPS 2014). Currently, captured bison are not culled based on being previously exposed to brucellosis. Instead, groups of bison are captured with the intent to place eligible bison testing negative for brucellosis exposure in the BCTP (Geremia 2022). Bison testing seropositive for brucellosis in quarantine are killed onsite or shipped to slaughter (USDI, NPS 2018).

Concerns about Brucellosis Limit Bison Abundance and Distribution—Tolerance for Yellowstone bison is limited to the park and nearby areas in Montana. For many decades, arguments against tolerance for bison in states surrounding the park were presented in terms of the risk of brucellosis transmission to cattle and effects to the livestock industry and state economies (Bidwell 2010). As elk were demonstrated to be the only recent transmission vectors to cattle, however, arguments shifted more towards concerns about bison competing with cattle for grass, human safety, and property damage (White et al. 2015c, National Academies of Sciences, Engineering, and Medicine 2017). During 2008 to 2022, counts of Yellowstone bison after calving increased from about 2,970 to 5,940, which is the largest number since the late 1800s and far larger than any other wild, unfenced population of plains bison (Geremia 2022). Hundreds to more than one thousand bison have migrated outside YNP and into Montana during winter, depending on bison density, forage production and availability, snow cover, and other factors (Geremia et al. 2011, 2014, 2015a; Geremia 2023).

Factor D—Inadequacy of Existing Regulatory Mechanisms

The petitioners believe existing federal and state regulatory mechanisms for bison conservation are inadequate. They suggest the IBMP is a threat to Yellowstone bison because of activities related to culling and brucellosis management, citing Halbert et al. (2012:368) that "[t]he continued practice of culling bison without regard to possible subpopulation structure has the potentially negative long-term consequences of reducing genetic diversity and permanently changing the genetic constitution within subpopulations and across the Yellowstone metapopulation."

Existing Regulatory Mechanisms are Inadequate—The potential concerns of Halbert et al. (2012) about reductions in genetic diversity and subpopulation structure have not been detected during subsequent research. In 2011-2012, geneticists identified 10 different mitochondrial DNA haplotypes in Yellowstone bison and an overall haplotype diversity of 0.78, indicating a healthy, diverse population (Forgacs et al. 2016). Between two and five groups of related alleles based on neutral markers exist across the park, and allelic diversity, allele frequencies, and inbreeding levels remained similar over more than two decades based on 44 microsatellites across the bison genome (Geremia 2022).

The severe, prolonged winter of 2022-2023 provided a sort of 'worst case' scenario for testing the adequacy of regulatory mechanisms at sustaining a viable population of bison while maintaining a low risk of brucellosis transmission from bison to cattle. The bison count during summer 2022 was the highest in recent history (near 6,000) and park biologists recommended removing animals near the northern park boundary through captures and harvests to reduce population growth, support the BCTP and tribal treaty hunts, and reduce conflicts from bison exiting the park (Geremia 2022). However, biologists cautioned against removing more than 25% of the population (1,500 bison) to avoid unintended consequences on sustainability and future tribal hunting opportunities and transfers of live bison to tribes (Geremia 2022).

The subsequent winter was the most severe of the IBMP era (2001-2023), with deep snow pack at middle to lower elevations in YNP and nearby areas (Geremia 2023). More than 4,100 bison migrated north of Mammoth, Wyoming, in YNP during the prolonged, severe winter, which was twice the previous high of about 2,000 bison in 2008 (Geremia 2023). More than 100 bison were outside the park in Montana on 83 days, 250 bison on 52 days, 500 bison on 23 days, and 1,000 bison on 3 days (Geremia 2023). However, there was no mingling of bison and cattle. The NPS ceased culling and the tribes decreased hunting substantially as they approached the upper recommended level of removals. Though a total of about 1,550 bison were removed, more than 4,000 bison remained in the population, which was higher than the 3,500 lower limit for bison that park biologists have recommended maintaining in the population to sustain a viable population and retain existing genetic diversity (Pérez- Figueroa et al. 2012, USDI, NPS 2023). Thus, existing mechanisms worked to conserve a viable bison population with no transmission of brucellosis from bison to cattle.

Under the IBMP, the NPS has lead responsibility for implementing bison management actions inside YNP while the State of Montana has lead responsibility outside the park (IBMP Members 2022). The NPS does not have regulatory authority or jurisdiction over hunts that occur outside YNP (Sholly 2020), and hunts conducted on national forests under permits from MFWP or tribes exercising their treaty rights do not require authorization from the USFS (Erickson 2019). As a result, some people have questioned how the federal government can ensure the bison population is not reduced to unsustainable levels by actions taken by other agencies or tribes outside the park. Most bison removals outside the park take place on national forest lands. If necessary, the USFS can preempt or supersede state laws and policy to meet its statutory and trust obligations regarding issues such as public safety and natural resource protection after consultation with the states (43 USC 1732). In addition, U.S. Supreme Court has indicated off-reservation treaty-based hunting rights do not guarantee Indians "absolute freedom" from regulation: "[w]e have repeatedly reaffirmed state authority to impose reasonable and necessary nondiscriminatory regulations on Indian hunting, fishing, and gathering rights in the interest of conservation. … This "conservation necessity" standard accommodates both the State's interest in management of its natural resources and the Chippewa's [tribe's] federally guaranteed treaty rights" (*Mille Lacs*, 526 US, 204-205). The Supreme Court later suggested during oral arguments for another case that the conservation necessity doctrine may be applicable to federal and state interests such as safety, mitigation of wildlife disease, and duration of hunting seasons, though they did not rule on these matters (*Herrera*, 138 S. Ct. 2707 (No. 17-532).

Bison Management Focuses on Managing Brucellosis Transmission Risk to Cattle—The IBMP was designed to ensure Yellowstone bison did not transmit brucellosis to cattle in Montana, while conserving about 3,000 bison in late winter and spring (which equates to about 3,500 or more bison after calving depending on the composition and growth rate of the population; Angliss 2003) and attempting to reduce the prevalence of brucellosis in bison through test-and-slaughter and vaccination (USDI, NPS and USDA, USFS, APHIS 2000). The primary strategy used to prevent direct brucellosis transmission from Yellowstone bison to cattle is to maintain separation between them, which has been successful with no detected transmissions. Managers have not focused on brucellosis suppression since at least 2014, when the NPS decided not to implement the remote vaccination of bison for brucellosis, and currently, bison are not culled based on their brucellosis exposure status (USDI, NPS 2014; Geremia 2022). The State of Montana only allows limited numbers of bison in certain areas and the federal government cannot force the state to tolerate more migrating bison; it is their decision (Bullock 2015). Allowing mass migrations of bison into local communities and areas with cattle, without management intervention, would thwart conservation efforts by reducing regional support (White et al. 2015c, Metcalf et al. 2016). Thus, agencies involved with the management of Yellowstone bison have agreed to regulate the size of the population (IBMP Members 2022).

Factor E—Other Natural or Manmade Factors Affecting its Survival

The petitioners indicated Yellowstone bison are threatened with a loss of genetic diversity and a loss of evolutionary potential due to domestication, human selection, and hybridization with cattle. In addition, they forecast climate warming will result in decreased precipitation, increased temperatures, and widespread drought that will cause bison to disperse south into Grand Teton National Park and the National Elk Refuge, where they could potentially interbreed with bison that may carry some genes from cattle (USDI, USFWS 2015).

Domestication—Concerns about confining wild bison for months or years during winter operations or quarantine appear to be unfounded. Bison introduced to northern YNP in the early 1900s were confined, fed, herded, and protected for decades to proliferate their numbers before managers decided they should live in a more natural state (Meagher 1973). Thereafter, these bison have been wild, wide-ranging, and subject to forces of natural selection and, today, their descendants are considered an excellent example of wild bison (Freese et al. 2007, White et al. 2015c). This successful restoration suggests there is no reason bison completing quarantine in a few years or less would not retain or redevelop their wild behaviors, and no reason they should not be used to augment or establish wild herds of bison in appropriate areas. Video of managers at the Fort Peck Indian Reservation attempting to capture Yellowstone bison relocated from quarantine clearly show released animals are not docile or habituated (Rather 2014). Furthermore, judicial evaluations have concluded Yellowstone bison completing quarantine are wild animals (*Citizens for Balanced Use et al. v. Director Maurier, Montana Department of Fish, Wildlife & Parks et al.*; Montana Seventeenth Judicial District, Blaine County; Cause No. DV–2012-1 [2012, 2014], overturned No. DA 12-0306 [Montana Supreme Court 2012]).

Human Selection—Yellowstone bison are not facing imminent threats to their genetic health and viability as suggested by the petitioners. However, humans have removed (through hunter harvests and culls) about 11,470 bison since 2001, which exceeds deaths from natural causes such as injuries, predation, and starvation (Geremia 2022, 2023). The NPS captured and culled bison in northern YNP during the winters of 2003, 2004, 2006, 2008, 2011, 2014 to 2020, 2022, and 2023. Public and tribal hunters harvested about 2,930 bison in Montana during winters from 2001 through 2022, and around 1,175 bison in the winter of 2022-2023. Another 916 bison were placed in quarantine during this period. In 2011 and 2023, the NPS held roughly 800 bison in captivity and fed them hay for several weeks to prevent mass migrations north of the park. These bison were released during spring, but confinement and feeding conflict with the management of bison as wildlife and could lead to food-conditioning, disease transmission during confinement, and disruption of traditional migratory patterns if conducted frequently. As a result, the NPS has recommended treating bison more like other wildlife in states surrounding YNP and supported increased tolerance for wild bison in suitable portions of the GYE (White et al. 2015c). In addition, the CGNF adopted a new Land Management Plan that includes components supporting habitat improvement projects to create or connect suitable bison habitat with enough bison present and distributed year-round to provide a self-sustaining population on the national forest in conjunction with bison herds in YNP (USDA, USFS 2022).

Hybridization with Cattle—Geneticists at Texas A&M University recently published findings that all bison in North American have some level of cattle introgression, including Yellowstone bison (Stroupe et al. 2022). A low level of cattle introgression in Yellowstone bison was detected by complete genome sequencing, which provided a conclusive description of the genetic makeup of 25 bison that were descendants from five remnant privately owned historic herds in the late 1800s, Yellowstone bison, or four cattle breeds (Stroupe et al. 2022). The detection of a low-level of cattle genes in Yellowstone bison is not surprising given the introduction of bison from other remnant herds into the park during the early 1900s to facilitate restoration and enhance genetic diversity following their slaughter and near extirpation by colonists in the late 1800s (Meagher 1973). Private bison managers often cross-bred bison and cattle, and in the early 1900s, park managers brought 21 privately owned bison into YNP to captively breed bison when they feared this last wild herd may go extinct. It appears at least one of these bison was hybridized with cattle genes (Stroupe et al. 2022). While this finding is disappointing, it does not substantially diminish the conservation value of Yellowstone bison, which remain the closest ancestral connection to the animals that once roamed North America (Plumb and Sucec 2006). Yellowstone bison are valuable because they live in herds of several thousands of individuals, moving and grazing across migratory landscapes, competing with other herbivores, and coping with predators and disease (White et al. 2015c). Letting nature influence Yellowstone bison allows the fittest to survive, helping them adapt to the environment as it changes, which should remove any genes, including cattle-related genes, that reduce their fitness.

Climate Warming and Bison Dispersal to Grand Teton National Park—Yellowstone bison have rarely dispersed to the nearest population in Grand Teton National Park, even though there are no physical barriers to such movements (Wallen and White 2015). The petitioners concerns about the potential effects of climate warming on bison and their movements are speculative, but plains bison are resilient and historically lived across North America from desert to near arctic climes. Evidence indicates there has been a substantial increase in the amount of carbon dioxide in the atmosphere over the past two centuries (Friedlingstein et al. 2019). Elevated carbon dioxide can increase plant growth by reducing water loss and facilitating photosynthesis. This increase may have indirectly contributed to more grass production and abundant forage for ungulates in YNP, especially in wetter areas where nonnative, cool-season grasses were planted for hay during the early 1900s and subsequently spread (Frank 2022). However, variations in precipitation and temperature strongly influence soil moisture, which can limit grass production (Frank et al. 2013 and references therein; Geremia and Hamilton 2019, 2022).

Average annual temperatures in the GYE increased about 2.3°F from 1950 to 2018, with a longer snow-free season (Hostetler et al. 2021). In northern YNP, these changes 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, Thoma et al. 2015, Yellowstone Center for Resources 2021). The regional warming trend is predicted to continue, with an increase in mean annual temperatures of about another 2°F across all seasons, milder winters with fewer days below freezing, earlier spring vegetation green-up, and more frequent drought (Hostetler et al. 2021). However, there is uncertainty around these predictions and somewhat divergent outcomes are possible.

Continuing trends toward warmer and drier conditions with more frequent drought could worsen the spread of invasive plants, such as winter annuals, and threaten some native bunchgrass communities that provide food for bison in the warmest and driest areas and regions with historical (tilling/plowing) and contemporary (roads) soil disturbance (Yellowstone Center for Resources 2021). Fires should continue to be infrequent in grassland and shrubland areas, mostly moving rapidly at low intensity. An increased frequency of fires could make grassland communities more vulnerable to the spread of nonnative grasses (Yellowstone Center for Resources 2021). These changes could reduce plant production and the forage capacity of the park to support bison and other wildlife, leading to larger migrations during some winters, with some animals being unable to obtain adequate fat and protein reserves for pregnancy and survival (Wilmers et al. 2013, Geremia et al. 2014, Middleton et al. 2018). However, warmer temperatures have already resulted in lower snowpack and soil moisture at elevations between 5,000 and 7,000 feet (1,525 and 2,135 meters; Thoma et al. 2015, Hostetler et al. 2021), and bison may respond to less snow on their winter ranges by remaining longer at higher elevations in the park and migrating to lower elevations near the boundary later in the winter.

If summers are hotter and drier than predicted, plant production across grasslands and shrub steppe could decrease because of reduced soil moisture which, in turn, would limit absorption of water and nutrients by plants and indirectly lower soil decomposition rates. Shorter, ephemeral pulses of nutrient availability in wet grassland areas could promote the growth of drought-tolerant plants, including annuals, winter annuals, and slow-growing graminoids (Yellowstone Center for Resources 2021). Thus, shrub and bunchgrass-dominated plant communities in dry upslope areas on the Blacktail Deer Plateau, Little America, and the slopes of the Lamar Valley could convert to infestations of annual plants with hotter and drier conditions. Increased fire frequency and intensity in ungrazed and lightly grazed areas could facilitate these plant community changes. Under this scenario, the numbers of bison could decrease from lower landscape-level plant production, which would contribute to decreased body condition, pregnancy, and survival (Yellowstone Center for Resources 2021). More intense droughts would further limit forage availability in late summer and winter. There could be mass migrations of bison and other ungulates from the park during limited forage years, with more ungulates remaining outside the park on agricultural land (Yellowstone Center for Resources 2021).

If summers start earlier and are wetter than predicted, the prolonged periods of warm and wet soils may increase decomposition rates and liberate soil carbon, nitrogen, and phosphorus. The longer periods of nutrient and water availability would naturally shift plant communities to faster-growing lifeforms, including rhizomatous and shallower rooted forms and nonnative annual plants (Yellowstone Center for Resources 2021). Plant production may increase, and more frequent wet years could enhance grazing feedbacks that further promote plant production, especially in higher-elevation wet areas. Grazing-tolerant, cool-season, nonnative cultivars would continue to spread in wet areas, with this spread enhanced by grazing (Yellowstone Center for Resources 2021). There could be an increase in body condition of bison and other ungulates by autumn, which would increase reproductive success and survival, resulting in increased population sizes for these species. More bison may remain in the park during winter due to increased forage availability, and earlier spring migrations to higher elevations would be timed with earlier snow melt (Yellowstone Center for Resources 2021).

Current Situation

A species status assessment evaluates the conservation biology principles of resiliency, redundancy, and representation, and forecasts the viability of the species (or distinct population segment) over time for various scenarios of future environmental conditions and conservation efforts (Gates and Ellison 2010, USDI, USFWS 2016). Resiliency refers to sustaining populations with a high probability of persisting for centuries due to their large size and high potential growth rate; this would enable them to withstand and recover from unpredictable events, such as severe weather or disease outbreaks. Redundancy refers to the preservation of a sufficient number of large, connected populations to withstand local catastrophic events, such as a virulent disease outbreak or large winterkill in a single population. Representation refers to preserving populations across the range of habitats historically used by the species to preserve genetic diversity, local adaptive capabilities, and enhance the likelihood of adaptation to future changes in environmental conditions, such as climate warming (Gates and Ellison 2010, USDI, USFWS 2016).

<u>Resiliency</u>

Yellowstone bison are one of a few wild, migratory populations of plains bison and the only population large enough to be considered ecologically and genetically viable (Hedrick 2009, Gross et al. 2010). The population has two primary breeding herds with modest reproduction and high survival of adults and young. As a result, numbers increase rapidly when conditions are good, with an average growth rate of 15% during 2001 to 2022 after adjusting for management removals (Geremia et al. 2015c, Geremia 2022). However, bison survival and calving are lower during and after some winters with large removals, with a population growth rate of less than 4% after such winters in 2005-2006, 2007-2008, and 2010-2011 (Geremia 2023). The population has recovered rapidly from substantial decreases in abundance during some winters (White et al. 2011, 2015; Geremia 2022). Geneticists from Texas A&M University concluded the population "appears to be genetically healthy, especially for a population with a history of intensive management that included periods of extreme reductions in size" (Forgacs et al. 2016).

For further recovery in the GYE, plains bison need similar access to habitat that other wildlife species such as elk are given without human intrusion, including year-round access to many USFS and other public lands in the ecosystem that are outside the NPS's jurisdiction (White et al. 2015b). Montana has allowed more tolerance for bison adjacent to YNP to facilitate conservation and hunting, including year-round in some areas (Bullock 2015). Public opinion is shifting toward more tolerance for bison in the GYE (Tulchin Research 2015); however, some state and local governments and private landowners do not support more tolerance for bison on public lands further from the park (Metcalf et al. 2016). Also, the continuing development of open space on private lands surrounding the park degrades and fragments habitat and migration corridors for wildlife, including bison (Hansen and Phillips 2018). As a result, it is unlikely additional tolerance for bison on public lands in the states surrounding YNP would keep pace with the potential growth of this population given the extremely high survival of calves and adults. In turn, it is foreseeable that Yellowstone bison will need to be continually culled and harvested from the population to limit abundance and distribution which will, in turn, limit recovery (White et al. 2015b).

<u>Redundancy</u>

The Yellowstone bison population is spatially separated from other populations of plains bison and, as a result, there has been no gene flow into the population for numerous generations (Wallen and White 2015). The nearest wild plains bison population is about 85 miles (137 kilometers) south in Grand Teton National Park and the National Elk Refuge, but Yellowstone bison have rarely dispersed there. No bison have dispersed from YNP to the Grand Teton area even though there are no physical barriers to such movements (Plumb and Sucec 2006, Wallen and White 2015). There are genetic differences between these populations because the Grand Teton population was founded partially from bison relocated from Theodore Roosevelt National Park, which has a different genetic lineage than Yellowstone bison (Dratch and Gogan 2010). There is limited opportunity for Yellowstone bison to disperse and expand their range in Montana because the Paradise and Madison valleys north and west of YNP support numerous livestock producers and rural residential development has increased rapidly during the past several decades; both of which are at times incompatible with the conservation and restoration of a free-ranging bison population (Haggerty and Travis 2006, Metcalf et al. 2016, Tilt 2020). Furthermore, Idaho and Wyoming have indicated they do not want wild bison outside of parks and refuges (Wallen et al. 2015a).

To mitigate the possible effects of genetic drift and protect against the loss of a unique genetic lineage, Geneticist Dr. Philip Hedrick at the University of Arizona indicated (2009:419) "[i]dentified differentiated populations (clusters) should be replicated with at least one other physically separated population with an effective population size of 1000. If it is not possible to have this replicated population in 1 location, then it could be in 2 or 3 locations with significant genetic exchange between them." Descendants of primarily indigenous bison from YNP were used to augment plains bison populations in Fort Niobrara National Wildlife Refuge in Nebraska, Grand Teton National Park/National Elk Refuge in Wyoming, National Bison Range in Montana, and Wind Cave National Park in South Dakota (Plumb and Sucec 2006, Halbert and Derr 2008, Hedrick 2009, Dratch and Gogan 2010, Stroupe et al. 2022). Also, several satellite populations of bison from the Yellowstone lineages were established on the Book Cliffs and Henry Mountains in Utah, Vermejo Ranch in New Mexico, and Flying D Ranch in Montana.

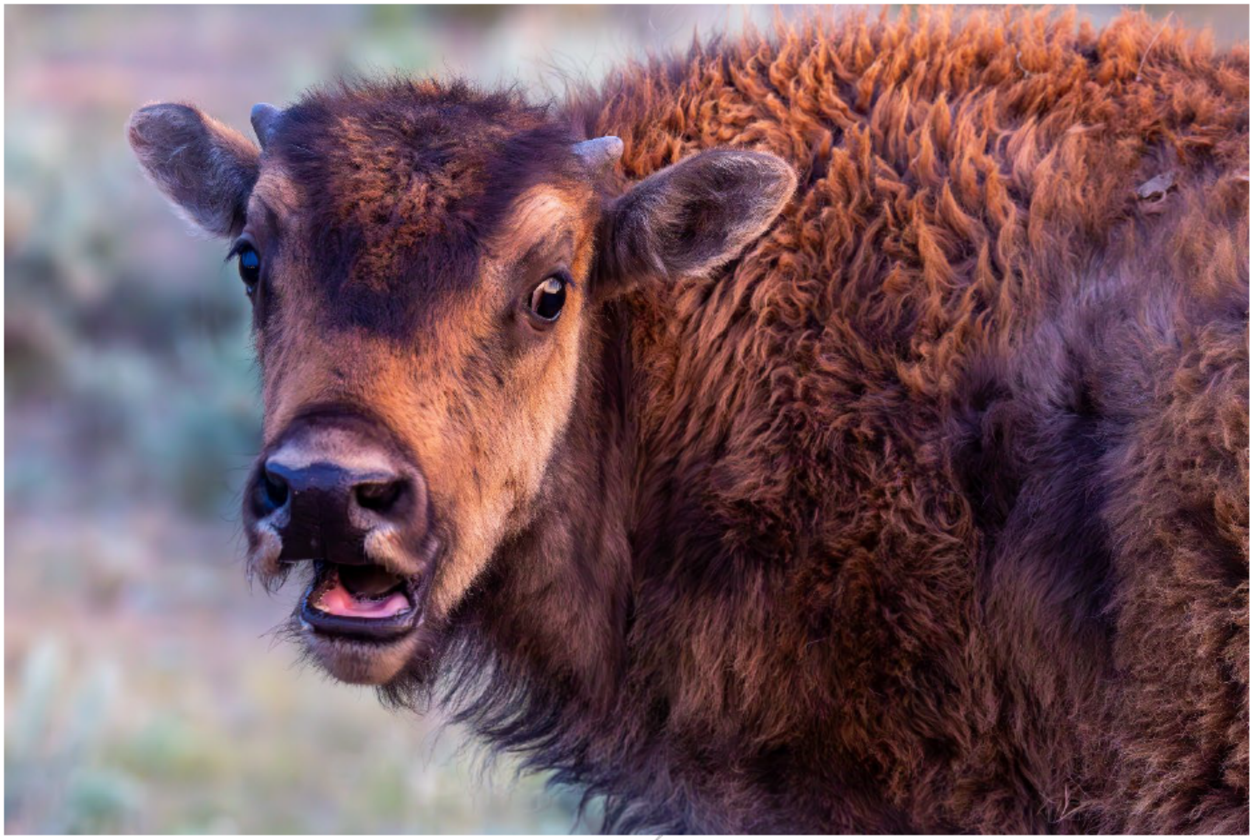
In 2010, a 5-year quarantine feasibility study with Yellowstone bison was successfully concluded, with the surviving bison and their offspring being declared brucellosis-free (Clarke et al. 2014). Montana relocated 87 bison completing quarantine to the Green Ranch in Montana in 2010 and sent another 61 bison to the Fort Peck Indian Reservation in 2012. In 2014, Montana sent the original quarantined bison plus 25% of the offspring (139 total) at the Green Ranch to the Assiniboine and Sioux Tribes at Fort Peck. Since 2019, the BCTP, implemented by the NPS and APHIS, has sent about 300 brucellosis-free Yellowstone bison to Fort Peck for one year of assurance testing and eventual release. The Fort Peck tribes now have about 400 Yellowstone bison across more than 18,000 acres (7,285 hectares) on their lands (Geremia et al. 2021). ITBC has transferred more than 170 bison of Yellowstone-origin from Fort Peck to 23 tribes across 12 states. Collectively, these populations total many thousands of bison. Geneticists from Colorado State University found "[g]enetic diversity levels in the quarantined herd were high and comparable to the YNP [Yellowstone] parent herd, suggesting a low risk of genetic loss soon. Based on these findings, the genetic diversity currently available within the BQFS [satellite] herd will provide a strong foundation for bison reintroduced herds and for the preservation of the species" (Herman et al. 2014:335).

Representation

Yellowstone bison represent a unique source of genetic diversity, not replicated among other Department of Interior populations, with high genetic diversity compared to many other populations (Hedrick 2009, Dratch and Gogan 2010). Yellowstone bison retain one of the highest levels of heterozygosity and allelic diversity in any conservation population of plains bison, and several geneticists have concluded abundance and gene flow among breeding herds are high enough to avoid inbreeding depression and maintain genetic variation (Hedrick 2009, Dratch and Gogan 2010, Gross et al. 2010, Pérez-Figueroa et al. 2012). Parentage analyses by Colorado State University indicated a high portion of adults contribute offspring to the population during their lifetimes (Herman et al. 2014). Also, geneticists at the University of Montana concluded mate competition among males was likely moderate to high, which should contribute to sustaining genetic variation for centuries (Pérez-Figueroa et al. 2012). In addition, geneticists from Texas A&M University conducted whole genome sequencing (mitochondrial DNA) with samples collected from contemporary bison in YNP, as well as two museum specimens from the Lamar Valley in northern Wyoming in 1856 and southern Montana in 1886 near the northern boundary of the park. Haplotypes in contemporary descendants of the indigenous bison were like those in the museum specimens (Forgacs et al. 2016).

To preserve genetic variation over centuries, the *Bison Conservation Initiative* by the USDI and the *North American Conservation Strategy for Bison* by the IUCN recommend that population (or subpopulation) sizes should be at least 1,000 bison, with approximately equal sex ratios to ensure considerable competition between breeding bulls (Dratch and Gogan 2010, Gross et al. 2010). This recommendation is derived from Hedrick (2009:419) who indicated "[i]ndividual herds or clusters [of plains bison] should have an effective population size of 1000 (census number of 2000–3000) to avoid inbreeding depression and maintain genetic variation. If it is not possible to have this primary herd in 1 location, then it could be in 2 or 3 locations with significant genetic exchange between them." Yellowstone bison are the only population of plains bison within their original range that meet these objectives, with hundreds to thousands of bison congregating in the central and northern regions of the park during the breeding season and hundreds of mature males competing for breeding opportunities (Hedrick 2009). Recent monitoring suggests there were significant movements, breeding, and gene flow between bison originating from central and northern YNP during the past two decades (White and Wallen 2012, Wallen and White 2015, Forgacs et al. 2016, Stroupe et al. 2023).

Yellowstone bison are one of only a few unfenced, wild, wide-ranging populations of plains bison in existence. They move across extensive portions of the unique landscape within and near YNP, with a full suite of native ungulates and predators, while being exposed to natural selection factors (Plumb et al. 2009, White et al. 2015b). Within the interior of the park, bison live in an environment not dominated by humans and whose behaviors, movements, survival, and reproduction are predominantly affected by their own daily decisions and natural selection (White 2016). As a result, Yellowstone bison have retained adaptive capabilities that are diminished in many other bison herds across North America 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 (McDonald 2001, White and Wallen 2012, White et al. 2015b). Only a few unfenced, wide-ranging populations of plains bison exist in the U.S. besides Yellowstone bison, including Book Cliffs, Henry Mountains, Grand Teton, and Wrangell-St. Elias. All these populations are relatively small with less than 1,000 bison (Dratch and Gogan 2010). Furthermore, most other conservation herds of bison on public lands also have low population sizes, along with limited distributions, protection from natural selection factors like large predators, and skewed sex and age ratios maintained to ease management (McDonald 2001). Additional wild, wide-ranging populations subject to the forces of natural selection need to be augmented or established at other sites to preserve the species. This would reduce the reliance on Yellowstone and a few other populations to preserve the species in the wild (White et al. 2015b,c).



Bison calf in the Lamar Valley of Yellowstone National Park.
Photograph by Ashton Hooker, National Park Service, 2023.

Acknowledgments

Special thanks to Dr. Robert Garrott, Professor Emeritus, Montana State University, and Attorney John Harrison, Confederated Salish and Kootenai Tribes, for reviewing a draft of this report and providing insightful comments and recommendations. This report benefited greatly from discussions with Jennifer Carpenter, Nancy Finley, Chris Geremia, Tim Reid, Tobin Roop, and Cameron Sholly from Yellowstone National Park; Dana Jacobsen, Jennifer Rigg, and Kate Williams-shuck from the Office of the Solicitor, U.S. Department of the Interior; Kelly Daigle, David Jacob, Gretchen Pinkham, Jennifer Rebenack, and Melissa Stedeford from the Environmental Quality Division, U.S. Department of the Interior, Lori Fox and Marlis Muschal from WSP, USA; and Susan Clark from Yale University. I also thank Kerry Gunther, Dan Stahler, Travis Wyman for providing information, and Charissa Reid for help with formatting.

Bison grazing in the Lamar Valley of Yellowstone National Park.
Photograph by Jacob W. Frank, National Park Service, 2023.

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Bison wallowing in Yellowstone National Park.
Photograph by Jim Peaco, National Park Service, 2015.