

**Petition to List the Yellowstone Bison as Threatened or
Endangered Under the Endangered Species Act**

Western Watersheds Project & Buffalo Field Campaign



**In the Office of Endangered Species
U.S. Fish and Wildlife Service
United States Department of Interior**

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Petitioners

Western Watersheds Project is a regional conservation organization with offices in Arizona, California, Idaho, Montana, Oregon, and Wyoming. The mission of Western Watersheds Project is to protect and restore watersheds and wildlife habitats on the nation's public lands through education, scientific study, public policy initiatives, and litigation.

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Summary

Western Watersheds Project and Buffalo Field Campaign are petitioning the Service to list the Yellowstone bison, the last remaining, free-roaming population of bison in the United States, as an endangered Distinct Population Segment (“DPS”) of plains bison, *Bison bison bison*. The Yellowstone bison exceed the criteria for designation as a DPS. The Yellowstone bison are the only plains bison population free from introgression with cattle-genes. The Yellowstone bison are a *discrete* population because they are physically and genetically isolated from other wild bison populations. The Yellowstone bison are *significant* because their continued persistence in the northern Greater Yellowstone ecosystem represents the only surviving natural occurrence of wild bison that has been never extirpated from its historic and ecological range. The extirpation of the Yellowstone bison would represent the complete loss of wild plains bison as a genetically-intact species, the loss of bison from the last stronghold of their historic and ecological range, the loss of unique ecological adaptations to the local environment, and the loss of valuable and unique genetic qualities.

The Yellowstone bison occur in and around Yellowstone National Park and are the largest remnant population of the plains bison that ranged across much of United States until it was eliminated post-settlement. Recent science shows that the Yellowstone bison is the only significant bison population that has not suffered introgression with domestic cattle genes. Thus, at a minimum the Yellowstone bison represent a distinct population segment of plains bison; and perforce, may in fact be the only remaining plains bison population in the United States. Whether the Yellowstone population represents the only plains bison population remaining in the United States, or represents a DPS of plains bison, multiple listing criteria apply to the population. Endangered Species Act protection is necessary to prevent the extinction of the species, and to protect the habitat and the ecosystems upon which Yellowstone bison depend.

The Yellowstone bison represent an evolutionary legacy for conservation of bison because they are the only surviving naturally occurring wild bison population in the United States (Freese *et al.*, 2007). The majority of bison in the United States today are privately managed as livestock, have evidence of hybridization with domestic cattle, or have been selected for specific commercial traits rather than for traits that would enable the species to function as wild in a natural setting.

Yellowstone bison have a relatively high degree of genetic variation compared to other herds and are the only plains bison population free of evidence of hybridization with cattle (Ward *et al.*, 1999; Halbert, 2003; Halbert and Derr, 2007; Dratch and Gogan, 2010; Schnabel, 2011). Ecological and genetic studies have provided solid evidence of population substructure within the Yellowstone bison (Kirkpatrick *et al.*, 1996; Taper *et al.*, 2000; Halbert, 2003; Gates *et al.*, 2005; Fuller *et al.*, 2007; Gardipee, 2007; Brodie, 2008). Yellowstone bison exhibit seasonal migrations along altitudinal gradients, with bison moving from higher elevation summer ranges to lower-elevations during winter, and returning to summer ranges during June and July (Geremia *et al.*, 2011). Yellowstone bison represent an ecological microcosm of historic bison populations and a genetic well-

spring for restoration of the species, thus requiring careful conservation efforts and legal protection under the Act to ensure their persistence in the wild. The Yellowstone bison is critical to the species' conservation and long-term survival, and its disappearance would create a significant gap in the species' range, or the complete elimination of the species.

Regulatory mechanisms are inadequate to protect the Yellowstone bison. Because the Yellowstone bison are an isolated remnant population, they are susceptible to threats such as disease outbreaks, natural catastrophes, and impairment of genetic and population structure due to ongoing management activities. These management actions do not protect bison from disease, limit bison access to essential range, result in the death or removal of many animals with differential effects on subpopulations, and are a threat to Yellowstone bison conservation.

Introduction

The wholesale slaughter and loss of the great herds of bison that once roamed the North American continent that occurred in the nineteenth century epitomizes the untempered impact of man on his environment. During the European settlement, the bison (*Bison bison*) populations that roamed North America were reduced from tens of millions to less than 1,000 by the late 1800's (Hornaday, 1889; Coder, 1975; Smits, 1994; Shaw, 1995). Following this near extermination, most of the few hundred remaining bison were captured and sent to zoos or adopted by private ranchers (Coder, 1975). Today, the plains bison is for all practical purposes ecologically extinct within its original range (Freese *et al.*, 2007; Sanderson *et al.*, 2008). While, historic conservation efforts have increased "bison" numbers widespread hybridization with cattle, loss of genetic diversity due to multiple bottlenecks, founder effects, small population sizes, and systematic domestication poses the risk of genomic extinction, and a drastic reduction in evolutionary potential (Boyd, 2003; Boyd and Gates, 2007; Freese *et al.*, 2007; Sanderson *et al.*, 2008; Hedrick, 2009; Halbert *et al.*, 2012; Bailey, 2013 pp. 133-149). The majority of former bison habitat has been lost to agricultural uses, development, alteration, and destruction (Boyd, 2005; Boyd and Gates, 2006).

Following the slaughter, only one small, bison herd, the nucleus of the extant Yellowstone bison population, remained *in situ* in the United States (Freese *et al.*, 2007). We are petitioning for these Yellowstone bison to be listed as an Endangered or Threatened Distinct Population Segment of plains bison under the Endangered Species Act of 1973 ("ESA"). Immediate and severe threats warrant listing as Endangered under the Act. The Yellowstone bison qualify for protection under the Act as an Endangered because the degree of threat exceeds the minimal requirement for listing.

The Yellowstone bison represent an ecological microcosm of historic bison populations and a genetic well-spring for restoration of the species. The Yellowstone bison represent an evolutionary legacy for bison because they are the only surviving naturally occurring wild bison population in the United States (Freese *et al.*, 2007). The

Yellowstone bison are the only remaining native population of plains bison that retain genetic integrity. Legal protection under the Act is required to ensure their persistence.

Yellowstone bison have a relatively high degree of genetic variation and are the only population free of evidence of hybridization with cattle (Ward *et al.*, 1999; Halbert, 2003; Halbert and Derr, 2007; Dratch and Gogan, 2010; Schnabel, 2011). Unique among the conservation herds they still exhibit some migratory behavior. Ecological and genetic studies also provide evidence of a population substructure within the population (Kirkpatrick *et al.*, 1996; Taper *et al.*, 2000; Halbert, 2003; Gates *et al.*, 2005; Fuller *et al.*, 2007; Gardipee, 2007; Brodie, 2008) that show differences in migration pattern (Halbert *et al.*, 2012 p. 9).

The Yellowstone bison meet all the requirements of the USFWS policy on Distinct Population Segments. Yellowstone bison are a discrete population because they are physically and genetically isolated from any public or private bison populations. The Yellowstone bison are significant because their continued persistence represents the only surviving natural occurrence of wild bison that has never been extirpated from its historic and ecological range (USDI/USDA, 2000). The extirpation of the Yellowstone bison from the northern Greater Yellowstone Ecosystem would represent the complete loss of wild bison from the last stronghold of their historic and ecological range, the loss of unique ecological adaptations to the local environment, and the loss of valuable and unique genetic qualities.

Petition History

On August 15, 2007¹, the U.S. Fish and Wildlife Service (“USFWS”) issued a 90-day finding on a January 5, 1999 petition to list the Yellowstone National Park bison population as threatened or to alternatively list plains bison as threatened. Although USFWS declined to conduct a full 12-month status review based on that 1999 petition, USFWS did determine that there is substantial information indicating that the Yellowstone National Park bison herd may meet the criteria of discreteness and significance as defined by its policy on DPS.

The January 5, 1999 petition was hand-written and without attached supporting scientific documents or other evidence; thus, the USFWS considered relatively little information and evidence in making its negative 90-day finding. Evidence not considered by USFWS in 2007 and new evidence that has become available since then, warrant a decision by USFWS to list the Yellowstone bison DPS under the ESA.

On February 24, 2011² the USFWS issued a 90-day finding on a June 22, 2009 petition to list the wild plains bison (*Bison bison bison*) or each of four distinct population segments as threatened under the Endangered Species Act of 1973, as amended. Again, the Service found that that petition did not present substantial

¹ 72 FR 45717

² 76 FR 10299

information indicating that listing may be warranted. However, this time the Service backtracked on its 2007 position on the Yellowstone bison:

The 2007 finding concluded that the Yellowstone herd may be discrete from other plains bison, because it was considered the only herd that has “remained in a wild state since prehistoric times” and because of physical distance and barriers. The best available information now indicates that the basis for our 2007 DPS determination was erroneous. We still use the term “wild plains bison” to describe the Yellowstone herd because they are managed as a conservation herd, rather than as a commercial herd. However, we no longer consider the Yellowstone herd to have remained in more of a “wild” state than any other conservation herd. Specifically, these wild plains bison are no longer thought to have remained in an unaltered condition from prehistoric times, as implied in the previous determination. In 1902, no more than 30 wild plains bison remained in Yellowstone (Halbert 2003, p. 24). In the same year, 18 female plains bison from the captive Pablo-Allard herd in Montana and 3 bulls from the captive Goodnight herd in Texas were purchased to supplement the Yellowstone herd (Halbert 2003, pp. 24-25). Additionally, intensive management (supplemental feeding, roundups, and selective culling) of the Yellowstone herd occurred from the 1920s through the late 1960s (Gogan *et al.* 2005, p. 1719). Wild plains bison from Yellowstone also have been used to start or augment many later conservation herds (Halbert and Derr 2007, p. 2). Despite geographic separation, the Yellowstone herd is essentially part of one metapopulation and is not markedly separate from other herds.

The petitioners disagree with the USFWS’s 2011 characterization of the Yellowstone bison. As we review herein, Yellowstone bison are not just geographically isolated from other bison but have been physically isolated from other bison populations for over 100 years. While many of the other conservation herds have been stocked with bison culled or selected from the Yellowstone herds, none of those herds exhibits the level of genetic diversity found in the Yellowstone bison. Furthermore, new information shows that Yellowstone bison are the only significant, wild population of plains bison with no evidence of hybridization with cattle - unlike most of the other conservation herds that USFWS and other agencies manage and erroneously groups into its “meta-population”. In essence, the Yellowstone bison are the *only* extant population of plains bison because they are the only population of plains bison that maintains its genetic integrity.

Biology and Natural History

Taxonomy

Despite the extensive history and the economic and symbolic importance of bison, there remains significant confusion and disagreement about bison taxonomy (Boyd, 2003; Gates *et al.*, 2010). Bison are large terrestrial mammals in the family Bovidae; however there is a lack of consensus as to the genus. A useful review of this taxonomic issue is provided in Gates *et al.*, 2010. They state:

When Linnaeus first classified the bison in 1758 for his 10th Edition of the *Systema Naturae*, he assigned the animal to *Bos*, the same genus as domestic cattle (Wilson and Reeder 2005). During the 19th Century, taxonomists determined that there was adequate anatomical distinctiveness to warrant assigning the bison to its own genus (Shaw and Meagher 2000). Therefore, in 1827, C. Hamilton Smith assigned the subgeneric name *Bison* to the American bison and the European bison (Skinner and Kaisen 1947). In 1849, Knight elevated the subgenus *Bison* to the level of genus (Skinner and Kaisen 1947). Since then, taxonomists have debated the validity of the genus, some arguing that bison are not sufficiently distinct from cattle, guar, yak, and oxen to warrant a distinct genus (Gardner 2002, personal communication). During the last two decades, as more molecular genetic and evolutionary evidence has emerged, scientists have used *Bos* with increasing frequency. Discrepancies in the genus are reflected in major cataloguing centres and books. For example, the Canadian Museum of Nature (Balkwill 2002, personal communication) and the Smithsonian National Museum of Natural History in its publication *Mammal Species of the World* (Wilson and Reeder 2005) use *Bison*, while the Royal Ontario Museum (Eger 2002, personal communication) and the Museum of Texas Tech University, in its *Revised Checklist of North American Mammals North of Mexico* (Jones, Jr. *et al.* 1992; Jones *et al.* 1997; Baker *et al.* 2003), have reverted to *Bos*.

Because bison have long been assigned to the genus *Bison*, and that generic assignment continues to be used by both the USFWS and the IUCN/SSC American Bison Specialist Group, herein we refer to bison as members of the genus *Bison*. However, inclusion in the genus *Bos* would have little effect on our arguments or conclusions.

The genus *Bison* is widely recognized as consisting of two extant species, the American bison, *Bison bison*, from North America, and *B. bonasus*, the European bison (or wisent), from Eurasia (Halbert, 2003, p. 1; Gates *et al.* 2010, p. 15). The two species diverged relatively recently, and can interbreed to produce fertile offspring (Pucek *et al.*, 2004 p. 13). However, mitochondrial genomic data suggests that *B. bison* is more closely related to *Bos grunniens* (yak) than to *B. bonasus* (Zeyland *et al.*, 2012). Of course, that finding also implies paraphyly within the genus *Bison*.

Representatives of the genus *Bison* emerged on the open Eurasian steppe by the mid-Pliocene, the ancestral steppe bison, *B. priscus*, spreading over the Bering land bridge during the mid-Pleistocene, with subsequent exchanges between Eurasia and North America (see Kerley *et al.*, 2012). Two species, *B. latifrons* and *B. antiquus*, appear in North American fossil records during this time. The larger of the two, *B. latifrons*, became extinct during the late Wisconsin glacial period (75,000 - 10,000 BP) however, *B. antiquus* survived into the Holocene. DNA evidence supports the *in situ* evolution of *B. bison* from *B. antiquus* through an intermediate usually called *B.*

occidentalis (Wilson *et al.*, 2008). Use of a genome-wide single nucleotide (SNP) genotyping platform using a bone sample from an ancient Russian specimen confirmed that *B. priscus* is basal to the modern *B. bison* clade (Decker *et al.*, 2009 p. 18646). Modern bison are considerably smaller in horn and body size than their progenitors (Guthrie, 1970 p. 7).

Extant American bison consist of two types, the plains bison (*B. bison bison*) and the wood bison (*B. bison athabascae*) (Reynolds *et al.*, 2003). Although plains and wood bison are phenotypically distinct (See *Description* below), the subspecies designations have been challenged (see Halbert, 2003 p. 10), and it has been argued that the two forms are merely ecotypes (Geist, 1991). However, there is a concordance of genealogy and phenotype for the two types even for populations historically moved to widely differing environments implying a genetic basis for the morphological differences (van Zyll de Jong *et al.* 1995). Molecular genetic analyses using blood typing, RFLP, microsatellite DNA, and genome-wide screening using SNP CHIP technology all indicate that plains and wood bison are genetically similar (Bork *et al.*, 1991; Wilson and Strobeck, 1999; Pertoldi *et al.*, 2010; Douglas *et al.*, 2011; Cronin *et al.*, 2013). Genotypic differentiation between wood bison and plains bison is significantly less than that seen among cattle breeds and subspecies (Cronin *et al.*, 2013). In a comparison of mitochondrial DNA genomes, the two identified wood bison haplotypes did not form a single clade and were mixed with plains bison haplotypes suggesting that wood bison were never a genetically distinct subspecies or that one of the two wood bison haplotypes is derived from the introduction of plains bison into the Canadian wood bison herds 90 years ago (Douglas *et al.*, 2011). Despite the inconclusive molecular genetic evidence for subspecific differentiation, the currently listed *B. bison athabascae* population is an important source of genetic diversity for the species, since the two wood bison haplotypes were not identified in any of the tested plains bison populations (Douglas *et al.*, 2011).

Description

Boyd (2003) and Gates *et al.*, 2010 differentiate plains and wood bison based on the following morphological differences:

Plains Bison, <i>B. bison bison</i>	Wood Bison, <i>B. bison athabascae</i>
Pelage Characteristics	
Dense woolly bonnet of hair between horns	Forelock dark, hanging in strands over forehead
Thick beard and full throat mane, extending below rib cage	Thin beard and rudimentary throat mane
Well-developed chaps	Reduced chaps
Well-demarcated cape, lighter in color than wood bison	No clear cape demarcation, hair usually darker than plains bison
Structural Characteristics	
Highest point of the hump over front legs	Highest point of the hump forward of front legs
Horns rarely extend above bonnet	Horns usually extend above forelock
Smaller and lighter than the wood bison (within similar age and sex classes)	Larger and heavier than plains bison (within similar age and sex classes)

Table 1: Comparison of Plains and Wood Bison Morphology. Data from Boyd, 2003.

The wood bison occurs in Canada and has been listed (as *B. bison athabascae*) under the Endangered Species Act since 1969. Although some earlier workers have referred to the indigenous bison at Yellowstone National Park as “Mountain Bison” (*B. bison athabascae*) (Christman, 1971; Meager, 1973) the current and indigenous Yellowstone bison herds have been confirmed to be plains bison (*B. bison bison*) (Wilson and Strobeck, 1999). Bailey has recently revived the term “Mountain Bison” as a bison ecotype that includes the Yellowstone bison (Bailey, 2013 pp.123-127).

Distribution

The range of the plains bison before European settlement extended from the east coast to west of the Rocky Mountains, and from the Great Plains of southern Canada south to northern Mexico (Hornaday, 1889 p. 377). Historically, habitat for the wild plains bison encompassed some 9.4 million square kilometers (3.6 million square miles), with about 7.9 million square kilometers (3.0 million square miles) west of the Mississippi River (Sanderson *et al.*, 2008, p. 255). Plains bison were most abundant on the Great Plains, but their range extended eastward into the Great Lakes region, beyond the Allegheny Mountains, and into Florida; westward into Nevada, the Cascade Mountains, and the Rocky Mountains; northward into mid-Alberta and Saskatchewan; and southward into Mexico (Hornaday, 1889 p. 377; Boyd, 2003 p. 20; Gates *et al.*, 2010 p. 56). Wild plains bison were eliminated west of the Rocky Mountains and east of the Mississippi River by the early 1800s (Halbert, 2003 p. 4). By 1889, only a few wild plains bison remained in the Texas Panhandle, Colorado, Wyoming, Montana, and the western Dakotas, as well as a small number in captive herds (Hornaday, 1889 p. 525). With the exception of a few hundred free roaming individuals that survived in the Greater Yellowstone Area, bison are ecologically extinct from >95% of their historic range (Boyd, 2003; Boyd and Gates, 2006; Freese *et al.*, 2007; Sanderson *et al.* 2008; Hedrick, 2009). The majority of former bison habitat has been lost to agricultural uses, development, alteration, and destruction (Boyd, 2003; Boyd and Gates, 2006).

Historic conservation efforts for plains bison involved restocking parks in the United States from the small surviving nucleus of animals. Overall trends in bison numbers and distribution have increased (Boyd, 2003; Freese *et al.*, 2007; Sanderson *et al.*, 2008; Gates *et al.*, 2010). Today, plains bison occur in parks, preserves, other public lands, and on private lands scattered throughout, and external to, their historical range. Most of these herds are heavily managed. Herds occurring on public lands are generally termed as “conservation herds” (Gates *et al.*, 2010).

The Yellowstone bison historically ranged across 20,000 km² in the headwaters of the Yellowstone and Madison rivers, within the northern Greater Yellowstone area (Meagher, 1973 p. 13-14; Schullery *et al.*, 1998; Gates *et al.*, 2005; Schullery and Whittlesey, 2006; Plumb *et al.*, 2009). Plumb *et al.* (2009) mapped the current and pre-settlement distributions of Yellowstone bison (Figure 1 below).

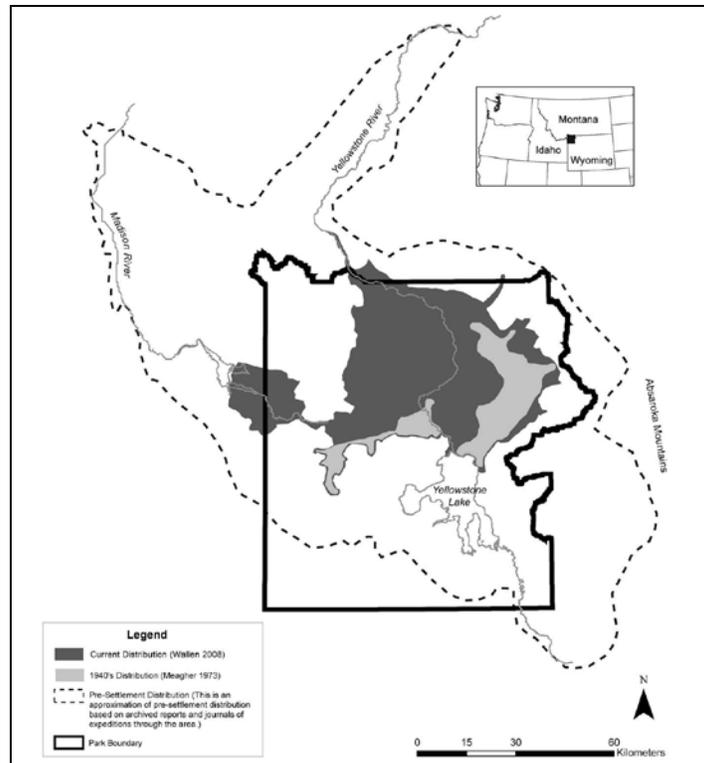


Figure 1: Historic and Current Range of the Yellowstone Bison. Yellowstone bison historically occupied some 20,000 km² in the northern Greater Yellowstone Area (Plumb *et al.*, 2009 p. 2378).

Bison Genetics & Cattle-Gene Introgression

Plains bison are plagued by loss of genetic diversity due to multiple bottlenecks, founder effects, small population sizes, widespread hybridization with cattle, and systematic domestication poses the risk of genomic extinction, and a drastic reduction in evolutionary potential (Polziehn *et al.*, 1995; Boyd, 2003; Boyd and Gates, 2007; Freese *et al.*, 2007; Sanderson *et al.*, 2008; Hedrick, 2009; Pertoldi *et al.*, 2010).

The collapse of the plains bison population following European settlement combined with early conservation efforts which relied on available bison including ranched bison resulted in a loss of genetic diversity due to bottlenecks, founder effects, and small population sizes (Boyd, 2003; Boyd and Gates, 2007; Freese *et al.*, 2007; Sanderson *et al.*, 2008; Hedrick, 2009; Pertoldi *et al.*, 2009; Pertoldi *et al.*, 2010). In the process of constructing a phylogeny for North American bison using mitochondrial DNA (mtDNA), Polziehn *et al.*, 1995 discovered a bovine (*Bos taurus*) haplotype (mitochondrial genotype) in the Custer State Park herd of South Dakota prompting wider surveys for bovine haplotypes in other bison populations of bison. Consequently, analyses of both mitochondrial (Polziehn *et al.*, 1995; Ward *et al.*, 1999) and nuclear (Halbert *et al.*, 2005) DNA have demonstrated cattle-gene introgression throughout almost all public and private bison populations due to hybridization with cattle (Halbert and Derr, 2007).

Hybridization between endangered species and more common species is a significant problem in conservation biology because it may result in extinction or loss of adaptation (Derr *et al.*, 2012). Hybrids are known to form among nearly all combinations of species from the *Bos* genus and although generally considered to be from different but closely related genera, bison and domestic cattle can produce fertile offspring from human-controlled crosses (see Halbert, 2003). The interspecific cross between cattle and bison is difficult, and the early ranchers could generally cross only bison bulls to domestic cows which results in a low birthrate of viable first-generation hybrid offspring and all the surviving progeny are female (see Hedrick, 2010). Each of the ranchers involved in establishing the 5 bison foundation herds in the late 1800s either experimented with domestic cattle–bison crosses or purchased bison from others who were involved in such experiments (Halbert, 2003). Recent studies indicate that cattle Y chromosome introgression has not occurred into bison populations probably reflecting the failure of bison bulls to domestic cows crosses to produce fertile male offspring (Ward *et al.*, 2001; Hedrick, 2010).

Derr *et al.*, 2012 examined the phenotypic effect of cattle gene introgression in *Bison* by comparing weight and height of bison with cattle or bison mitochondrial DNA (mtDNA) from Santa Catalina Island, a nutritionally stressful environment for bison, with a group of age-matched feedlot bison males in Montana, a nutritionally rich environment. The environmental and nutritional differences between these 2 bison populations were very different and demonstrated the phenotypic effect of domestic cattle mtDNA in bison over a broad range of conditions. For example, the average weight of feedlot males that were 2 years of age was 2.54 times greater than that of males from Santa Catalina Island. In both environments, bison with cattle mtDNA had lower weight compared with bison with bison mtDNA, and on Santa Catalina Island, the height of bison with cattle mtDNA was lower than the height of bison with bison mtDNA. The study of Derr *et al.*, 2012 thus shows that cattle gene introgression does result in phenotypic effects and that genomic integrity is an important consideration for the conservation of the American plains bison.

Halbert *et al.*, 2005 used 14 unlinked microsatellite markers with nonoverlapping allele size ranges between bison and domestic cattle to identify 6 of 14 US and Canadian public bison populations with evidence of nuclear domestic cattle introgression. To date, evidence of mitochondrial or nuclear domestic cattle introgression has been identified in most US plains bison conservation herd populations (Ward *et al.*, 1999; Halbert *et al.*, 2005; Schnabel, 2011 p. 11). All major public bison populations in the U.S. and Canada have now been examined using mtDNA, microsatellite markers, or a combination of these 2 technologies (Gates *et al.*, 2010 p. 23). The latter authors reported that at that time cattle-gene introgression had been detected in all United States herds except for the Yellowstone, Grand Teton National Park (the Jackson Herd), the Henry Mountains, the Wind Cave National Park, and the small Sully's Hill National Game Preserve herds.

Subsequently, Schnabel (2011 p. 11) using an SNP CHIP genotyping platform (Decker *et al.*, 2009) looked at cattle-gene introgression in a number of bison herds. Data from relevant herds is shown in Table 2 below.

Population	Non-Introgressed	Introgressed	% Introgression	Block Size	Number Blocks	% Cow DNA
Jackson	0	7	100.00%	4,024,869	3.86	0.25%
Wind Cave NP	28	74	72.50%	4,412,274	2.53	0.19%
Sully Hill	4	35	89.70%	4,466,352	2.91	0.25%
Yellowstone	19	0	0.00%	0	0	0

Table 2: Cattle-gene Introgression in Four Plains Bison Herds. Data from Schnabel, 2011.

Schnabel found that only the Yellowstone bison remain free of cattle-gene introgression. The seven bison he tested from the Jackson herd, the closest conservation herd to the Yellowstone bison, were all introgressed showing an average of 0.25% cattle DNA (Schnabel, 2011). The apparent success of bison recovery efforts over the past 150 years is thus threatened by widespread introgression with domestic cattle-genes.

The Yellowstone bison clearly represent a primary resource for plains bison restoration efforts not only because they exhibit a high level of genetic diversity relative to other bison populations, but because they are the only significant wild population of plains bison with no evidence of hybridization with cattle (Ward *et al.*, 1999; Ward, 2000; Halbert, 2003; Freese *et al.*, 2007; Halbert and Derr, 2007; Sanderson *et al.*, 2008; Schnabel, 2011 p. 11).

The Yellowstone bison herds possess genetic characteristics that distinguish them from other public and private bison populations. Wilson and Strobeck (1999) found an average of 5.36 alleles per locus and heterozygosity of 54.2% among 33 Yellowstone bison included in their study. Halbert (2003) genotyped 488 Yellowstone bison with 54 microsatellite loci and found an average of 6.48 alleles per locus, and observed and expected heterozygosities of 61.5% and 62.7%, respectively.

Halbert (2003) compared genetic diversity among 9 federal bison herds (including Yellowstone bison) and 1 state herd. Her analysis revealed that only 4 of the 10 populations significantly contributed to allelic richness and gene diversity - Yellowstone, the National Bison Range, Wind Cave National Park and Wichita Mountains. The Yellowstone bison made the highest contribution to overall allelic richness (Halbert, 2003 p. 46). She estimated F_{ST} , a measure of genetic differentiation which ranges from 0.00 (no genetic differences) to 1.00 (complete genetic differentiation). Population comparisons with an F_{ST} value of >0.05 provide evidence of genetic distinction. The F_{ST} estimates between the Yellowstone bison and the other herds were all >0.05 , ranging from 0.0855 (Wind Cave National Park) to 0.2347 (Texas State Bison Herd) (Halbert, 2003 p. 49). The closest genetic neighbor of Yellowstone bison is Wind Cave National Park bison ($D_S = 0.188$, $(\delta\mu)^2 = 0.375$) (Halbert, 2003 p. 58). The Wind Cave National Park bison population was originally founded with fourteen bison donated from the New York Zoological Society and six Yellowstone bison introduced in 1916 (Halbert, 2003 p. 16). Evidently, the Yellowstone bison used to supplement the Wind Cave National Park herd markedly influenced the genetic constitution of the herd. Unfortunately, the

Zoological Society bison evidently brought cattle-genes with them; 74 of 102 Wind Cave National Park bison tested were introgressed (Schnabel, 2011 p. 11).

The Yellowstone bison also possess other genetic characteristics that distinguish them from other bison populations, such as several unique alleles not found in any other bison populations (Halbert, 2003). Genetic evidence showed that the Yellowstone bison population is separated into at least two distinct subpopulations that show genetic differentiation comparable to that seen in populations that have been geographically separated for over 40 years (Halbert *et al.*, 2012).

Life History

The average lifespan for bison in natural settings average from 10 to 15 years, and some bison may live as long as 20 years (Meagher, 1973 p. 46; Brodie, 2008). Bison reach sexual maturity at 2-4 years of age, although the occasional female may conceive as a yearling and some 2 year old males may breed in the absence of older males (Meagher, 1973 p. 50-51). Fully mature bison males (8 years and older) are the most sexually active and only mature males tend females during the breeding season (Meagher, 1973 p. 51). The bison rut begins around mid-July, peaks in August, and may last through early September. During the rut, bulls use their olfactory senses to detect whether females are in estrus (Lott, 2002 p. 15). Bulls curl their lips in an upward motion in close proximity to the female genital area or urine stream, a behavior known as flehmen (Lott, 2002 p. 85). Mature bulls will compete for access to mates during this time (Meagher, 1973 p. 47; Lott, 2002 p.8). A bison cow may choose not to mate with a bull, and will flee through the herd with her tail raised (Lott, 2002 p. 16). The gestation period is estimated at 285 days, and the sex ratio at birth slightly favors males (Meagher, 1986; Lott, 2002 p. 34; Brodie, 2008). Calving season in the wild generally extends from mid-April through May with births often concentrated from the end of April through the first two weeks of May (Meagher, 1986). Females produce one calf per year; twins are extremely rare (Meagher, 1973 p. 58). The bison rut occurs when most calves are about four months old (Lott, 2002, p. 34).

Survivorship varies widely among public bison populations due to differences in environmental influences, predation, and harvest regimes (Brodie, 2008). Survival increases with age up to 14 years, and declines sharply after 15 years of age (~ 50%) (Brodie, 2008). Calf survival rates are the most variable and are lowest in bison populations, such as the Yellowstone bison, that co-exist with large predators such as wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) (Mattson, 1997; Brodie, 2008). Harsh winters affect survival rates (Meagher, 1973 p. 73; Meagher, 1986; Brodie 2008). Annual calf survivorship in Yellowstone's central and northern range breeding herds has been documented to be 61% and 76% respectively. Adult survivorship ranges from 91-93% among adult Yellowstone bison excluding hunting and disease risk management removals, and is reduced to 83% when those factors are included (Brodie, 2008).

Higher calf survivorship (> 90%) and adult female longevity (up to 20-30 years) are common among bison herds on private ranches because they are managed for

maximum commercial value. Some adult female bison in domestic herds have been documented to live and breed well past 20 years of age. In contrast, most bull bison in private ownership are slaughtered before the age of 6 years for commercial meat production (Boyd and Gates, 2006; Freese *et al.*, 2007; Sanderson *et al.*, 2008). Usually, commercial herds have skewed sex ratios with only a small proportion of bison bulls kept to breed a large number of females for up to 6 to 8 years before slaughter (Lott, 2002 p. 198; Boyd and Gates, 2006; Freese *et al.* 2007; Sanderson *et al.*, 2008).

History of Bison in Yellowstone National Park

In 1872, President Grant created Yellowstone National Park to protect all natural resources, including bison, within its borders. However, by 1894 continued poaching had reduced the park bison population from 200 to only 25 animals (Danz, 1997 p. 124). On May 7, 1894, President Cleveland signed the National Park Protective Act (Lacey Act). The Lacey Act ameliorated longstanding problems with jurisdiction and law enforcement in Yellowstone National Park and was the first federal law to provide specific protection for bison. It carried a two-year jail term and a \$1,000 fine for anyone removing mineral deposits, cutting timber, or killing game in Yellowstone National Park (Danz, 1997 p. 124).

In 1902, 18 female bison from the captive Pablo-Allard herd in Montana and 3 bulls from the captive Goodnight herd in Texas were purchased to supplement the Yellowstone herd (Halbert, 2003, pp. 24-25). Descendants of these introduced bison began to join the wild bison in 1915 (Meagher, 1973 p. 15). No other bison have been introduced to the Yellowstone bison population since then.

Earlier workers referred to the bison indigenous to Yellowstone National Park as “mountain bison”, *Bison bison athabasca* as compared to the introduced “plains bison” (Christman, 1971; Meagher, 1973 p. 14; Jackson, 2008). The last stronghold of the indigenous bison was the Pelican Valley/Mirror Plateau (Meagher, 1973 p. 26; Jackson, 2008 at 1). The introduced bison diluted the indigenous input to the current gene pool to about 40% (Meagher, 1973 p. 29; Wilson and Strobeck, 1999 p. 484).

Yellowstone Bison Metapopulation Range and Movement Patterns

Yellowstone National Park is an 8,983 km² reserve, located in the northern Greater Yellowstone Ecosystem in the northwest corner of Wyoming. Most (96%) of the park is in Wyoming. The western, northern, and northeast borders of the park encompass smaller portions of Montana (3%) and Idaho (1%) (Gates *et al.*, 2005). In 1978, Yellowstone National Park received global recognition as one of the first designated World Heritage Sites (UNESCO, 1978³). UNESCO recognized “the extraordinary scenic treasures of Yellowstone include the world’s largest collection of geysers, the Grand Canyon of the Yellowstone River, numerous waterfalls, and great herds of wildlife”. The Greater Yellowstone Ecosystem is a large (12 to 18 million acres) landscape overlapping

³ UNESCO, 1978. Committee Decisions CONF 010 VIII.38. Online at: <http://whc.unesco.org/en/decisions/2127>.

portions of Wyoming, Montana and Idaho in the western United States. This ecosystem includes two National Parks (Yellowstone and Grand Teton), portions of six National Forests, three National Wildlife Refuges, and tracts of other federal, state, tribal, and private lands. The headwaters of three major watersheds originate in the Greater Yellowstone Ecosystem: the Mississippi-Missouri, Snake-Columbia, and Green-Colorado (Marston and Anderson, 1991). Yellowstone National Park and contiguous lands to the north is the only area within the Greater Yellowstone Ecosystem where natural patterns of population structure and gene flow in plains bison can be observed (Sanderson *et al.*, 2008).

The unique landscape and habitats of Yellowstone National Park have been formed through the forces of extensive volcanism, glaciations, and erosion over millions of years (Meagher and Houston, 1998). One of the world's largest calderas lies beneath the central portion of Yellowstone National Park, extending from Old Faithful to Mount Washburn in the north, and east to Yellowstone Lake (Meagher and Houston, 1998). The active caldera and associated magma layers located just 3-8 miles below the surface provide a source of heat for the unusually high concentration of geothermal features (geysers, hot springs, mud pots, and fumaroles) which influence bison habitat within the park. Summer in Yellowstone National Park is short, occurring from late June to early September, with occasional droughts occurring over several years. The winters in Yellowstone National Park are characterized as severe, long, and extremely cold with average temperatures as low as 4.3°C in Mammoth and 0.2°C at Yellowstone Lake, and the mean duration of snow cover is about 213 days (Gates *et al.*, 2005). Annual mean Snow Water Equivalent (SWE) range from 6 cm in the Gardiner Basin to 20 cm at Mary Mountain area located within the central range of the park (Gates *et al.*, 2005). However, the recent climate monitoring indicates considerable change is underway (Saunders *et al.*, 2011; Yellowstone Center for Resources, 2014).

The Yellowstone bison are an isolated meta-population of two to three genetically distinct herds (Halbert *et al.*, 2012). The presence of these subpopulations contributes to the high levels of genetic variation observed among Yellowstone bison compared to other populations (Halbert *et al.*, 2012 p. 9). The Yellowstone bison congregate in three geographically distinct breeding areas: Hayden Valley, Lamar Valley, and Mirror Plateau during the mid-summer rut (Meagher, 1973 p. 76; Taper *et al.*, 2000; Meagher *et al.*, 2002; Gardipee, 2007 p. 32; Geremia *et al.*, 2009). Bison that rut in the Lamar Valley and Mirror Plateau are generally termed the northern range herd. Their winter ranges extend from the central and northern ranges within Yellowstone National Park to public and private lands outside the park in Montana. Northern range bison move between the Gardiner Basin (elev. 5,900 ft), the Lamar Valley floor, up to the Cache Calfee ridge, and the Mirror Plateau (elev. 8,200 ft). The central range bison herd which ruts in Hayden Valley, ranges from Pelican Valley, Hayden Valley, Mary Mountain (elev. 8,200 ft), Firehole River basin, the Madison Junction, and to their traditional winter ranges located outside the west and north entrances of Yellowstone National Park. Cannon (2007 and 2008) found evidence that bison ranged among elevations over 9,900 ft within the Greater Yellowstone Ecosystem. Christman, 1971 (page 47) provides a map of high elevation localities. The Yellowstone bison are the only free-roaming, wild population

known to have continuously ranged across high altitudinal gradients, which represents the conservation of a unique ecological adaptation for American bison.

Bison typically follow the path of least resistance to access seasonal home ranges. Five primary winter range movement corridors for Yellowstone bison have been identified. The Gardiner Basin to Lamar Valley is located along the Yellowstone River and the road to Cooke City within the northern range. The Mirror Plateau corridor occurs over a network of historic bison travel routes that extend from the southeastern Lamar Valley to northeastern Pelican Valley. Bison from the central range access the northern range via the corridor that extends from the Firehole to Mammoth. Two interior central ranges are connected by the Pelican Valley to Hayden Valley corridor. Historic evidence suggests that bison accessed winter ranges west of Yellowstone National Park along the Madison River (Meagher, 1973 p. 23). Central range bison also access the winter ranges located west of park boundaries via the corridor that extends from the Firehole to the town of West Yellowstone and Hebgen Lake. Interestingly, the central range bison utilize a significant proportion of geothermal area within their winter ranges (from 5% in Pelican Valley to 14% in Mary Mountain), and movement corridors (5.2% to 9.2%) (Gates *et al.*, 2005). The inclusion of geothermal areas as a significant portion of habitat use represents an unusual ecological adaptation unique to Yellowstone bison.

Approximately, one-third (3,175 km²) of the Yellowstone National Park interior currently serves as primary bison habitat (Plumb *et al.*, 2009). A significant portion of crucial winter range for the Yellowstone bison is located west and north outside park boundaries (Gates *et al.*, 2005; Plumb *et al.*, 2009). Yellowstone bison frequently migrate to these ranges when snowpack within the park's interior increases the energetic costs of foraging, often before either breeding herd has exceeded its food-limited carrying capacity (Plumb *et al.*, 2009). Archeological evidence and historic accounts identify areas immediately adjacent to Yellowstone National Park as essential winter ranges for the Yellowstone bison population (Schullery *et al.*, 1998; Schullery and Whittlesey, 2006; Cannon, 2008; Plumb *et al.*, 2009). Dispersal of Yellowstone bison to seasonal ranges outside the park represents an attempt to naturally re-colonize former ranges (Schullery *et al.*, 1998; Schullery and Whittlesey, 2006; Cannon, 2008; Plumb *et al.*, 2009). However, access to these ranges is now precluded by brucellosis risk management operations which involve hazing, shooting, capture, and slaughter of Yellowstone bison, which results in a loss of critical range and creates a dispersal sink (Plumb *et al.*, 2009). These ranges are threatened by habitat destruction, disturbance and degradation.

Meagher (1989) considered the unusually severe winter of 1975-1976 to have provided the initial impetus that led to the westward movements or stress dispersal of bison on the northern winter range and subsequent regular movement of larger numbers of bison out of the Park in the mid 1970's. This brought the Yellowstone bison back to an important portion of their natural, historic range. However, it also initiated an unprecedented period of excessive management that continues to today. As Lancaster (2005 p. 451) states, "This is the classic example of the boundaries of an ecosystem not matching artificially human created borders. The bison's ecosystem overlaps and crosses the artificially created jurisdictional boundaries between government entities."

Yellowstone bison have been observed to assemble in matrilineal groups or family units that may include several generations of related individuals. Halbert (2003 p. 150) found several cases of dams with multiple offspring of different ages, including a multigenerational matriarchal group which spanned 4 generations ranging from a 7 year-old female to a male calf.

Yellowstone bison have historically used winter ranges outside park boundaries even when population estimates were much lower than those currently observed. In the winter of 1893-94, poachers slaughtered about 116 bison that had shifted across the west boundary of Yellowstone National Park (McHugh, 1975 p. 385). In 1943, the Yellowstone bison population had been reduced to around 747 individuals following the removal of several hundred animals within the previous year (USDI/USDA, 2000; Gates *et al.*, 2005). Harsh winter conditions resulted in at least 160 migrating to winter ranges north of the park boundary (Gates *et al.*, 2005 pp. 84-85; Franke, 2005 p. 83). Several bison travelled as far as 50-80 km from the park that winter (Franke, 2005 p. 84). Despite two years of drastic culls to reduce bison numbers on the northern range, 68 of the 313 bison in the Lamar herd moved north of the park boundary in 1948 (Franke, 2005 p. 84). In 1953, when the Yellowstone bison population had rebounded to about 1,477 animals, a group of bison wandered across the north boundary (Franke, 2005 p. 90). Over 130 bison were removed from the population that year (USDI/USDA, 2000; Franke, 2005 pp. 90-91). These frequent and sometimes long-range emigrations north of park boundaries were seen as evidence that the Yellowstone bison's range probably extended at least to Livingston (Franke, 2005 p. 84). Results of modelling of bison migration to low elevation areas out of Yellowstone National Park using a hierarchical Bayesian framework found that migration differed at the herd scale (Geremia *et al.*, 2011). Migration beyond the northern park boundary was affected by herd size, accumulated snow, and aboveground dried biomass. Migration beyond the western park boundary was less influenced by these predictors. Their simulation results suggest that future large-scale, recurrent migrations and numbers exiting the park boundaries will be much greater than the predictions underlying the Interagency Bison Management Plan (Geremia *et al.*, 2011 page 7).

Bison movements and spatial distribution of travel corridors are influenced by topographic and habitat characteristics such as slope, landscape roughness, access to forage, distance to streams, and forest cover (Clow, 1995; Bruggeman *et al.*, 2007). Streams and river bottoms are the most influential features affecting bison winter travel routes, particularly in response to variable climactic conditions (Clow, 1995; Bruggeman *et al.*, 2007). In fact, many plains tribes who subsisted on bison intimately understood the influence of streams and river bottoms on bison travel routes, and used this insight for efficiently hunting them (Clow, 1995; Barsh and Marlor, 2003). For example, the Blackfeet tribe practiced selective harvest of beaver to maintain adequate water supply along traditional bison travel corridors and insure availability of bison for subsistence hunting (Barsh and Marlor, 2003). A significant proportion of travel corridors used by Yellowstone bison to access winter ranges west and north of park boundaries follow river bottoms and stream beds (Gates *et al.*, 2005; Plumb *et al.*, 2009). These observations provide evidence that innate ecological behavior is the primary motivation which drives

the Yellowstone bison to emigrate to winter range outside park boundaries and attempt to re-colonize historic ranges.

In addition to regular use of winter range in Montana north and west of Yellowstone National Park, substantial herds (50-100 bison) frequently move into the Silver Gate - Cooke City area of Montana northeast of the Park boundary.⁴ Yellowstone bison also move into historic range near Henry's Lake in Idaho where they are usually shot by the Idaho Department of Agriculture Division of Animal Industries which is responsible for managing bison in the state⁵. According to Division of Animal Industries records some 10 bison bulls were killed between 2004 and 2012. Yellowstone bison also move out east and southeast of the Park boundaries into the Absaroka Bison Management Area (Hunt Area 1) of Wyoming (WGFD, 2008). The WGFD estimates some 5-20 bison used the area each year for the years 1988-2007 (WGFD, 2008 p. 12).

Analysis of genotypes at 49 microsatellite loci from samples collected from bison that were captured and removed from winter ranges at Park boundaries suggested the presence of three subpopulations within Yellowstone National Park using the STRUCTURE program (Pritchard *et al.*, 2000) to test the probability of population substructure using a clustering algorithm for multilocus genotypes (Halbert, 2003). Halbert *et al.*, 2012 found genetic evidence showing that the Yellowstone bison population is separated into at least two distinct subpopulations that show genetic differentiation comparable to that seen in populations that have been geographically separated for over 40 years. Halbert *et al.*, 2012 also identified differences in migration patterns between these two subpopulations. The identification of cryptic population subdivision and genetic differentiation of this magnitude highlights the importance of this biological phenomenon in the management of wildlife species. The two major subpopulations correspond to the Central range and Northern range herds. Based on historical observations Meagher (1973) had described a third distinctive herd in the Pelican Valley. Halbert *et al.*, 2012 had only two capture samples from bison in the Pelican Valley. Radio-telemetry studies indicate extensive co-mingling of bison between the Pelican Valley and the Hayden Valley during the summer breeding season (Olexa and Gogan, 2007) suggesting a high likelihood of genetic exchange between bison at those locations (Halbert *et al.*, 2012 p. 8). However, the extent of genetic exchange between subpopulations cannot be determined without knowing when and where individual bison breed (Olexa and Gogan, 2007 p. 1536), so the possibility of a third genetic cluster cannot be discounted. That there are at least two genetically distinct populations coexisting geographically in Yellowstone provides important information for future population management of the herd.

Gardipee (2007) also found evidence of genetic population substructure among Yellowstone bison using mitochondrial DNA extracted from fecal samples collected within breeding areas located within Yellowstone National Park during the rut season. Two of eight haplotypes (haplotypes 6 and 8) previously identified by Ward *et al.* (1999) were found among 179 samples tested. The frequencies of these two haplotypes among

⁴ See for example: <http://www.riding-the-usa.com/2010/10/day-18-cooke-city-worland-part-2.html>

⁵ Idaho Statute 25 Chapter 6, at <http://legislature.idaho.gov/idstat/Title25/T25CH6SECT25-618.htm>

the northern and central range breeding herds contributed to a significant F_{ST} value (0.367, $P < 0.001$).

Gardipee's (2007) study revealed evidence of female philopatry to breeding areas, providing new insight into the behavioral ecology of free-roaming, wild, bison. This behavior has not been documented through genetic evidence in any other wild bison population and may be unique to the Yellowstone bison. Female philopatry among Yellowstone bison contributes to genetic population structure, and assists in the conservation of unique genetic qualities and local adaptations within each breeding herd. For example, she found that haplotype 8 occurs at a much higher frequency (0.54) in the northern range herd than in the central range herd (< 0.10) (Gardipee, 2007). Given the significant role Mitochondrial DNA plays in fitness, viability and fecundity (Gemmell *et al.*, 2004; Hedrick, 2009; Derr *et al.*, 2012), conserving the frequency and distribution of mtDNA haplotypes among the Yellowstone bison is important.

The Yellowstone bison are not just a physically isolated "population" but are an isolated meta-population of two to three genetically distinct herds (Halbert *et al.*, 2012). Halbert and her colleagues proposed that the presence of these subpopulations contributes to the high levels of genetic variation observed among Yellowstone bison compared to other populations (Halbert *et al.*, 2012 p. 9).

Population Estimates and Status

A comprehensive review of the status of all American bison conducted by the International Union for Conservation of Nature (IUCN) generated serious concern regarding the future of the species. Subsequently, in 2010 American bison were uplisted from Lower risk/conservation dependent (designated in 1996) to a Near Threatened designation on the IUCN Red List. The IUCN uplisted the conservation status of bison because of their increasing dependence upon conservation programs, the existence of only five viable populations and small isolated populations.

The IUCN cites a number of serious threats to the conservation of bison such as: habitat loss; genetic manipulation of commercial bison for market traits; small population effects in most conservation herds; few herds are exposed to a full range of natural limiting factors; cattle gene introgression; loss of genetic non-exchangeability through hybridization between bison subspecies; and the threat of depopulation as a management response to infection of some wild populations hosting reportable cattle diseases (e.g. Yellowstone bison) (IUCN, 2014). In particular, the IUCN cites culling of bison populations to prevent spread of bovine diseases as a major threat to their conservation (IUCN, 2014).

The Park Service monitored overall trends in the Yellowstone bison population both before and after the moratorium on culling in the park was instituted in 1969. Figure 2 below shows the variation in bison numbers and breakdown among the Lamar Valley, Pelican Valley, and Mary Mountain herds until the 1969 moratorium. Figure 2 also

shows the breakdown by individual herd of the Park's culling reductions. It is clear from the figure that the proportion of each herd culled has not been constant in the past.

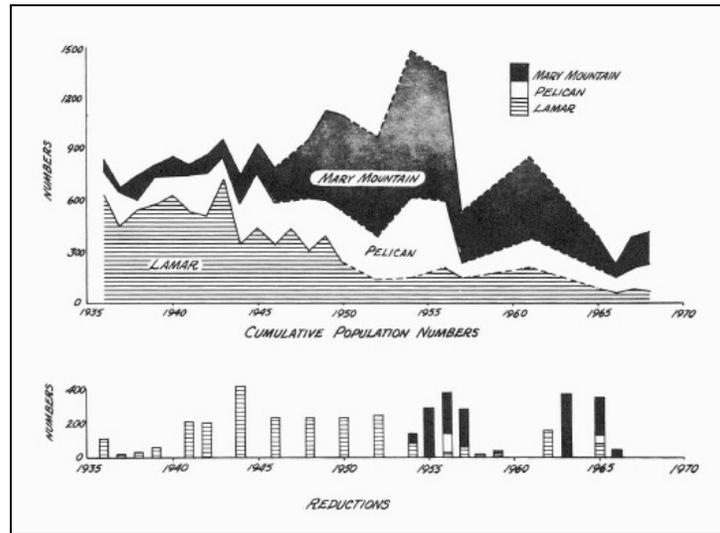


Figure 2: Yellowstone Bison Population Trends 1936-1968. From Meagher, 1973 (page 66).

Following the Park's moratorium on culling, bison numbers increased. The total population has fluctuated from about 2,100 to 4,800 over the last 25 years (Figure 3).

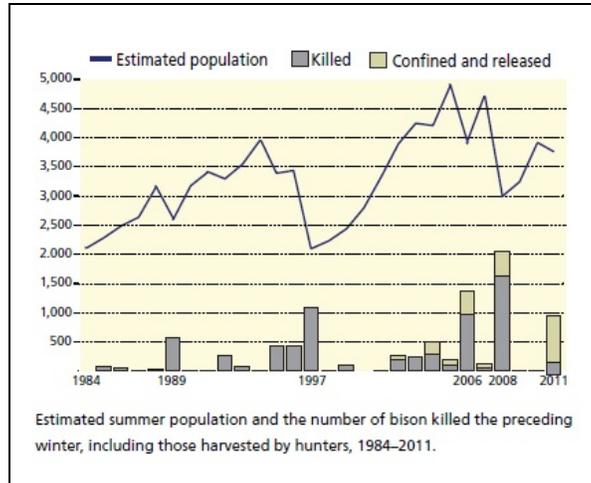


Figure 3: Yellowstone Bison Population Trends 1984-2011. From Yellowstone Center for Resources, 2011 (page 11).

As we reviewed above (pages 15-20) bison move in and out of the Park after winter forage. Once outside the Park, the bison are also outside of Park Service jurisdiction and may be hunted. The fluctuations in overall numbers (Figure 2) clearly reflect the killing (culling and hunting) that is occurring inside and outside the park boundary under the auspices of the IBMP. Under the IBMP, 3,207 bison were culled from 2000-2010.

Halbert *et al.*, 2012 confirmed that the culling occurring near the Park boundary is still having differential impacts on individual herds. Based on 1996-1997 counts, they estimated that culling of bison removed 57% of the entire Northern subpopulation compared to 20% of the Central subpopulation (Halbert *et al.*, 2012 p. 9). The different rate of loss between the subpopulations has significant implications for Yellowstone bison conservation because IBMP culling is based on overall population numbers. The winter of 2007-2008 is recorded as the largest scale slaughter of wild plains bison since the 19th Century with over 1,716 wild buffalo killed. More than 1,000 bison were also killed during the winter of 2005-2006. The Park’s 2014 Central herd count was estimated at 1,400 bison, a sharp decline from the 3,531 bison in 2005 (Geremia *et al.*, 2011 p. 2). These culls removed more calf and female bison from the central breeding herd which, if continued over time, could result in unintended consequences on the demography of Yellowstone bison (White *et al.* 2011). Pringle (2011) has also raised concerns that culling migratory bison could reduce the overall health and resilience of the Yellowstone bison by favoring less migratory bison, which may also select for a mitochondrial gene defect that decreases their fitness for escaping predators and tolerating the cold. The continued practice of culling bison without regard to 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 (Halbert *et al.*, 2012 p. 9).

The most recent count estimates released by the Park Service (based on aerial surveys) and cull data are:

Year	Total	Northern	Central	Calves	Killed*
2011	3700	2300	1400	583	33
2012	4230	2600	1600	600	254
2013	4600	3200	1400	700	653
2014	4900	3500	1400	740	

*Culls occur in the winter, surveys are conducted in summer (June).

Table 3: Recent Aerial Counts of Yellowstone Bison.

Between 2011 and 2014 the Northern Range bison increased by 1,200 (i.e. an increase of 52% since 2011) while the Central Range population stayed the same. This suggests that culling continues to have a differential effect on the Yellowstone bison subpopulations.

Individual herds or clusters should have an effective population size of 1,000 (census number of 2,000-3,000) to avoid inbreeding depression and maintain genetic variation (Hedrick, 2009 p. 419). “Effective population sizes” differ from actual census counts because factors such as unequal sex ratios, differential reproductive success, overlapping generations, and non-random mating result in the “effective” population size always being less than the census size. For bison, estimates of the ratio of effective population size to the census population size vary from 0.09 to 0.42. The effective population sizes for the two or three Yellowstone bison subpopulations are unknown, and a through population viability analysis to determine the appropriate effective population size for the long-term sustainability of the subpopulations has not been conducted (Gates

et al., 2005 p. 123; Halbert *et al.*, 2012 p. 9). However, the size of the Northern range herd is marginal and that of the Central range herd is clearly below an effective population size of 1,000. The Northern range herd count also includes the Pelican Valley bison. Pelican Valley was the location of the original remnant wild herd and these bison may form a third distinctive herd (Meagher, 1974 p. 26; Halbert *et al.*, 2012 p. 8). Thus, the biologically significant Yellowstone bison sub-populations are below viability.

The Yellowstone Bison Are a Distinct Population Segment of Plains Bison

The Yellowstone bison are the only population of plains bison that has persisted *in situ* within the species' historic and ecological range in the United States (Halbert, 2003; Freese *et al.*, 2007; Sanderson *et al.*, 2008; Hedrick, 2009). All other bison in the United States are reconstituted herds and are confined with fencing, or otherwise range restricted (USFWS, 2007). The Yellowstone bison are the only major conservation herd in the United States that shows no evidence of cattle-gene introgression (see above). The Yellowstone population is one of only a few "occupying extensive native landscapes where human influence is minimal and a full suite of natural limiting factors is present" (Gates *et al.*, 2010). The Yellowstone bison uniquely includes two genetically distinct subpopulations that show longitudinal differences in migration patterns (Halbert *et al.*, 2012 p. 9).

The extirpation of the unique Yellowstone bison would represent the complete loss of wild bison from the last stronghold of their historic and ecological range, loss of unique ecological adaptations to the local environment, and the loss of valuable and unique genetic qualities.

The ESA provides for listing any "species" as threatened or endangered by the Secretary on his own initiative or in response to a petition by an interested person. 16 U.S.C. §§ 1533(a)(1), 1533(a)(3)(A). "The term 'species' includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." 16 U.S.C. § 1532(16). The addition of distinct population segment ("DPS") to the definition of species allows the Service to list smaller entities than entire species or subspecies, where a segment may be imperiled though the entire species or subspecies is not.

In 1996, the Service adopted a DPS Policy to implement that statutory provision, which sets forth three elements to consider in identifying and deciding whether to list a DPS: 1) the **discreteness** of the population segment in relation to the remainder of the species to which it belongs; 2) the **significance** of the population segment to the species to which it belongs; and 3) the population segment's **conservation status** in relation to the Act's standards for listing (i.e., is the population segment, when treated as if it were a species, endangered or threatened?).

A population must be **both** discrete and significant to qualify as a DPS. Nat'l Ass'n of Home Builders v. Norton, 340 F.3d 835, 842 (9th Cir. 2003). Northwest Ecosystem Alliance, 475 F.3d at 1142. "The purpose of the discreteness standard is to ensure that a DPS is adequately defined and described, allowing for the effective administration of the ESA. This standard distinguishes a population from other members of its species, but does not require absolute separation." National Ass'n of Home Builders v. Norton, 340 F.3d 835, 842 (9th Cir. 2003); W. Watersheds Project v. Hall, CV 06-0073-S-EJL, 2007 WL 2790404 (D. Idaho Sept. 24, 2007) aff'd, 338 F. App'x 606 (9th Cir. 2009).

In 2007, the USFWS determined that there is substantial information indicating that the Yellowstone National Park bison meet the criteria of discreteness and significance under the service's policy on distinct vertebrate population segments (USFWS, 2007). The Service based this determination on information showing that the Yellowstone National Park bison population is geographically separated from other bison herds because of physical distance and barriers and thus meets the criterion of discreteness.

In 2007, the Service also recognized that the absence of cattle-gene introgression within the Yellowstone National Park bison populations may meet the criterion for significance for two reasons. First, loss of this unique population would result in a significant gap in the range of the plains bison because it is the only significant herd without cattle-gene introgression. Second, because maintenance of genetic diversity is an important long-term goal for management of species populations and this population is the only substantial bison population without cattle-gene introgression its survival is significant to the survival of the entire species.

In 2011, the Service backtracked on its finding that the Yellowstone Bison met the discreteness standard by stating that "despite geographic separation, the Yellowstone herd is essentially part of one metapopulation and is not markedly separate from other Herds" (USFWS, 2011). They supported this conclusion with claims that the Yellowstone herd was supplemented by bison from Texas in 1902, that the population is heavily managed and thus not wild, and that bison from the Yellowstone herd have been used to stock other populations. As we explain below, the 2011 conclusion is erroneous and the Yellowstone bison population clearly meets the discreteness criterion.

The Yellowstone Bison Meet the Criteria for Discreteness

According to FWS' DPS Policy, a population segment of a vertebrate species may be considered discrete if it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. 61 FR 4725.

Physical and Geographic Isolation

With the exception of the Yellowstone bison herds, all other plains bison herds have been created solely by human intervention. Yellowstone bison are physically isolated from any other public or private bison populations (USDI/USDA, 2000; Halbert, 2003; Gardipee, 2007) and have been so for about a century. Bison from other populations have not been introduced to the Yellowstone bison population since 18 bison cows from the Pablo-Allard herd in Montana and 3 bison bulls from the Charles Goodnight herd were moved to the area in 1902. Sometime after 1915, descendants of these introduced plains bison mingled with the native bison at Yellowstone (Meagher, 1973 p. 26). The extant Yellowstone bison include some 40% of the original wild bison strain (Meagher, 1973 p. 29; Wilson and Strobeck, 1999 p. 484).

Trans-jurisdictional management of bison exiting Yellowstone National Park includes capture, slaughter, and hazing back into the park boundaries. Thus, trans-jurisdictional management actions prevent the migration of Yellowstone to current winter ranges, recolonization of historic seasonal ranges outside the park, and immigration into other bison populations. The presence of brucellosis among bison and elk in the greater Yellowstone area currently limits management agencies from allowing the introduction of bison from any populations (USDI/USDA, 2000).

The Jackson bison herd at the southern end of the Greater Yellowstone Ecosystem is the only bison population in close proximity to the Yellowstone bison. However, there is no evidence of any migration of bison from the Jackson bison herd that congregates in two areas (Antelope Flats and Wolf Ridge Road) within Grand Teton National Park during the rut to Yellowstone (Halbert, 2003; Gardipee, 2007; USDI/USDA, 2007).

On rare occasions, bison from Yellowstone National Park have been known to move south and join the Jackson bison herd in the Grand Teton National Park (Gates *et al.* 2005, p. 93). In a footnote, they report, “In winter 1995/96, 3 bulls from the Hayden Valley and wintered in the vicinity of Polecat Creek; they were captured and radio collared. For several years after that they returned each year to Hayden Valley during the rut then back to the Jackson Lake area to spend the winter. During the harsh winter of 1996-97 a mixed group of 3 cows and 3 juveniles followed the road from YNP through the south gate and spent winter in the same area as the 3 bulls. Then they moved south and joined the Jackson herd; this mixed group did not return to YNP. Source: Interview with Steven Cain, 11 August 2004.” There have been other reports of isolated bulls moving south from Yellowstone.⁶

Thus, there is substantial evidence that Yellowstone bison are geographically isolated from all other bison populations. The USFWS currently manages its bison herds to minimize genetic loss across all Refuges with bison within the National Wildlife Refuge System (Jones and Roffe, 2007 p. 9). The Service aspires to treat its bison as a single “meta-population” of herds because the small size of most of its herds does not reach the “minimal genetically viable population level of 1000 to 1500” (Jones and Roffe, 2007 p. 8-9). However, the fact that the Service is attempting to preserve the genetic integrity of its herds by managing its herds as a single population is irrelevant to the wild Yellowstone bison situation that is not part of its management scheme. And it would seem fortuitous too that the Yellowstone bison are not part of the USFWS’s managed bison population since almost all the larger National Wildlife Refuge herds suffer cattle-gene introgression.

The Yellowstone bison are not just geographically isolated from other bison but have been physically isolated from other bison populations for over 100 years. While many of the other conservation herds have been stocked with bison culled or selected

⁶ For example, on Saturday, March 13, 2004 Associated Press released a story on “Boris the bison” that reportedly travelled the 200 miles round-trip from Hayden Valley to Jackson Hole and back on an annual basis. Online at: <http://www.freerepublic.com/focus/f-news/1097164/posts>

from the Yellowstone herds, there has been no introduction of bison to Yellowstone since 1902. There is no evidence that any of the herds stocked maintain the high levels of genetic variation observed among Yellowstone bison compared to other populations (Wilson and Strobeck, 1999; Halbert and Derr, 2008).

The Yellowstone bison are more than a physically isolated “population” but are an isolated meta-population of two to three genetically distinct herds (Halbert *et al.*, 2012). The presence of these subpopulations contributes to the high levels of genetic variation observed among Yellowstone bison compared to other populations (Halbert *et al.*, 2012 p. 9). The presence of natural population substructure has important implications for the long-term evolution of these populations and the plains bison itself.

Yellowstone National Park is the only area in the lower 48 States where bison have existed in a wild state since prehistoric times (Gates *et al.*, 2005, p. 245). Unlike many other species that have gone through major population bottlenecks through the action of humankind the geographic isolation of the original wild bison at Yellowstone has ensured that bison have remained *in situ* in this one region. That same geographic isolation persists to this day. Clearly, the Yellowstone bison are isolated from other members of the taxon.

Physiological Isolation

Maintenance of genetic integrity and diversity is an important long-term goal for management of species populations. Hybridization between endangered species and more common species is a significant problem in conservation biology because it may result in extinction or loss of adaptation (Derr *et al.*, 2012). As we reviewed above, the Yellowstone bison are the only major Federal herd that does not display genetic introgression with cattle (see pages 11-14).

In its 2011 90-Day Finding on a Petition To List the Wild Plains Bison the Service stated, “the frequent interchange between herds that has occurred since the late 1800s has provided a physical connectivity between herds, and has maintained genetic homogeneity.” 76 FR 10309. Fortunately for the persistence of plains bison as a genetically intact species, this is not the case for the Yellowstone bison. Although some Yellowstone bison have been exported to found or supplement other bison populations there have been no introductions to the Yellowstone herd for over 100 years. The very lack of physical connection to other bison has in fact ensured the survival of the only genetically unpolluted, free roaming wild bison herd in the United States.

Yellowstone bison also possess genetic characteristics that distinguish them from other public and private bison populations. Halbert (2003) estimated F_{ST} , a measure of genetic differentiation which ranges from 0.00 (no genetic differences) to 1.00 (complete genetic differentiation) for comparisons among 9 federal bison herds (including Yellowstone bison) and one state bison herd. Population comparisons with an F_{ST} value of > 0.05 provide evidence of genetic distinction. The F_{ST} estimates among bison sampled from Yellowstone, eight other federal bison herds and one state bison herd range

from 0.0855 (Wind Cave National Park) to 0.2347 (Texas State Bison Herd) (Halbert, 2003). The closest genetic neighbor of Yellowstone bison are Wind Cave National Park bison ($D_S = 0.188$, $(\delta\mu)^2 = 0.375$) (Halbert, 2003 p. 58). The Wind Cave National Park bison population was originally founded with fourteen bison donated from the New York Zoological Society and six Yellowstone bison introduced in 1916 (Halbert, 2003 p. 16). Evidently, the Yellowstone bison used to supplement the Wind Cave National Park herd markedly influenced the genetic constitution of the herd. Unfortunately, the Zoological Society bison evidently contributed cattle-genes to the herd; 74 of 102 Wind Cave National Park bison tested were introgressed (Schnabel, 2011 p. 11). Over the last 64 years, the Yellowstone bison have diverged into at least two distinct subpopulations (Halbert *et al.*, 2012 p. 8). Thus, although the Wind Cave National Park herd may share some genetic characteristics in common with Yellowstone bison, they are descended only in part from Yellowstone bison, after 100 years have diverged to an extent, and are introgressed with cattle-genes.

The Yellowstone Bison Meet the Criteria for Significance

No other plains bison population is as important to survival of the species as the Yellowstone bison. Yellowstone bison are the only surviving natural occurrence of wild bison that was never completely extirpated from its historic and ecological range. The Yellowstone bison are the only major conservation herd in the United States that shows no evidence of cattle-gene introgression. The Yellowstone bison are the only remnant population that has remained in a wild state since prehistoric times and, therefore, is important to the management of bison genetic diversity. The extirpation of the Yellowstone bison would represent the complete loss of genetically-intact, wild bison from the last stronghold of their historic and ecological range, loss of unique ecological adaptations to the local environment, and the loss of other valuable and unique genetic qualities.

The significance of a DPS may be determined by consideration of (but is not limited to) the following factors: (1). Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon, (2). Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon; (3). Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or (4). Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

Persistence of the Discrete Population Segment in an Ecological Setting Unusual or Unique for the Taxon

The portion of the northern Greater Yellowstone Ecosystem occupied by Yellowstone bison is the only place where natural patterns of population structure and gene flow in plains bison can be observed (Sanderson *et al.*, 2008; Halbert *et al.*, 2012). The unique landscape and habitats of Yellowstone National Park have been formed

though the forces of extensive volcanism, glaciations, and erosion over millions of years (Meagher and Houston, 1998). The active caldera and associated magma layers provide a source of heat for an unusually high concentration of geothermal features (geysers, hot springs, mud pots, and fumaroles). These features influence bison habitat and bison behavior by providing thermal refugia within the park. Yellowstone's central range bison utilize a significant proportion of geothermal area within their winter ranges (from 5 % in Pelican Valley to 14% in Mary Mountain), and movement corridors (5.2 to 9.2 %) (Gates *et al.*, 2005). The inclusion of geothermal areas as a significant portion of habitat use represents an unusual ecological adaptation unique to the Yellowstone bison population.

Loss of the Discrete Population Segment Would Result in a Significant Gap in the Range of a Taxon

The Yellowstone bison are the single largest free-roaming bison population. Arguably, they are in fact the only wild bison population in the United States since all other conservation herds exhibit varying degrees of introgression with cattle-genes. The extirpation of the Yellowstone bison would represent the complete loss of genetically-intact, wild bison from the last stronghold of their historic and ecological range, loss of unique ecological adaptations to the local environment, and the loss of other valuable and unique genetic qualities.

The Yellowstone bison represent a primary resource for plains bison restoration efforts because they exhibit a high level of genetic diversity relative to other bison populations, and are the only wild population of plains bison with no evidence of hybridization with cattle (Ward *et al.*, 1999; Ward, 2000; Freese *et al.*, 2007; Halbert and Derr, 2007; Sanderson *et al.*, 2008; Schnabel, 2011). Loss of the genetic diversity, evolutionary potential, and disruption of genetic population substructure that is currently represented within the Yellowstone bison would result in the loss of the most significant genetic resource for the ecological restoration of bison (Freese *et al.*, 2007; Halbert and Derr, 2008; Sanderson *et al.*, 2008; Hedrick, 2009).

The Discrete Population Segment Represents the Only Surviving Natural Occurrence of a Taxon that May Be More Abundant Elsewhere as an Introduced Population Outside its Historic Range

Yellowstone National Park is the only area in the lower 48 States where bison have existed in a wild state since prehistoric times (Gates *et al.*, 2005, p. 245). Unlike many other species that have gone through major population bottlenecks through the action of humankind the geographic isolation of the original wild bison at Yellowstone has ensured that bison have remained *in situ* in this one region. Bison from other populations have not been introduced to the Yellowstone bison population since 18 bison cows from the Pablo-Allard herd in Montana and 3 bison bulls from the Charles Goodnight herd were moved to the area in 1902. Sometime after 1915, descendants of these introduced plains bison mingled with the native bison at Yellowstone (Meagher, 1973 p. 26). The extant Yellowstone bison include some 40% of the original wild bison strain (Meagher, 1973 p. 29; Wilson and Strobeck, 1999 p. 484). The Yellowstone bison

are thus the only bison population in the United States that represents a surviving natural occurrence of the taxon.

There are large numbers of re-introduced bison elsewhere in the historic range. However these are either domestic herds, or conservation herds with evidence of cattle-gene introgression. The only other bison herd that may lack cattle-gene introgression is the small Henry Mountain Herd which is an extralimital population founded with 18 bison removed from Yellowstone in 1948.

The Discrete Population Segment Differs Markedly From Other Populations of the Species in its Genetic Characteristics

As reviewed in more detail above, the Yellowstone bison exhibit a high level of genetic diversity relative to other bison populations (Ward *et al.*, 1999; Ward, 2000; Freese *et al.*, 2007; Halbert and Derr, 2007; Sanderson *et al.*, 2008; Halbert *et al.*, 2012). They are the only significant, wild population of plains bison with no evidence of hybridization with cattle (Ward *et al.*, 1999; Halbert, 2003; Halbert and Derr, 2007; Schnabel, 2011). The Yellowstone bison are the only remnant population that has remained in a wild state since prehistoric times and, therefore, is important to the management of bison genetic diversity. Halbert (2003, pp. 44-45) found only four Federal herds that were sufficiently unique to contribute significantly to overall bison genetic diversity. The Yellowstone bison are the only one of Halbert's four Federal herds that does not show evidence of cattle-gene introgression.

Wilson and Strobeck (1999) found an average of 5.36 alleles per locus and heterozygosity of 54.2% among 33 Yellowstone bison included in their study. Halbert (2003) genotyped 488 Yellowstone bison with 54 microsatellite loci and found an average of 6.48 alleles per locus, and observed and expected heterozygosities of 61.5% and 62.7%, respectively. Halbert (2003) used samples collected from bison that were captured and removed from winter ranges inside Yellowstone National Park near park boundaries. Analysis of genotypes at 49 microsatellite loci using the STRUCTURE program (Pritchard *et al.*, 2000) to test the probability of population substructure using a clustering algorithm for multilocus genotypes suggested the presence of three subpopulations within the Yellowstone bison (Halbert, 2003). Gardipee (2007) found evidence of genetic population substructure among Yellowstone bison using mitochondrial DNA extracted from fecal samples collected within breeding areas located within Yellowstone National Park during the rut season.

Gardipee's (2007) also found evidence of female philopatry to breeding areas. This behavior has not been documented through genetic evidence in any other wild bison population and may be unique to the Yellowstone bison. Female philopatry among Yellowstone bison contributes to genetic population structure, and may also result in the conservation of unique genetic qualities and local adaptations within each breeding herd.

The Discrete Population Segment Differs Markedly From Other Populations of the Species in its Behavioral Characteristics

The Yellowstone bison congregate in three geographically distinct breeding areas during the mid-summer rut (Meagher 1973 p. 76; Taper *et al.*, 2000; Meagher *et al.*, 2002; Gardipee, 2007; Geremia *et al.*, 2009). Females exhibit philopatry to breeding areas (Gardipee, 2007), a behavior that has not been documented in any other wild bison population and may be unique to the Yellowstone bison. Bison rutting in the Lamar Valley and Mirror Plateau are generally termed as the Northern range herd. Northern range bison move between the Gardiner Basin (elev. 5,900 feet), the Lamar Valley floor, up to the Cache Calfee ridge, and the Mirror Plateau (elev. 8,200 feet). The central range bison herd ranges from Pelican Valley, Hayden Valley, Mary Mountain (elev. 8,200 feet), Firehole river basin, the Madison Junction, and to their traditional winter ranges located outside the west and north entrances of Yellowstone National Park. Cannon (2007 and 2008) found archeological evidence that bison ranged among elevations over 9,900 feet within the Greater Yellowstone Ecosystem. Therefore, the Yellowstone bison are the only free-roaming, wild population known to have continuously ranged across high altitudinal gradients, which represents the conservation of a unique ecological adaptation for American bison.

Halbert *et al.* (2012) demonstrated the existence of two genetically distinct subpopulations of bison within Yellowstone National Park that showed longitudinal differences in migration patterns. The bison moving to the park boundary in the vicinity of West Yellowstone are consistently from the Central subpopulation, whereas those moving to the park boundary in the vicinity of Gardiner may originate from either the Central or Northern subpopulation. This differential migratory behavior has been seen in no other bison herds.

Threats

Under Section 4 of the Endangered Species Act the U.S. Fish and Wildlife Services (USFWS) considers five factors in determining whether a species qualifies for listing as either Endangered or Threatened, according to the degree of threat. These factors are: (A) The 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) The inadequacy of existing regulatory mechanisms; or (E) Other natural or manmade factors affecting its continued existence. If the Service finds that, based on the best available science, one or more of these factors imperil the survival of the species, they are required list. Here more than one factor is implicated.

A wide variety of threats affect bison, most of which are anthropogenic in origin. The IUCN cites a number of serious threats to the conservation of plains bison such as: habitat loss; genetic manipulation of commercial bison for market traits; small population effects in most conservation herds; lack of exposure to a full range of natural limiting factors; cattle gene introgression; loss of genetic non-exchangeability through hybridization between bison subspecies; and the threat of depopulation as a management response to infection of some wild populations hosting reportable cattle diseases (IUCN, 2014). In particular, the IUCN cites culling of bison populations to prevent spread of bovine diseases as a major threat to their conservation (IUCN, 2014). Yellowstone bison are threatened by all of the threats identified by the IUCN as well as other threats presented in this petition. The Yellowstone bison merit protection under the ESA based on each of the five listing factors as described below.

The Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range.

Range Curtailment

The Yellowstone bison are the only identified U.S. bison population herd that is sufficiently unique to contribute significantly to overall bison genetic diversity (Halbert, 2003, pp. 44-45) that is free of cattle-gene introgression. As such it is the only free-roaming remnant of the once immense plains bison herds that ranged across the continent. Historically, within the northern Greater Yellowstone Ecosystem bison ranged across some 20,000 km² in the headwaters of the Yellowstone and Madison rivers (Meagher, 1973 p. 13-14; Gates *et al.*, 2005; Schullery and Whittlesey, 2006; Plumb *et al.*, 2009). Figure 1 on page 11 shows the historic and current range of Yellowstone bison. The current occupied range is approximately 3,175 km² (Plumb *et al.*, 2009 p. 2379) or about 16% of the historical range.

Outside the National Park boundary Yellowstone bison have only limited, temporary access to some 300 km² acres of habitat on federal lands in the Gardiner Basin of Montana (Montana Fish, Wildlife and Parks, 2012). Disease risk-management operations which occur under the guidance of the IBMP prevent the Yellowstone bison

from permanently accessing a significant portion of their winter ranges located outside park boundaries, and preclude natural re-colonization of historic range (Freese *et al.*, 2007; Plumb *et al.*, 2009). These operations, which include hazing, capture, and slaughter, effectively exclude Yellowstone bison from a significant portion of their range.

Livestock Grazing

Livestock impacts have been implicated in the initial decline in plains bison populations that followed settlement due to the spread of exotic diseases (e.g., tuberculosis and brucellosis from cattle), and competition for grazing and water sources with growing populations of cattle, horses, and sheep (Flores, 1991 p. 481; Halbert *et al.*, 2007 p. 23; Halbert *et al.*, 2012 p. 1). For the same reasons, livestock grazing on public lands that are bison habitat outside Yellowstone National Park continue to threaten the Yellowstone bison.

First, livestock and livestock grazing management directly and indirectly impact bison and their habitat. Livestock directly affect vegetation structure, alter plant communities, alter soil characteristics, and impact other habitat elements (e.g. Fleischner, 2010). Public lands livestock grazing requires developments such as fencing, cattle-guards and roads to control livestock movements. These range developments impair bison movements and distribution. The proximity of livestock poses a significant threat of disease transmission to free-roaming bison.

Second, continued livestock grazing on bison habitat on public lands promotes the perceived need for disease risk-management operations such as those occurring under the guidance of the IBMP. Unfortunately, rather than managing domestic cattle to avoid bison habitat, the agencies instead manage bison out of its habitat all to benefit powerful livestock industry interests.

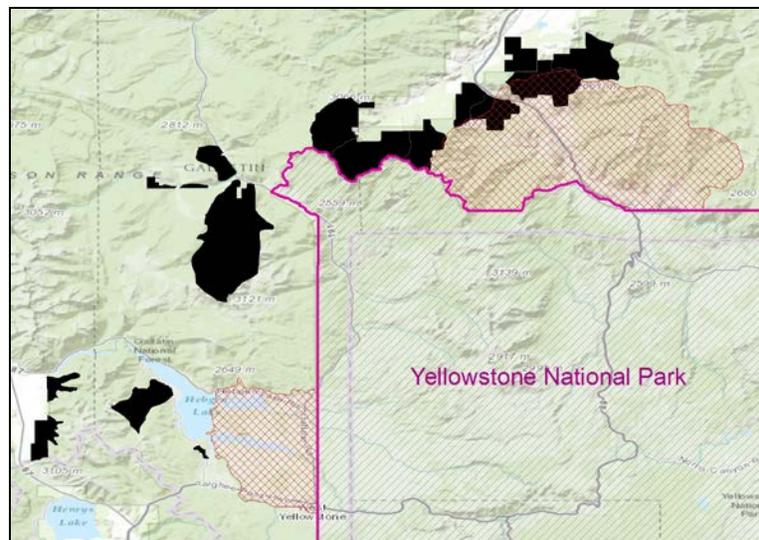


Figure 4: Forest Service and BLM Livestock Grazing Allotments in Yellowstone Bison Habitat. Active allotments are shown in black. IBMP north and west management zones are shown with red hatching.

Figure 4 shows active livestock allotments on public lands around the northwest corner of Yellowstone National Park in the immediate vicinity of the northern and western bison use areas. Although the Forest Service has allowed the relinquishment of some grazing privileges and closed some allotments to livestock grazing, bison are not allowed free-use of those closed allotments.

Livestock grazing is also permitted on public lands on Shoshone National Forest in large portions of the Absaroka Management Area and on adjacent Bureau of Land Management lands to the east.

Livestock are grazed on private lands within the north and west bison use areas in Montana. Of particular concern is grazing by domestic sheep which may act as reservoirs for malignant catarrhal fever (see below). Bighorn sheep have been observed comingling with domestic sheep on private land between the Yellowstone River and US 89 west of the junction with Papesh Road and about 0.5 miles from the Yellowstone National Park boundary raising concerns of disease risk for the bighorn population⁷. The IBMP Annual Report for 2013 notes that 3 bison bulls comingled with domestic sheep at this same location (IBMP Annual Report 2013 p. 58). Similar concerns of risk of disease from domestic sheep grazed in the bison use area extend to the Yellowstone bison.

Development and Infrastructure

Most of the original range of plains bison has changed to competing land uses including cultivation, cattle ranching, commercial bison ranching, natural resource extraction, and urban expansion (Boyd and Gates, 2006 p. 16). This is true for the Yellowstone bison habitat outside the Park. Extensive amounts of land within the northern Greater Yellowstone Ecosystem are unprotected and threatened by land use intensification, policies such as zoning are needed that can affect large areas including regionally coordinated growth management efforts to preserve biodiversity by redirecting future development (Gude *et al.*, 2007 p. 1017). The same authors conclude, “Future habitat conversion to exurban development outside the region’s nature reserves is likely to impact wildlife populations within the reserves.”

Extensive residential housing development has occurred in the West Yellowstone and Gardiner areas over the last decade. In the West Yellowstone area the lower and upper Beartrap subdivisions (near the junction of highways 191 and 287), Horse Butte Village (on the Horse Butte Peninsula), and the corridor along the north shore of Hebgen Lake, including the Red Canyon area have all seen increased numbers of residential houses and subdivisions built in the past 10 years. In the Gardiner Basin, the Church Universal and Triumphant has constructed many structures on their extensive properties, including housing developments, meeting houses, and bomb shelters and was responsible for a major diesel fuel spill in the early 1990s⁸.

⁷ See: http://www.bozemandailychronicle.com/news/wildlife/article_67966a20-5baf-11e3-a220-0019bb2963f4.html

⁸ See: <http://articles.latimes.com/keyword/church-universal-and-triumphant>

The current bison capture and quarantine facilities immediately to the north of Yellowstone National Park and on the east side of highway 89 pose a threat to wild bison because of their extensive size. The facilities include a 400-acre double-fenced property that is dissected into three large pastures (50 to 100 acres) and three smaller (1-4 acres) assembly pens, and two additional 30-acre pastures at the Slip and Slide Ranch.

Invasive Species

Olliff *et al.*, 2001 provide a useful review of nonnative invasive plants in Yellowstone National Park and the surrounding area. Nonnative plants negatively impact ecosystem structure and function by altering soil properties and related processes (Lacey *et al.*, 1989), plant community dynamics and related disturbance regimes (D'Antonio and Vitousek, 1992), and distribution, foraging activity, and abundance of native ungulates (Trammell and Butler, 1995; Thompson, 1996). Geothermal habitats unique to Yellowstone and important as winter refugia for bison have been altered by exotic plants (Olliff *et al.*, 2001 p. 347).

Exotic plants are substantially impacting Yellowstone National Park's natural resources with particularly severe infestations in bison winter range in the Lamar Valley (Olliff *et al.*, 2001; Chong *et al.*, 2011) where ranch management practices including seeding and tilling occurred (Meagher, 1973 p. 12). Olliff *et al.*, 2001 documented some 185 exotic plant species in Yellowstone National Park and the latest report has increased that number to 219 (Yellowstone Center for Resources, 2013). The Park's emphasis is on eradicating small, new infestations of highly invasive species such as sulfur cinquefoil (*Potentilla recta* L.) and leafy spurge (*Euphorbia esula* L.). Control efforts focus on about 30 priority species, such as spotted knapweed (*Centaurea maculosa* Lam.), oxeye daisy (*Chrysanthemum leucanthemum* L.), and hoary cress (*Cardaria draba* [L.] Desv.). Most of the occurrences are in the lower elevation bison winter habitats.

Most of these noxious weeds occur in the bison winter habitat off the Park. Leafy spurge, *Euphorbia esula* has been shown to significantly impact forage value for bison in Theodore Roosevelt National Park in North Dakota. Bison and deer use of *E. esula*-infested areas was 83 and 70% less than noninfested sites, respectively (Trammell and Butler, 1995; DiTomaso, 2000). Leafy spurge is spreading actively in Paradise Valley north of the Park (Yellowstone Resources Handbook, 2012, p. 74). Securing appropriate funds to support the Park's weed management program has been challenging (Olliff *et al.*, 2001 p. 350).

Cheatgrass, *Bromus tectorum*, which thrives in disturbed areas and is an early colonizer that out-competes native species in establishment (Knapp, 1996), occurs through the region including the Park (Chong *et al.*, 2011). Vectors identified to spread cheatgrass propagules, include livestock, machinery and vehicles.⁹ Livestock are effective agents in dispersing exotic species and cattle may disperse more than an order of magnitude more seeds than elk and deer per animal (Bartuszevige and Endress, 2008).

⁹ <http://www.fs.fed.us/database/feis/plants/graminoid/brotec/all.html>

Cattle break soil crusts that may reduce the ability of invasive species to become established.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes.

Hunting

In order to benefit the livestock industry, Yellowstone bison using winter ranges at Park boundaries are subject to disease risk management operations conducted under the guidance of current IBMP. These actions, driven by commercial interests perturb the current population substructure (Halbert, 2003; Gardipee, 2007; Freese *et al.*, 2007; Halbert *et al.*, 2012). Disproportionate culling of genetically distinct breeding herds under these management operations threatens the genetic viability of the Yellowstone bison and could result in the loss of unique genetic qualities, maternal lineages, and the loss of overall genetic diversity (Halbert, 2003; Gardipee, 2007; Halbert *et al.*, 2012). Pringle (2011) has also raised concerns that culling migratory bison could reduce the overall health and resilience of the Yellowstone bison by favoring less migratory bison, which may also select for a mitochondrial gene defect that decreases their fitness for escaping predators and tolerating the cold. Since 2005, hunting has been allowed on bison using habitat outside the National Park.

According to publically-posted state records, 790 Yellowstone bison have been killed since the State of Montana allowed bison hunting in 2005.¹⁰ This included 343 in the Gardiner area and 275 at West Yellowstone. Of the 790 total, sex was recorded for 465 animals - 305 bulls and 160 cows. Thus, cows account for some 34% of the kill. However, this was not uniform between management zones. In the Gardiner area, 195 bulls and 50 cows were reported; i.e. cows were some 20% of the total kill. In contrast, for the West Yellowstone area, an even number of cows (110) and bulls (110) bulls were reported killed. Small numbers of Yellowstone bison have also be killed by hunting in Wyoming in Hunt Area 1 including 12 in 1995-1996 and 16 in 1996-1997 with an additional five female bison shot by Wyoming Game and Fish Department on the North Fork of the Shoshone River in 1994-95, prior to a hunting season being in place (WGFD, 2008 p. 12).

The agencies have made no attempt to determine the herd origin for these hunt killed animals. However, since the Northern range bison tend to leave the Park at Gardiner whereas the Central range bison migrate through both portals, the smaller Central range bison herd clearly bears the brunt of the hunting take. This contributes to the disproportionate culling of genetically distinct breeding herds that is currently fostered by IBMP management operations. This threatens the genetic viability of the Yellowstone bison and could result in the loss of unique genetic qualities, maternal lineages, and the loss of overall genetic diversity (Halbert, 2003; Gardipee, 2007; Halbert *et al.*, 2012).

¹⁰ Bison Harvest Data 2005-2013. Online at: <http://fwp.mt.gov/hunting/planahunt/huntingGuides/bison/>

Disease or Predation.

Predation

Bison have few predators other than man. Grizzly bears may take small numbers of adult (Meagher, 1973 p. 71; Wyman, 2002) and young bison (Varley and Gunther, 2002). Historically, gray wolves apparently played a critical role in plains bison population dynamics, and not just as culling agents of diseased and old animals (Flores, 1991 p. 478). Gray wolves do take some bison at Yellowstone and there is evidence that predation on Yellowstone bison calves by gray wolves may be increasing (White and Garrott, 2005; Smith *et al.*, 2013). This shift by wolves toward predation on bison will be an important development to track in the future but is not considered a significant concern at this time (Smith *et al.*, 2013).

Disease

Bison are susceptible to many of the infectious diseases carried by domestic livestock (Tessaro, 1989; Hoberg *et al.*, 2008) and epidemics of livestock disease have been implicated in the post-settlement, historic demise of plains bison (Flores, 1991). Surveys have detected the same bacterial, viral, and macroparasites among farmed bison that are usually found in other domestic livestock such as cattle and sheep including bovine tuberculosis, Johne's disease (paratuberculosis), yersiniosis, leptospirosis, brucellosis, anthrax, salmonellosis, colibacillosis, tetanus, blackleg, malignant oedema, pulpy kidney, bluetongue, bovine viral diarrhoea virus, Parainfluenza 3, bovine respiratory syncytial virus, and unclassified coronaviruses (Mackintosh *et al.*, 2002; Haigh *et al.* 2002).

The American Bison Specialist Group recognizes nine federally listed diseases of concern for bison conservation in North America: anaplasmosis, anthrax, bluetongue, bovine spongiform encephalopathy, bovine brucellosis, bovine tuberculosis, bovine viral diarrhoea, Johne's disease, and malignant catarrhal fever (sheep associated) (Gates *et al.*, 2010 p. 32). Of these, hemorrhagic septicemia (outbreaks have occurred in the past), malignant catarrhal fever (outbreaks of which have occurred in the region), and bovine brucellosis (with which Yellowstone bison suffer chronic infection) pose the most immediate threats to Yellowstone bison.

Hemorrhagic Septicemia

Hemorrhagic septicemia is an acute, highly fatal form of pasteurellosis that affects cattle and bison. Hemorrhagic septicemia was the first contagious disease verified in bison when an outbreak occurred at Yellowstone in 1911 (Tessaro, 1989). Hemorrhagic septicemia caused considerable mortality in the introduced herd in the Lamar Valley in 1912, 1919, and 1922 (Meagher, 1973 p. 70). Losses for those years were 28, 18 and 45 bison respectively (Meagher, 1973 p. 144-145). Hemorrhagic septicemia is highly infectious and twenty-two animals died between December 3 and December 15, 1911

(Mohler and Eichhorn, 1911). Although there have been no recent reported cases from Yellowstone, an outbreak occurred at the National Bison Range in 1965-1967 (Heddleston and Wessman, 1973).

Malignant Catarrhal Fever

Malignant catarrhal fever is a viral disease syndrome primarily of ruminants, caused by a group of closely related rhadinoviruses (Li *et al.*, 2003). Malignant catarrhal fever is the most important viral disease found among bison and presents the greatest threat to their conservation (Schultheiss *et al.*, 2000; Haigh *et al.*, 2002; Li *et al.*, 2006). Bison are extremely susceptible, and outbreaks have resulted in mortality rates as high as 51 to 90%. Domestic sheep are reservoirs for malignant catarrhal fever virus and almost all domestic sheep tested in Idaho, Montana and Wyoming tested positive for the virus (Li *et al.*, 1995). Aerosol transmission can occur (Li *et al.*, 2006). Malignant catarrhal fever has been documented in bison herds one mile (Schultheiss *et al.*, 2000) and three miles away from the closest domestic sheep Gates *et al.*, 2010 p. 33). In 2003, an outbreak of malignant catarrhal fever in ranch bison at a feedlot in southern Idaho caused 41 bison deaths in a single day with an overall 51% mortality rate (Li *et al.* 2006). An outbreak among three bison herds in Colorado during 1997-1999 resulted in mortality rates as high as 90% (Schultheiss *et al.*, 2000). Sheep ranching operations are common on public and private lands within the northern Greater Yellowstone Ecosystem. Goats are reservoirs for a malignant catarrhal fever virus that has caused outbreaks in white tailed deer (Li *et al.*, 2003). The Park County Cooperative Weed Management Area encourages the use of domestic goats and sheep herds to control leafy spurge and spotted knapweed.¹¹ The IBMP Annual Report for 2013 notes that 3 Yellowstone bison bulls commingled with domestic sheep on April 19, 2013 on private land between the Yellowstone River and US 89 west of the junction with Papesh Road about half a mile from the Yellowstone National Park boundary (IBMP Annual Report 2013 p. 58).

Brucellosis

Boyd and Gates (2006) identified brucellosis as the disease which presents the primary threat to plains bison conservation. This disease, which causes reproductive failure, was first discovered in Yellowstone bison in 1917 most likely transmitted from cattle maintained for Park employees (Meagher and Meyer, 1994). Opportunistic and systematic serological surveys of Yellowstone bison have revealed sero-prevalences varying between 20% and 70%, while bacterial cultures indicated an infection prevalence of approximately 10% (Gates *et al.*, 2010 p. 33). Demographic analysis indicates that brucellosis has a significant reproductive effect on Yellowstone bison and that the growth rate of the population could increase by 29% in the absence of brucellosis (Fuller *et al.*, 2007). However, the direct effects of the disease itself pale in comparison to the impacts of agency disease-management on the Yellowstone bison.

Brucellosis affects Yellowstone bison primarily because of the potential risk the disease poses to the livestock industry (Keiter, 1997). Bison using their habitat outside

¹¹ See <http://parkcountycwma.com/index.html>

the Park boundary could potentially transmit the disease to domestic cattle grazing on adjacent National Forest and private lands in Montana, Wyoming or Idaho. Bison dispersal and winter range use outside Yellowstone National Park is managed through culling, hunting and hazing back into the Park ostensibly to reduce the risk of brucellosis transmission to livestock (Cheville *et al.*, 1998; USDI/USDA, 2000).

This killing/hazing disease-management approach is not designed to eliminate brucellosis from Yellowstone bison. Culling of Yellowstone bison to prevent transmission to cattle has been ineffective at reducing brucellosis infection in bison (Treanor *et al.*, 2011; White *et al.*, 2011). And given the extensive spread of brucellosis through the elk population, this disease-management approach does not reduce transmission risks to cattle either. Transmission of brucellosis from bison to cattle has been demonstrated in captive studies but there are no confirmed cases of transmission in the wild (see Gates *et al.*, 2010 p. 33). In contrast, transmission from elk to cattle is well established and elk have been definitively identified in the Greater Yellowstone Area based on DNA genotyping of isolates as the source of outbreaks of brucellosis in cattle in Idaho in 1999 and Wyoming 2003 (Beja-Pereira *et al.*, 2009). Elk are also suspected to transmitted brucellosis to the Jackson bison (Cheville *et al.*, 1998).

Implementation of disease-management operations under the guidance of current IBMP includes hazing and recurrent, large-scale removals of bison at park boundaries. Under the guise of disease-management Yellowstone bison are precluded from free-access to winter habitat on public lands outside the Park by hazing. In severe winters when Yellowstone bison seek to access forage outside the Park in large numbers, culling and hunting has episodically reduced the Yellowstone bison population by 25-30% and generated concern because non-random culling of genetically-distinct subpopulations could lead to long term loss of maternal lineages, genetic diversity, and evolutionary potential (Halbert, 2003; Freese *et al.*, 2007; Halbert *et al.*, 2012). The management plan underestimated bison abundance, distribution, and migration, which contributed to larger risk management culls (total >3000 bison) than anticipated; the culls differentially affected breeding herds and altered gender structure, created reduced female cohorts, and dampened productivity (White *et al.*, 2001).

The maintenance of subpopulations of comparatively large effective size high explains the high levels of genetic variation observed among Yellowstone bison compared with other populations (Halbert *et al.*, 2012 p. 9). However triggers for winter culling are based on the overall population size. As we discussed above (pages 15-23), this leads to the disproportionate culling of subpopulations in years when bison move out of the Park in numbers and places subpopulation viabilities at risk. Halbert *et al.*, (2012) also point out an additional mechanism whereby IBMP management influences the genetic integrity of the subpopulations. When the total census is less than 3,000 bison, the IBMP calls for 125 bison that test negative for brucellosis to be held through the winter and released into the Park in the spring. Because brucellosis seronegative bison are most commonly calves, these naive bison may join the Northern subpopulation rather than return to the Central range, thus eroding the genetic distinctiveness between the 2 groups (Halbert *et al.*, 2012 p. 9)

In summary, bison are highly susceptible to diseases carried by domestic livestock. Infectious diseases directly impact the Yellowstone bison. Disease management practices do not benefit Yellowstone bison; to the contrary, they pose a significant threat to the continued persistence, genetic diversity, and the conservation of evolutionary potential of the Yellowstone bison.

Inadequacy of Existing Regulatory Mechanisms.

Regulatory mechanisms provide the necessary assurances that essential habitat needs will be addressed and that long-term habitat protections for a species are in place. For Yellowstone bison, there are no specific laws or regulations that serve to protect and preserve them as a genetically intact species or protect their habitats.

Although “One mission of the National Park Service is to preserve native wildlife species and the processes that sustain them”¹², within the boundaries of Yellowstone National Park, bison management includes hazing, capture, and culling. Under a 2000, court-mediated settlement, the Secretaries of Agriculture and Interior and the Governor of Montana signed an agreement that limits bison abundance and distribution in Montana by culling bison that venture near the Park boundaries. As discussed above, these actions by the National Park Service are resulting in differential impacts to sub-populations, and are preventing the Yellowstone bison from moving out of the Park into important winter range. This management benefits livestock grazing interests. It does not preserve the species or help the bison move into crucial winter range that can sustain them through the winter. Thus, current National Park Service management provides an inadequate regulatory mechanism to assure that essential habitat needs are addressed or the long-term genetic health of the Yellowstone bison population.

The United States Forest Service administers most of the public land that provides Yellowstone bison habitat outside the Park. Although bison are extremely rare in both Forest Service regions, are designated Near Threatened on the IUCN Red List, are a species of national interest, are the subject of great controversy, and are clearly impacted by agency actions such as the issuance of livestock grazing permits and other activities in bison habitat, neither Region 1 (which includes Yellowstone bison habitat in Montana and parts of Idaho) nor Region 2 (which includes Yellowstone bison habitat in Wyoming) consider bison to be a sensitive species or a species of conservation concern.

The situation in the states is even worse. State wildlife officials in Montana¹³ and Idaho¹⁴ have lost most of their jurisdiction over wild bison to their livestock counterparts, who are treating these bison as diseased domestic livestock (Keiter, 1997 p. 2). State livestock departments have neither the expertise nor the institutional support to manage wildlife. While state livestock departments rightly control domesticated bison these commercial bison herds make no contribution to bison conservation because of

¹² <http://www.nps.gov/yell/naturescience/bisoninfo.htm>

¹³ <http://leg.mt.gov/bills/mca/81/2/81-2-120.htm> and <http://leg.mt.gov/bills/mca/87/1/87-1-216.htm>

¹⁴ <http://legislature.idaho.gov/idstat/Title25/T25CH6SECT25-618.htm>

widespread evidence of hybridization with cattle (Freese *et al.*, 2007; Hedrick, 2009). The commercial bison industry is subject only to the same laws and regulations mandated by agricultural agencies. There are currently no conservation laws restricting the commercial overutilization of private bison, and none are likely to be created.

Current Yellowstone bison management outside the Park is governed by the IBMP. However, the IBMP was not designed to protect bison and their habitat but rather to keep bison out of their habitat outside of the Park. Although the threat of brucellosis transmission could be more easily pacified through management of domesticated cattle rather than bison, the agencies have chosen the wrong ungulate to manage (Lancaster, 2005 p. 450). The IBMP is not an adequate regulatory mechanism for many reasons. First, the IBMP is not enforceable, and thus is not a regulatory mechanism for purpose of the ESA. Second, the IBMP “thresholds” relate only to when management agencies will or may halt lethal practices, but do not ensure bison populations will remain at such levels given weather, disease, or other influences. Third, the IBMP “thresholds” do not ensure genetic diversity and viability will be maintained.

The IBMP established demographic conservation thresholds without regard to the genetic effects of recurrent large-scale population reductions, frequently experienced by the Yellowstone bison, under the guidance of this management agreement. Genetic monitoring is crucial for the management and conservation of wildlife populations (Schwartz *et al.*, 2007). The FEIS for the IBMP states that viable population size is affected by genetic, demographic, environmental stochasticity, and catastrophes (USDI/USDA, 2000). Yet, the IBMP did not establish a genetic monitoring program to assess effects of disease risk management operations or other stochastic events to genetic diversity and conservation of evolutionary potential in Yellowstone bison.

Concern for the detrimental genetic effects of frequent population reductions due to disease risk management operations conducted under the IBMP *is* a real concern. The Yellowstone population represents the stronghold of genetically intact wild bison remaining in the United States (see pages 11-14). Protection of this large, genetically intact population and its subpopulations is crucial for the ecological restoration of wild bison (Freese *et al.*, 2007; Sanderson, *et al.*, 2008; Hedrick, 2009; Halbert *et al.*, 2012).

IBMP adaptive management strategies do not consider the combined synergistic effects of disease risk management operations, demographic stochasticity, and environmental stochastic events (e.g. severe winter mortality or disease outbreak) on Yellowstone bison population viability and genetic diversity (USDI/USDA, 2000). The adaptive management threshold of 2,100 is triggered only when the number of bison removed under disease risk management operations reduces the population below the summer population estimate. It does not consider additive winter mortality (or mortality from other causes) within the park before management actions are implemented. The adaptive management strategies established by the IBMP are thus insufficient to protect Yellowstone bison from experiencing catastrophic declines resulting from synergistic negative influences which may occur during disease risk management operations.

The conservation threshold population sizes (e.g. 2,100) set forth in the IBMP appear to have been arbitrarily determined without an in-depth analysis of the population ecology of Yellowstone bison. The IBMP cited no peer-reviewed publications regarding bison population demographics that support the population thresholds established and a detailed population viability analysis was not conducted to determine the minimum viable population size for either the entire population or its genetically different subpopulations. Instead, simple deterministic and stochastic models were used to determine population thresholds and environmental conditions that would result in emigration of bison out of Yellowstone National Park, and predict brucellosis seroprevalence rates under various population sizes (USDI/USDA, 2000).

Both models assumed the Yellowstone National Park bison population would never exceed 3,500 animals because of environmental stochasticity or emigration with subsequent lethal removals (USDI/USDA, 2000). However, the Yellowstone National Park bison population has exceeded 3,500 animals in the last five years (Plumb *et al.*, 2009). Historic documentation of bison migration out of Yellowstone National Park at lower population sizes was ignored. Neither model considered the probability of extinction, quasi-extinction, or effects to genetic diversity. The models ran for only 18 years which is only approximately three bison generations, and results were presented for just 15 years or the life of the IBMP. The smallest time frame for considering risk of extinction recommended by the IUCN is 100 years (IUCN, 2012). Population viability analyses should consider a range of time frames much longer (>100 years) than those dictated by political or legal considerations, especially for longer lived species such as bison (Lande, 2002; Allendorf and Ryman, 2002). The time frame used in population viability analyses is even more critical when genetic issues are taken into consideration (Allendorf and Ryman, 2002; Frankham, 2005).

It is also important to use modeling to estimate quasi-extinction thresholds rather than absolute extinction thresholds, and the probability of a populations declining below these thresholds (Hildenbrandt *et al.*, 2006; Mills, 2007). None of these recommendations were included in the models used for assessing effects of the IBMP's proposed alternatives on Yellowstone bison viability and genetic diversity. Thus, the models used were insufficient for assessing long-term, detrimental effects of brucellosis risk management operations to population viability and genetic effective population size. IBMP guidance does not provide a regulatory mechanism to insure against adverse effects to the long-term viability and genetic diversity of the Yellowstone bison from brucellosis risk management operations.

The lack of realistic parameters precludes the stochastic model described in the IBMP FEIS from adequately evaluating effects and outcomes of all proposed alternatives on brucellosis epidemiology and seroprevalence (Gross *et al.*, 2002 p. 28). The model examined reduction of seroprevalence under alternatives specifically tailored to meet their goals within 18 years. It is more practical and efficient to model disease dynamics under a range of parameters and conditions to develop alternatives that would have the highest probability of reducing seroprevalence in the shortest period of time, rather than post-hoc modeling of alternatives predetermined by political and social interests

(McCallum *et al.*, 2001; Lloyd-Smith *et al.*, 2005; McCallum and Hocking, 2005).

Despite the assertion in the IBMP FEIS that brucellosis transmission occurs under a frequency-dependent transmission mode, the stochastic model and all alternatives were inappropriately drafted under the assumption of a density-dependent transmission mode. Population size and culling have little to no effect on reducing disease prevalence under frequency-dependent transmission because it is the proportion of infected individuals that determines the probability that a susceptible animal becomes infected, and the proportion of infected animals remains relatively constant regardless of population size (McCallum *et al.*, 2001; Gross *et al.*, 2002; Lloyd-Smith *et al.*, 2005). Dobson and Meagher (1996) identified that brucellosis is a frequency-dependent transmitted disease, and demonstrated through their models that the Yellowstone bison population would have to be nearly eradicated ($\ll 200$ individuals) in order to significantly reduce brucellosis prevalence. Gross *et al.* (2002) demonstrated that population control reduces risk but does little for reducing the prevalence of brucellosis or eradication of this disease, and test and slaughter operations are only effective if a large proportion of the population is captured and tested. They also demonstrated that test and slaughter of 10-25% of the population would be ineffective in reducing prevalence and result in the slaughter of a large number of animals leading to major reductions in population size (Gross *et al.*, 2002 p. 31).

The models used to evaluate brucellosis epidemiology and seroprevalence under the proposed alternatives of the IBMP failed to address these issues and did not consider effects of management actions conducted under these alternatives to population viability. Further, the use of unrealistic parameters and lack of details renders all proposed alternatives of the IBMP unachievable and increases the probability that they would fail to achieve their goals or provide adequate conservation measures to protect the Yellowstone bison from irreparable harm. This proved to be the case on implementation. Brucellosis prevalence in the bison population was not reduced; the management plan underestimated bison abundance, distribution, and migration, which contributed to larger risk management culls (total >3000 bison) than anticipated; and culls differentially affected breeding herds and altered gender structure, created reduced female cohorts, and dampened productivity (White *et al.*, 2011).

An evaluation of a minimum viable population should include an assessment of population substructure (Palsbøll *et al.*, 2006). Population substructure is important for monitoring natural and anthropogenic influences on movement and gene flow among subpopulations (Schwartz *et al.*, 2007). The Yellowstone bison exist as at least two genetically distinct breeding herds (Halbert, 2003; Gardipee, 2007; Halbert *et al.*, 2012). Plumb *et al.* (2009) presented a spatially-explicit model that integrated both abiotic variables and biotic processes to determine the food-limited carrying capacity for the Yellowstone bison which included population substructure as well. For the northern range herd the model provided a range of food-limited carrying capacity estimates from 1,820 to 3,530 bison (mean = 2,417; median = 2,670). Carrying capacity estimates for the central breeding herd were much higher ranging from 2,430 to 5,630 (mean = 3,776; median = 4,030) (Plumb *et al.*, 2009).

The actual maximum population estimates for Yellowstone bison within a single year occurred during 2005 with 3,531 bison in the central range breeding herd and 1,484 bison in the northern range breeding herd (Wallen, 2008). This study provided strong evidence of an overall food-limited carrying capacity of 6,200 for the Yellowstone bison population, yet recommended managing for a population sizes between 2,500 and 4,500 as a compromise to satisfy the collective interests of various stakeholders concerned with brucellosis risk management and achieve conservation objectives for the Yellowstone bison. However, to meet the need for bison to adapt to new areas where they are reintroduced and to adapt to large current (e.g., exotic diseases) and future (e.g., climate change) alterations in their habitats, as well as for the intrinsic value of conserving genetic diversity, a minimum population of 2,000 was necessary to achieve a 98% probability of retaining 95% allelic diversity over 200 years (Gross and Wang, 2005; Gross *et al.*, 2006). This would translate into a minimum viable population of 4,000 bison or more if conservation of genetic substructure among Yellowstone bison is considered.

Traill *et al.* (2007) derived a cross-species frequency distribution of minimum viable population from 3,577 to 5,129 (95% C.I) individuals, with a median of 4,169, and recommend a generalized minimum viable population of 5,000 to achieve long-term evolutionary and demographic conservation goals. Hedrick (2009) recommended an N_e of 1,000 to avoid inbreeding depression and maintain genetic diversity. This would translate into a census of at least 2,000-3,000 for each Yellowstone breeding herd, if the polygynous mating system of bison, high probability of differential reproductive success, small founding population, and recurrent population reductions are considered (Kalinowski and Waples, 2002; Hedrick, 2009).

The minimum conservation threshold defined by the IBMP is less than half the minimum viable population recommendations suggested by current analyses (Gross *et al.*, 2006; Plumb *et al.*, 2009; Traill *et al.*, 2007; Traill *et al.*, 2010). Further, the IBMP conservation threshold of 2,100 individuals ignores population substructure, and does not consider the detrimental effects of frequent, recurrent, large-scale removals on genetic effective population size and evolutionary potential in Yellowstone bison (Halbert *et al.*, 2012). Finally, genetic population substructure was not considered in determining the IBMP conservation threshold, and no program is in place to monitor the rate of culling to each breeding herd.

Implementation of the IBMP has not reduced brucellosis in the Yellowstone bison; the management plan underestimated bison abundance, distribution, and migration, which contributed to larger risk management culls (total >3000 bison) than anticipated; and culls differentially affected breeding herds and altered gender structure, created reduced female cohorts, and dampened productivity (White *et al.*, 2011). Disproportionate culling during disease risk management operations could result in the loss of entire maternal lineages, decrease genetic effective population size, and an overall loss of genetic diversity among the Yellowstone bison. Thus, no conservation population thresholds exist under the IBMP that would sufficiently minimize the rate of loss of genetic diversity, promote conservation of evolutionary potential, and provide a buffer against demographic or environmental stochasticity.

Under the IBMP, numbers of Yellowstone bison have held in quarantine for eventual distribution to third parties under the Bison Quarantine Feasibility Study. Prior recipients include Turner Enterprises and the Fort Peck and Fort Belknap tribes. Montana Fish, Wildlife and Parks is currently seeking proposals for agencies and organizations to receive approximately 139 bison that have completed all phases of the quarantine study and are currently being held at the Green Ranch near Bozeman Montana (MFWP, 2014). According to the Request For Proposals, “While long-term bison conservation efforts are the Department’s priority for these animals, MFWP will ultimately consider all feasible options as necessary.” Thus, the State of Montana has made no commitment that the remaining quarantined Yellowstone bison be conserved as wildlife.

In Wyoming, the current (2008) Absaroka Management Plan seeks to maintain the current low number and specific distribution of bull bison in the North Absaroka and Washakie Wilderness Areas (no more than 25), and on Shoshone National Forest (SNF) lands along the North Fork of the Shoshone River (no more than 15) (WGFD, 2008). In addition, the plan allows up to 25 bison in the Yellowstone River drainage within the Teton Wilderness. Once numbers are exceeded, hunting is allowed to remove the bison. The Yellowstone River drainage within the Teton Wilderness is the only part of the management area that can be used by female bison. Thus even in the federally designated North Absaroka and Washakie Wilderness Areas female bison are not safe. This management approach is simply designed not to conserve the bison population but to limit use of the range.

Given the clear inadequacy of existing regulatory mechanisms Yellowstone bison warrant and need protection under the ESA.

Other Natural or Manmade Factors Affecting its Continued Existence.

Genomic Extinction

Genomic extinction poses one of the most imminent threats to bison conservation. This type of species extinction occurs when the genetic composition of a species changes substantially over time as a result of natural evolutionary processes, anthropogenic selection, and inter-specific hybridization (Rhymer and Simberloff, 1996; Allendorf *et al.*, 2001; Freese *et al.*, 2007). Bison are at extremely high risk of genomic extinction because of domestication and anthropogenic selection, and hybridization with cattle (Freese *et al.* 2007). More than 95% of bison exist under private ownership and are subject to agricultural practices which promote anthropogenic selection for traits to meet the market standards of the commercial bison industry (Freese *et al.*, 2007). There is widespread evidence of hybridization with cattle among private bison herds. Selection for particular traits which may be conferred by cattle alleles has the potential to increase current levels of introgression (Ward *et al.*, 1999; Halbert, 2003; Halbert *et al.*, 2005; Freese *et al.*, 2007; Halbert and Derr, 2007). Evidence of hybridization with cattle has now been found in all major conservation herds except for the Yellowstone bison (see pages 11-14). As such, the Yellowstone bison are the last remnant of genetically intact plains bison. Conservation biologists rightly recommend placing greater value on pure or

non-hybridized populations of species, especially when hybridized populations pose a significant conservation threat (Allendorf *et al.*, 2001).

The only other U.S. bison herd that may be free of cattle-gene introgression is the small Henry Mountains herd in Utah (Ward, 2000) but it has not been tested using recent sensitive SNP CHIP techniques. The herd was founded with 18 bison from Yellowstone National Park in 1941, and is currently maintained between 300-400 individuals. The Henry Mountains herd represents only a subset of the genetic diversity of the Yellowstone bison (Ward, 2000 p. 22) and may have lost its original local phenotypic and genetic adaptations after 75 years separation. The Henry Mountains herd is not considered sufficiently large and unique enough to contribute to overall bison genetic diversity (Halbert, 2003).

Yellowstone bison exist in at least two genetically distinct breeding groups between which various rates of gene flow may exist (Halbert, 2003; Gardipee, 2007; Halbert, *et al.*, 2012). The existence of population substructure contributes to the maintenance of overall genetic diversity within the entire population (Hedrick, 2009; Halbert, *et al.*, 2012).

Female philopatry contributes to genetic population structure which may result in the conservation of unique genetic qualities and local adaptations within each breeding herd (Gardipee, 2007). However, these unique genetic traits and local adaptations may be lost through disproportionate culling during disease risk management operations (Halbert, 2003; Freese *et al.*, 2007; Hedrick, 2009; Halbert, *et al.*, 2012).

Yellowstone bison have exhibited remarkable demographic resiliency in response to recurrent large-scale population reductions, however this does not translate into long-term genetic resiliency (Kalinowski and Waples, 2002; Hedrick, 2009). The recurrent large-scale removals frequently experienced by the Yellowstone bison during disease risk management operations pose a significant threat to the conservation of genetic diversity and evolutionary potential, and will continuously decrease the ratio of N_e relative to census population size (Kalinowski and Waples, 2002; Halbert, 2003; Freese *et al.*, 2007; Hedrick, 2009; Halbert, *et al.*, 2012). The introduction of individuals from other bison populations into the Yellowstone bison population to mitigate any potential loss of genetic diversity resulting from management operations is precluded by hybridization issues and by the presence of brucellosis among bison and elk within the greater Yellowstone area (USDI/USDA, 2000; Freese *et al.*, 2007; Halbert and Derr, 2007; Hedrick, 2009).

Yellowstone bison warrant immediate protection under the Endangered Species Act to avoid further loss of genetic diversity, loss of evolutionary potential, and conserve potential genetic contributions to plains bison restoration. Loss of the genetic diversity, evolutionary potential, and disruption of genetic population substructure that is currently represented within the Yellowstone bison herds would result in the loss of the most significant genetic resource for the ecological restoration of plains bison; and because the Yellowstone bison are the only significant population of non-hybridized bison, would result in the loss of genetically intact plains bison.

Climate Change

Human activities have led to large increases in the atmospheric concentration of heat-trapping gases, which is changing the climate in Greater Yellowstone. According to Saunders *et al.* (2012) in Greater Yellowstone, the last decade was 1.4°F above the region's 20th century average. Summer temperatures in Greater Yellowstone have gotten hotter by an even larger margin, with the summers of the past decade 2.3°F above the average for 20th century summers. Yellowstone National Park has documented that precipitation has been declining as temperatures have been increasing (Yellowstone Center for Resources, 2013). According to that report, total annual precipitation at the Mammoth Hot Springs since 1976 has been generally below the long-term mean of 15.3 inches; at the Northeast Entrance, the 5-year running mean of the average annual daily minimum temperature has increased by 4.6°F and the average annual daily maximum temperature by 3.5°F since 1989; the 5-year running mean of annual peak snowpack (expressed as snow water equivalent, SWE) at the Northeast Entrance has declined 22% since 1975 (from 14.5 inches to 11.3 inches); and, the 10-year running mean of winter length (annual number of days with SWE > 0) has decreased from 208 in 1980 to 185 days in 2012.

The Lamar Valley provides important year-round range for Yellowstone bison. Bartlein *et al.* (1997) predict that the present Lamar Valley climate will become more widespread to include the middle elevations in Yellowstone National Park and the mountain ranges outside the park to the north and west. While this may superficially appear beneficial for the bison, the spread of the Lamar Valley climate outside the park boundaries will increase conflicts as bison seek to use this habitat. There is evidence that bison populations are driven by both density-independent and density-dependent mechanisms (Koons *et al.*, 2012). The effect of population density is more severe in dry relative to wet conditions, indicating that competition for forage could be severe in drought conditions. *ibid.* Thus as the climate dries, more bison will move out of the park.

In addition to these expected and ongoing habitat changes, the decrease in snow pack raises additional concerns. As we discussed above, bison from Yellowstone National Park have been known to move south and join the Jackson bison herd in the Grand Teton National Park on rare occasions. Any shifts in bison use to higher elevation areas combined with the decreased snow pack increases the risk that bison may disperse south in larger numbers because movement corridors will be open for longer periods of time. The predicted and observed effects of climate change within the Park are thus increasing the risk of interactions between Yellowstone bison and the cattle-gene introgressed bison in the Jackson herd. Thus climate change poses a serious, predictable threat to the genetic integrity of the Yellowstone bison. And, since Yellowstone bison are the only non-introgressed herd of plains bison, by extension climate change poses a serious, predictable threat to the genetic integrity of the species as a whole.

As a corollary, increased dispersal of bison will also increase risks for contact between Yellowstone bison and domestic livestock thus increase the risk of outbreaks of contagious disease. Bison are susceptible to many of the infectious diseases carried by

domestic livestock (see pages 37-40 above). Climate change is influencing the scope and context of many ungulate pathogens in North America (Hoberg *et al.*, 2008). For example, climate change has affected the distribution of vectors and therefore the occurrence of bluetongue and other Orbivirus diseases (Gates *et al.*, 2010 p. 30; MacLachlan and Guthrie, 2010; Guis *et al.*, 2012). Thus climate change poses a serious threat to Yellowstone bison due to the increased risk of outbreaks of contagious diseases.

Conclusion

The Endangered Species Act requires that the Service promptly issue an initial finding as to whether this petition “presents substantial scientific or commercial information indicating that the petitioned action may be warranted.” 16 U.S.C. § 1533(b)(3)(A). The information and best available science provided in this petition establish that the Yellowstone bison are a distinct population segment of plains bison and that listing this species is warranted because Yellowstone bison are imperiled under each of the five factors that the U.S. Fish and Wildlife Services considers in determining whether a species qualifies for listing as Endangered or Threatened. Yellowstone bison are threatened by curtailment of habitat or range, by disease and disease management, by overutilization by trapping and by hunting, by genomic extinction, and by climate change. The existing regulatory mechanisms threaten rather than protect the Yellowstone bison. Prompt listing under the Endangered Species Act is required if this last remnant population of plains bison is to survive and recover.

Submitted this 13th day of November, 2014 on behalf of all parties,

A handwritten signature in black ink that reads "Michael J. Connor". The signature is written in a cursive style and is underlined with a single horizontal line.

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Literature Cited

Electronic copies of the cited papers are provided with the Petition.

- Allendorf, F. W., Leary, R. F., Spruell, P. and Wenburg, J. K. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology and Evolution*, 16: 613-622.
- Allendorf, F. W. and Ryman, N. 2002. The role of genetics in population viability analysis. *In*: S.R. Bessinger and D.R. McCullough, editors. *Population Viability Analysis*, The University of Chicago Press, Chicago and London. pp. 50-85.
- Bailey, J. A. 2013. *American Plains Bison: Rewilding an Icon*. Sweetgrass Book. 238 pp.
- Barsh, R. L. and Marlor, C. 2003. Driving bison and Blackfoot science. *Human Ecology*, 31(4): 571-593.
- Bartlein, P. J., Whitlock, C. and Shafer, S. L. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology*, 11(3): 782-792.
- Bartuszevige, A. M. and Endress, B. A. 2008. Do ungulates facilitate native and exotic plant spread? Seed dispersal by cattle, elk and deer in northeastern Oregon. *Journal of Arid Environments*, 72: 904-913.
- Beja-Pereira, A., Bricker, B., Chen, S., Almendra, C., White, P. J. and Luikart, G. 2009. DNA genotyping suggests that recent brucellosis outbreaks in the Greater Yellowstone Area originated from elk. *Journal of Wildlife Diseases*, 45(4): 1174-1177.
- Bork, A. M., Strobeck, C. M., Yeh, F. C., Hudson, R. J. and Salmon, R. K. (1991). Genetic relationship of wood and plains bison based on restriction fragment length polymorphisms. *Canadian Journal of Zoology*, 69(1): 43-48.
- Boyd, D. P. 2003. *Conservation of North American bison: Status and recommendations*. Masters Thesis. University of Calgary, Calgary, Alberta.
- Boyd, D. P. and Gates, C. C. 2006. A brief review of the status of plains bison in North America. *Journal of the West*, 45: 15-21.
- Brodie, J. F. 2008. A review of American bison (*Bos bison*) demography and population dynamics. *Wildlife Conservation Society Working Paper No. 38*, July 2008.
- Bruggeman, J. E., Garrott, R. A., White, P. J., Watson, F. G. and Wallen, R. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications*, 17(5): 1411-1423.

Cannon, K. P. 2007. "They went as high as they choose:" What an isolated skull can tell us about the biogeography of high-altitude bison. *Arctic, Antarctic, and Alpine Research*, 39(1): 44-56.

Cannon, K. P. 2008. Biogeography of holocene bison in the Greater Yellowstone Ecosystem. Ph.D. dissertation, University of Nebraska, Lincoln.

Cheville, N. F., McCullough, D. R. and Paulson, L. R. 1998. *Brucellosis in the Greater Yellowstone area*. National Academy Press, Washington, D.C.

Chong, G., Barnett, D., Chemel, B., Renkin, R. and Sikkink, P. 2011. Vegetation monitoring to detect and predict vegetation change: Connecting historical and future shrub/steppe data in Yellowstone National Park. *In: Anderson, C., ed. Proceedings: Questioning Greater Yellowstone's Future: Climate, Land Use, and Invasive Species*. pp. 84-92.

Christman, G. M. 1971. The mountain bison. *American West*, 8(3): 44-47.

Clow, R. 1995. Bison ecology, Brulé and Yankton winter hunting and the starving winter of 1832-1833. *Great Plains Quarterly*, 15: 259-270.

Coder, G. M. 1975. The national movement to preserve the American buffalo in the United States and Canada between 1880 and 1920. Ph.D. Dissertation. Ohio State University, Columbus.

Cronin, M. A., MacNeil, M. D., Vu, N., Leesburg, V., Blackburn, H. D. and Derr, J. N. 2013. Genetic Variation and Differentiation of Bison (*Bison bison*) Subspecies and Cattle (*Bos taurus*) Breeds and Subspecies. *J. Hered.* 104(4): 500-509. doi: 10.1093/jhered/est030

D'Antonio, C. M., and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review Ecology Systematics*, 23: 63-87.

Danz, H. P. 1997. *Of Bison and Man: from the Annals of a Bison Yesterday to a Refreshing Outcome from Human Involvement with America's Most Valiant of Beasts*. Colorado University Press, Boulder, CO.

Decker, J. E., Pires, J. C., Conant, G. C., McKay, S. D., Heaton, M. P., Chen, K. and 25 others. 2009. Resolving the evolution of extant and extinct ruminants with high-throughput phylogenomics. *Proceedings of the National Academy of Sciences*, 106(44): 18644-18649.

Derr, J. N., Hedrick, P. W., Halbert, N. D., Plough, L., Dobson, L. K., King, J., Duncan, C., Hunter, D. L., Cohen, N. D. and Hedgecock, D. 2012. Phenotypic Effects of Cattle Mitochondrial DNA in American Bison. *Conservation Biology*, 26(6): 1130-1136. doi: 10.1111/j.1523-1739.2012.01905.x.

DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science*, 48(2): 255-265.

Dobson, A. and Meagher, M. 1996. The population dynamics of brucellosis in the Yellowstone National Park. *Ecology*, 77(4): 1026-1036.

Douglas, K. C., Halbert, N. D., Kolenda, C., Childers, C., Hunter, D. L., and Derr, J. N. 2011. Complete mitochondrial DNA sequence analysis of *Bison bison* and bison-cattle hybrids: Function and phylogeny. *Mitochondrion*, 11: 166-175. DOI: 10.1016/j.mito.2010.09.005.

Dratch, P. A. and Gogan, P. J. P. 2010. *Bison Conservation Initiative: Bison Conservation Genetics Workshop: report and recommendations*. Natural Resource Report NPS/NRPC/BRMD/NRR-2010/257. National Park Service, Fort Collins, Colorado.

Fleischner, T. L. 2010. Livestock grazing and wildlife conservation in the American West: historical policy and conservation biology perspectives. *In: Wild rangelands: Conserving Wildlife While Maintaining Livestock in Semi-arid Ecosystems*. pp. 235-265.

Flores, D. 1991. Bison ecology and bison diplomacy: the southern plains from 1800-1850. *Journal of American History*, 9: 465-485.

Franke, M. A. 2005. *To save the wild bison: Life on the edge in Yellowstone*. University of Oklahoma Press, Norman. 328 pp.

Frankham, R. 2005. Genetics and extinction. *Biological Conservation*, 126(2): 131-140.

Freese, C. H., Aune, K. E., Boyd, D. P., Derr, J. N., Forrest, S. C., Gates, C. C., Gogan, P. J., Grassel, S. M., Halbert, N. D., Kunkel, K. and Redford, K. H. 2007. Second chance for plains bison. *Biological Conservation*, 136: 175-184.

Fuller, J. A., Garrott, R. A., White, P. J., Aune, K. E., Roffe, T. J. and Rhyan, J. C. 2007. Reproduction and survival of Yellowstone bison. *Journal of Wildlife Management*, 10: 2365-2372.

Gardipee, F. M. 2007. Development of fecal DNA sampling methods to assess genetic population structure of Greater Yellowstone bison. Masters Thesis, The University of Montana, Missoula.

Gates, C. C., Stelfox, B., Muhly, T., Chowns, T. and Hudson, R.J. 2005. *The Ecology of Bison Movements and Distribution In and Beyond Yellowstone National Park*. Faculty of Environmental Design, University of Calgary, Calgary, Alberta.

Gates, C. C., Freese, C. H., Gogan, P. J. and Kotzman, M. 2010. *American bison: status survey and conservation guidelines 2010*. IUCN. 154 pp.

Geist, V. 1991. Phantom subspecies: the wood bison *Bison bison* “*athabascae*” Rhoads 1897 is not a valid taxon, but an ecotype. *Arctic*, 44(4): 283-300.

Gemmell, N. J., Metcalf, V. J. and Allendorf, F. W. 2004. Mother’s curse: the effect of mtDNA on individual fitness and population viability. *Trends in Ecology and Evolution*, 19: 238-244.

Geremia, C., P.J. White, R.A. Garrott, R. Wallen, K. Aune, J. Treanor, and J. Fuller. 2009. Demography of Central Yellowstone Bison: Effects of Climate, Density, and Disease. Pages 255-279, in R.A. Garrott, P.J. White, and F.G. Watson, editors. *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*, Elsevier, Academic Press, San Diego, California.

Geremia, C., White, P. J., Wallen, R. L., Watson, F. G., Treanor, J. J., Borkowski, J., Potter, C. S. and Crabtree, R. L. 2011. Predicting bison migration out of Yellowstone National Park using Bayesian models. *PloS one*, 6(2), e16848.

Gross, J. E., Lubow, B. C. and Miller, M. W. 2002. Modeling the epidemiology of brucellosis in the Greater Yellowstone Area. *In* T. Kreeger, editor. *Brucellosis in elk and bison in the Greater Yellowstone Area*, Wyoming Fish and Game Department for the Interagency Brucellosis Committee. Pp. 24-37.

Gross, J. E. and Wang, G. 2005. Effects of population control strategies on retention of genetic diversity in National Park Service bison (*Bison bison*) herds. Final Report, Yellowstone Research Group, USGS-BRD. United States Geological Survey, Bozeman, Montana. 38 pp.

Gross, J. E., Wang, G., Halbert, N. D., Gogan, P. A., Derr, J. N., and Templeton, J. W. 2006. Effects of Population Control Strategies on Retention of Genetic Diversity in National Park Service Bison (*Bison bison*) Herds. Final Report, Yellowstone Research Group, USGS-BRD. United States Geological Survey, Bozeman, Montana. 31 pp.

Gude, P. H., Hansen, A. J. and Jones, D. A. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications*, 17(4): 1004-1018.

Guis, H., Caminade, C., Calvete, C., Morse, A. P., Tran, A. and Baylis, M. 2012. Modelling the effects of past and future climate on the risk of bluetongue emergence in Europe. *Journal of the Royal Society Interface*, *J. R. Soc. Interface*, 9: 339–350.

Guthrie, R. D. 1970. Bison Evolution and Zoogeography in North America During the Pleistocene. *The Quarterly Review of Biology*, 45(1): 1-15.

Haigh, J. C., Mackintosh, C. and Griffith, F. 2002. Viral, parasitic and prion diseases of farmed deer and bison. *Review of scientific technology, Epizootology*, 21: 219-248.

- Halbert, N. D. 2003. The utilization of genetic markers to resolve modern management issues in historic bison populations: implications for species conservation. Ph.D. Dissertation, Texas A&M University, College Station.
- Halbert, N. D. and Derr, J. N. 2007. A comprehensive evaluation of cattle introgression into US federal bison herds. *Journal of Heredity*, 98: 1-12.
- Halbert, N. D., Ward, T. J., Schnabel, R. D., Taylor, J. F. and Derr, J. N. 2005. Conservation genomics: disequilibrium mapping of domestic cattle chromosomal segments in North American bison populations. *Molecular Ecology*, 14: 2343-2362.
- Halbert, N. D., Gogan, P. J., Hiebert, R. and Derr, J. N. 2007. Where the buffalo roam: The role of history and genetics in the conservation of bison on US federal lands. *Park Science*, 24: 22-29.
- Halbert, N. D., Gogan, P. J., Hedrick, P. W., Wahl, J. M. and Derr, J. N. 2012. Genetic population substructure in bison at Yellowstone National Park. *J. Heredity*, 103(3): 360-370.
- Heddleston, K. L. and Wessman, G. 1973. Vaccination of American bison against *Pasteurella multocida* serotype 2 infection (hemorrhagic septicemia). *J. Wildlife Disease*, 9: 306-310.
- Hedrick, P. W. 2009. Conservation genetics and North American bison (*Bison bison*). *Journal of Heredity*, 100: 411-420.
- Hedrick, P. W. 2010. Cattle ancestry in bison: explanations for higher mtDNA than autosomal ancestry. *Mol. Ecol.*, 16: 3328-3335. doi: 10.1111/j.1365-294X.2010.04752.x.
- Hildenbrandt, H., Müller, M. S. and Grimm, V. 2006. How to detect and visualize extinction thresholds for structured PVA models. *Ecological Modelling*, 191: 545-550.
- Hoberg, E. P., Polley, L., Jenkins, E. J. and Kutz, S. J. 2008. Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. *Revue Scientifique et Technique (International Office of Epizootics)*, 27: 511-528.
- Hornaday, W. T. 1889. *The Extermination of the American Bison*. Smithsonian Institute Press, Washington and London.
- IBMP Annual Report 2013. 2013 Annual Report of the Interagency Bison Management Plan, 1 November 2012 - 31 October 2013. 64 pp.
http://www.ibmp.info/Library/AnnualReports/2013_IBMP_AnnualReport_FINAL.pdf

IUCN. 2012. IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK: IUCN. iv + 32pp.
http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf

IUCN. 2014. Gates, C. and Aune, K. 2008. *Bison bison*. The IUCN Red List of Threatened Species. Version 2014.2. <<http://www.iucnredlist.org/details/2815/0>>.

Jackson, B. 2008. The Mountain Bison of Yellowstone: A Breed Apart. April 24, 2008. 4 pp. Online at:
http://www.peer.org/assets/docs/nps/08_23_4_yellowstone_mountain_bison.pdf

Jones, L. C. and Roffe, T. J. 2007. Management of bison in the National Wildlife Refuge system. US Fish and Wildlife Service. Unpublished Report. 11 pp.

Kalinowski, S. T. and Waples, R. S. 2002. Relationship of effective to census size in fluctuating populations. *Conservation Biology*, 16: 129-136.

Keiter, R. B. 1997. Greater Yellowstone's bison: Unraveling of an early American wildlife conservation achievement. *Journal of Wildlife Management*, 61(1): 1-11.

Kerley, G. I. H., Kowalczyk, R. and Cromsigt, J. P. G. M. 2012. Conservation implications of the refuge species concept and the European bison: king of the forest or refugee in a marginal habitat? *Ecography*, 35(6): 519-529.

Kirkpatrick, J. F., McCarthy, J. C., Gudermuth, D. F., Shideler, S. E. and Lasley, B. L. 1996. An assessment of the reproductive biology of the Yellowstone bison (*Bison bison*) subpopulations using non-capture methods. *Canadian Journal of Zoology*, 74: 8-14.

Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: History, persistence, and influences to human activities. *Global Environmental Change*, 6: 37-52.

Koons, D. N., Terletzky, P., Adler, P. B., Wolfe, M. L., Ranglack, D., Howe, F. P., Hersey, K., Paskett, W. and Du Toit, J. T. 2012. Climate and density-dependent drivers of recruitment in plains bison. *Journal of Mammalogy*, 93(2): 475-481.

Lacey, J. R., Marlow, C. B. and Lane, J. R. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology*, 3: 627-631.

Lancaster, Z. L. 2005. Restraining Yellowstone's roaming bison. *Journal of Land Use*, 20(2): 427-454.

Lande, R. 2002. Incorporating stochasticity in population viability analysis. *In*: S. R. Bessinger and D. R. McCullough, editors. *Population Viability Analysis*, The University of Chicago Press, Chicago and London. Pp. 18-40.

- Li, H., Shen, D. T., O'Toole, D., Knowles, D. P., Gorham, J. R. and Crawford, T. B. 1995. Investigation of sheep-associated malignant catarrhal fever virus infection in ruminants by PCR and competitive inhibition enzyme-linked immunosorbent assay. *Journal of Clinical Microbiology*, 33(8): 2048-2053.
- Li, H., Wunschmann, A., Keller, J., Hall, D. G. and Crawford, T. B. 2003. Caprine herpesvirus-2-associated malignant catarrhal fever in white-tailed deer (*Odocoileus virginianus*). *Journal Veterinary Diagnostic Investigation*, 15(1): 46-49.
- Li, H., Taus, N. S. Jones, C., Murphy, B., Everman, J. F. and Crawford, T. B. 2006. A devastating outbreak of malignant catarrhal fever in a bison feedlot. *Journal of Veterinary Diagnostic Investigation*, 18: 119-123.
- Lloyd-Smith, J. O., Cross, P. C., Briggs, C. J., Daugherty, M., Getz, W. M., Latto, J., Sanchez, M. S., Smith, A. B. and Swei, A. 2005. Should we expect thresholds for wildlife disease? *Trends in Ecology and Evolution*, 20: 511-519.
- Lott, D. F. 2002. *American bison: a natural history*. University of California Press, Berkeley and Los Angeles.
- MacLachlan, N. J. and Guthrie, A. J. 2010. Re-emergence of bluetongue, African horse sickness, and other Orbivirus diseases. *Veterinary Research*, 41(6) Art. 35.
- Mackintosh, C., Haigh, J. C. and Griffin, F. 2002. Bacterial diseases of farmed deer and bison. *Review of scientific technology, Epizootology*, 21(2): 249-263.
- Marston, R.A. and Anderson, J. E. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*, 5: 338-346.
- Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation*, 81(1): 161-177.
- McCallum, H., Barlow, N. and Hone, J. 2001. How should pathogen transmission be modelled? *Trends in Ecology and Evolution*, 16: 295-300.
- McCallum, H. and Hocking, B. A. 2005. Reflecting on ethical and legal issues in wildlife disease. *Bioethics*, 19: 336-347.
- McHugh, T. 1972. *The Time of the Buffalo*. University of Nebraska Press, Lincoln, Nebraska.
- Meagher, M. M. 1973. *The bison of Yellowstone National Park*. Government Printing Office, Scientific Monographs 1. National Park Service, Washington, D.C.

- Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. *Journal of Mammalogy*, 70(3): 670-675.
- Meagher, M. and Houston, D. B. 1998. *Yellowstone and the Biology of Time*. Univ. Oklahoma Press. Norman. 287 pp.
- Meagher, M. M. and Meyer, M. E. 1994. On the origin of brucellosis in bison of Yellowstone National Park: A review. *Conservation Biology*, 8: 645-53.
- Meagher, M. M., Taper, M. L. and Jerde, C. L. 2002. Recent changes in population distribution: The Pelican bison and the domino effect. *Proceedings of the 6th Biennial Scientific Conference, Yellowstone National Park*, pp. 135-147.
- Mills, L. S. 2007. *Conservation of wildlife populations: Demography, genetics, and management*. Blackwell Publishing, Malden, Massachusetts.
- MFWP. 2014. Montana Fish, Wildlife and Parks. Request for Proposals Disposition of Quarantine Facility Bison. 3 pp. Available at: http://fwp.mt.gov/news/publicNotices/environmentalAssessments/speciesRemovalAndRelocation/pn_0067.html
- Mohler J. and Eichhorn A. 1912. Immunization against hemorrhagic septicemia. *American Veterinary Review*, 42/43: 409-418.
- Montana Fish, Wildlife and Parks. 2012. Joint Decision Notice Adaptive Management Adjustments to the Interagency Bison Management Plan February 2012. 21 pp.
- Olexa, E. M. and Gogan, P. J. P. 2007. Spatial population structure of Yellowstone bison. *J. Wildlife Management*, 71: 1531-1538.
- Olliff, T., Renkin, R., McClure, C., Miller, P., Price, D., Reinhart, D. and Whipple, J. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. *Western North American Naturalist*, 61(3): 347-358.
- Palsbøll, P. J., Bérubé, M. and Allendorf, F. W. 2006. Identification of management units using population genetic data. *Trends in Ecology and Evolution*, 22: 11-16.
- Pérez-Figueroa, A., Wallen, R. L., Antao, T., Coombs, J. A., Schwartz, M. K., White, P. J. and Luikart, G. 2012. Conserving genomic variability in large mammals: Effect of population fluctuations and variance in male reproductive success on variability in Yellowstone bison. *Biological Conservation*, 150(1): 159-166.
- Pertoldi, C., Tokarska, M., Wójcik, J. M., Demontis, D., Loeschcke, V., Gregersen, V. R., Coltman, D., Wilson, G. A., Randi, E. Hansen, V. R. and Bendixen, C. 2009. Depauperate genetic variability detected in the American and European bison using genomic techniques. *Biology Direct*, 4: 48. doi:10.1186/1745-6150-4-48

- Pertoldi, C., Tokarska, M., Wójcik, J. M., Kawałko, A., Randi, E., Kristensen, T. N., Loeschcke, V., Coltman, D., Wilson, G. A., Gregersen, V. R. and Bendixen, C. 2010. Phylogenetic relationships among the European and American bison and seven cattle breeds reconstructed using the BovineSNP50 Illumina Genotyping BeadChip. *Acta Theriologica*, 55(2): 97-108.
- Plumb, G. E., White, P. J., Coughenour, M. B. and Wallen, R. L. 2009. Carrying capacity, migration, and dispersal of Yellowstone bison. *Biological Conservation*, 142: 2377-2387.
- Polziehn, R. O., Strobeck, C., Sheraton, J. and Beech, R. 1995. Bovine mtDNA discovered in North American Bison Populations. *Conservation biology*, 9(6): 1638-1643.
- Pringle, T. H. 2011. Widespread mitochondrial disease in North American bison. *Nature Precedings*,
<<http://precedings.nature.com/documents/5645/version/1/files/npre20115645-1.pdf>>.
- Pritchard, J. K., Stephens, M. and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics*, 155: 945-959.
- Pucek, Z., Belousova, I. P., Krasnińska, M., Krasniński, Z. A. and Olech, W. 2004. European Bison: Status Survey and Conservation Action Plan. IUCN/SSC Bison Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. ix + 54 pp.
- Reynolds, H. W., Gates, C. C. and Glaholt, R. D. 2003. Bison (*Bison bison*). In: G. A. Feldhamer, B. C. Thompson and J. A. Chapman (eds.), *Wild Mammals of North America: Biology, Management and Conservation*, pp.1009-1060.
- Rhymer, J. M. and Simberloff, D. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, 27: 23-34.
- Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J., Carter, D., Curtin, C., Derr, J., Dobrott, S., Fearn, E., Fleener, C., Forrest, S., Gerlach, C., Gates, C. C. Gross, J. E., Gogan, P., Grassel, S., Hilty, J. A., Jensen, M., Kunkel, K., Lammers, D., List, R., Minkowski, K., Olson, T., Pague, C., Robertson, P. B. and Stephenson, B. 2008. The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology*, 22: 252-266.
- Saunders, S., Findlay, D., Easley, T. and Christensen, S. 2011. Greater Yellowstone in Peril. *The Threats of Climate Disruption*. 48 pp. Available on line at: <http://www.rockymountainclimate.org/images/YellowstoneInPeril.pdf>

- Schnabel, R. 2011. High Throughput Genomic Technologies for Bison. Presentation to the American Bison Society. Tulsa, OK. March 24, 2011. Available on line at: http://www.americanbisonsocietyonline.org/Portals/7/110325_Tulsa_Schnabel.pdf
- Schullery, P. and Whittlesey, L. H. 2006. Greater Yellowstone bison distribution and abundance in the early historic period. *In*: Biel, A.W. (Ed.), Greater Yellowstone Public Lands: Proceedings of the Eighth Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Yellowstone National Park, Wyoming, pp. 135-140.
- Schullery, P., Brewster, W. and Mack, J. 1998. Bison in Yellowstone: a historical overview. *In*: Irby, L. and Knight, J. (Eds.), International Symposium on Bison Ecology and Management in North America. Montana State University, Bozeman, pp. 326-336.
- Schultheiss, P. C., Collins, J. K., Spraker, T. R. and DeMartini, J. C. 2000. Epizootic malignant catarrhal fever in three bison herds: Differences from cattle and association with ovine herpesvirus-2. *J. Veterinary Diagnostic Investigation*, 12: 497-502.
- Schwartz, M. K., Luikart, G. and Waples, R. S. 2007. Genetic Monitoring as a promising tool for conservation and management. *TRENDS in Ecology and Evolution*, 22: 25-33.
- Shaw, J. H. 1995. How many bison originally populated western rangelands? *Rangelands*, 17(5): 148-150.
- Smith, D. W., Stahler, D. R., Stahler, E., Metz, M., Quimby, K., McIntyre, R., Ruhl, C., Martin, H., Kindermann, R., Bowersock, N. and McDevitt, M. 2013. Yellowstone Wolf Project: Annual Report, 2012. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2013-02.
- Smits, D. D. 1994. The frontier army and the destruction of the buffalo: 1865-1883. *The Western Historical Quarterly*, 25: 312-338.
- Taper, M. L., Meagher, M. and Jerde, C. L. 2000. The phenology of space: Spatial aspects of bison density dependence in Yellowstone National Park. Montana State University, Bozeman, MT. Unpublished manuscript. 113 pp.
- Tessaro, S. V. 1989. Review of the diseases, parasites and miscellaneous pathological conditions of North American bison. *The Canadian Veterinary Journal*, 30(5): 416-422.
- Thompson, M. J. 1996. Winter foraging response of elk to spotted knapweed removal. *Northwest Science*, 70: 10-19.
- Traill, L. W., Bradshaw, C. J. A. and Brook, B. W. 2007. Minimum viable population size: a meta-analysis 30 years of published estimates. *Biological Conservation*, 139: 159-166.

- Trails, L. W., Brock, B. W., Frankham, R. R. and Bradshaw, C. J. A. 2010. Pragmatic population targets in a rapidly changing world. *Biological Conservation*, 143: 28-34.
- Trammell, M. A. and Butler, J. L. 1995. Effects of exotic plants on native ungulate use of habitat. *J. Wildlife Management*, 59: 808–816.
- Treanor, J. J., Geremia, C., Crowley, P. H., Cox, J. J., White, P. J., Wallen, R. L. and Blanton, D. W. 2011. Estimating probabilities of active brucellosis infection in Yellowstone bison through quantitative serology and tissue culture. *Journal of Applied Ecology*, 48(6): 1324-1332.
- Ungerer, M. C., Weitekamp, C. A., Joern, A., Towne, G. and Briggs, J. M. 2013. Genetic Variation and Mating Success in Managed American Plains Bison. *Journal of Heredity*, 104(2): 182-191.
- USFWS. 2007. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the Yellowstone National Park bison herd as endangered. *Federal Register*, 72(157): 45717-45722.
- USDI/USDA. 2000. Final Environmental Impact Statement for the Interagency Bison Management Plan for the State of Montana and Yellowstone National Park. U.S. Department of the Interior, National Park Service and U.S. Department of Agriculture, Forest Service.
- USDI/USDA. 2007. Bison and Elk Management Plan: National Elk Refuge, Grand Teton National Park. Jackson, Wyoming. U.S. Department of the Interior, National Park Service: Grand Teton National Park, Fish and Wildlife Service: National Elk Refuge and U.S. Department of Agriculture, Forest Service.
- Van Zyll de Jong, C., Gates, C., Reynolds, H. and Olson, W. 1995. Phenotypic variation in remnant populations of North American bison. *Journal of Mammalogy*, 391-405.
- Varley, N. and Gunther, K. A. 2002. Grizzly bear predation on a bison calf in Yellowstone National Park. *Ursus*, 13: 377-381.
- Wallen, R. L. 2008. Bison population abundance survey, National Park Service, Yellowstone National Park, Mammoth, Wyoming. 7 pp.
- Ward, T. J. 2000. An evaluation of the outcome of interspecific hybridization events coincident with a dramatic demographic decline in North American bison. Ph.D. Dissertation, Texas A&M University, College Station.
- Ward, T. J., Bielawski, J. P., Davis, S. K., Templeton, J. W. and Derr J. N. 1999. Identification of domestic cattle hybrids in wild cattle and bison species: a general approach using mtDNA markers and the parametric bootstrap. *Animal Conservation*, 2: 51-57.

Ward, T. J., Skow, L. C., Gallagher, D. S., Schnabel, R. D., Nall, C. A., Kolenda, C. E., Davis, S. K., Taylor, J. F. and Derr, J. N. 2001. Differential introgression of uniparentally inherited markers in bison populations with hybrid ancestries. *Animal Genetics*, 32(2): 89-91.

WGFD. 2008. Brucellosis Management Action Plan for Bison Using the Absaroka Management Area. Wyoming Game and Fish Department. 20 pp.

White, P. J., Wallen, R. L., Geremia, C., Treanor, J. and Blanton, D. W. 2011. Management of Yellowstone bison and brucellosis transmission risk-Implications for conservation and restoration. *Biological Conservation*, 144: 1322-1334.

White, P. J. and Garrott, R. A. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. *Biological Conservation*, 125(2): 141-152.

Wilson, M. C., Hills, L. V. and Shapiro, B. 2008. Late Pleistocene northward-dispersing *Bison antiquus* from the Bighill Creek Formation, Gallelli gravel pit, Alberta, Canada, and the fate of *Bison occidentalis*. *Canadian Journal of Earth Sciences*, 45(7): 827-859.

Wilson, G. A. and Strobeck, C. 1999. Genetic variation within and relatedness among wood and plains bison populations. *Genome*, 42(3): 483-496.

Wyman, T. 2002. Grizzly bear predation on a bull bison in Yellowstone National Park. *Ursus*, 13: 375-377.

Yellowstone Center for Resources. 2011. Yellowstone National Park: Natural Resource Vital Signs. National Park Service, Mammoth Hot Springs, Wyoming, YCR-2011-07.

Yellowstone Center for Resources. 2013. Yellowstone National Park: Natural and Cultural Resources Vital Signs. National Park Service, Mammoth Hot Springs, Wyoming, YCR-2013-03.

Zeyland, J., Wolko, Ł., Lipiński, D., Woźniak, A., Nowak, A., Szalata, M., Bocianowski, J. and Słomski, R. 2012. Tracking of wisent-bison-yak mitochondrial evolution. *Journal of Applied Genetics*, 53(3): 317-322.