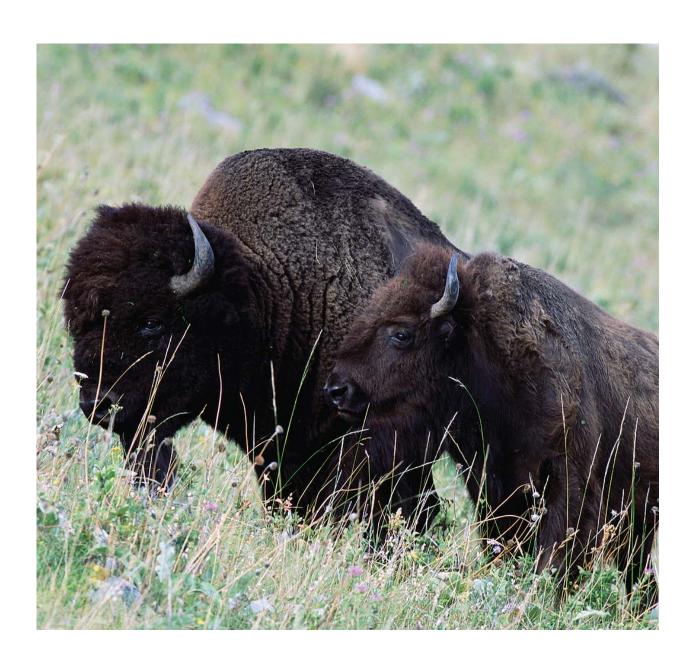


Bison Conservation Initiative

Bison Conservation Genetics Workshop: Report and Recommendations

Natural Resource Report NPS/NRPC/BRMD/NRR—2010/257



Bison Conservation Initiative

Bison Conservation Genetics Workshop: Report and Recommendations

Natural Resource Report NPS/NRPC/BRMD/NRR—2010/257

Peter A. Dratch

National Park Service Natural Resource Program Center 1201 Oakridge Drive, Suite 200 Fort Collins, Colorado 80525

Peter J. P. Gogan

U.S. Geological Survey Northern Rocky Mountain Science Center 2327 University Way, Suite 2 Bozeman, Montana 59715

October 2010

U.S. Department of the Interior National Park Service Natural Resource Program Center Fort Collins, Colorado The National Park Service, Natural Resource Program Center, publishes a range of reports that address natural resource topics of interest and applicability to a broad audience in the National Park Service and others in natural resource management, including scientists, conservation and environmental constituencies, and the public.

The Natural Resource Report Series is used to disseminate high-priority, current natural resource management information with managerial application. The series targets a general, diverse audience, and may contain NPS policy considerations or address sensitive issues of management applicability.

All manuscripts in the series receive the appropriate level of peer review to ensure that the information is scientifically credible, technically accurate, appropriately written for the intended audience, and designed and published in a professional manner. This report received formal peer review by subject-matter experts who were not directly involved in the collection, analysis, or reporting of the data, and whose background and expertise put them on par technically and scientifically with the authors of the information.

Views, statements, findings, conclusions, recommendations, and data in this report do not necessarily reflect views and policies of the National Park Service, U.S. Department of the Interior. Mention of trade names or commercial products does not constitute endorsement or recommendation for use by the U.S. Government.

This report is available from the Biological Resource Management Division and the Natural Resource Publications Management website (http://www.nature.nps.gov/publications/NRPM).

Please cite this publication as:

Dratch, P. A., and P. J. P. Gogan. 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.

Contents

Figures	iv
Tables	v
Appendixes	vi
Executive Summary	vii
Introduction	1
Background	3
Brief History of American Bison Conservation	3
General Principles for Maintaining Genetic Diversity in Bison	5
Current Evidence of Cattle Ancestry	6
Workshop Recommendations	9
Management to Limit Introgression	9
Management to Retain Genetic Diversity	10
Research Recommendations	12
Conclusions	14
Literature Cited	19

Figures

Figure 1 . Neighbor-joining tree diagrams for DS (top) and (δμ)2 (bottom) distance measures for DOI bison herds as of 2003
Figure C-1. Badlands National Park bison herd population, 1963 to 2009
Figure C-2 . Fort Niobrara National Wildlife Refuge bison herd population, 1913 to 2009 28
Figure C-3. Jackson Bison Herd (Grand Teton National Park/National Elk Refuge) population, 1948 to 2008
Figure C-4 . National Bison Range bison herd population, 1909 to 2009
Figure C-5. Neal Smith National Wildlife Refuge bison herd population, 2006 to 2009 31
Figure C-6. Rocky Mountain Arsenal bison herd population, 2007 to 2009
Figure C-7. Sullys Hill bison herd population, 1918 to 2009
Figure C-8. Theodore Roosevelt National Park bison herd population, 1956 to 2009 34
Figure C-9 . Witchita Mountains Wildlife Refuge bison herd population, 1907 to 2009 35
Figure C-10. Wind Cave National Park bison herd population, 1913 to 200936
Figure C-11. Yellowstone National Park bison herd population, ca. 1900 to 2009

Tables

Table 1 . Summary of herd size and indicators of genetic diversity for U.S. Department of the Interior bison herds.	8
Table 2. Recommendations to limit bison introgression in federal bison herds.	15
Table 3. Recommendations to retain genetic diversity in federal bison herds	16
Table 4. Recommendations for research priorities in bison genetics.	18

Appendixes

Appendix A. Participants in the Bison Conservation Genetics Workshop	24
Appendix B. Workshop Agenda	25
Appendix C. U.S. Department of the Interior Herd Histories	27
Appendix D. Source and Movement of DOI Herd	38

Executive Summary

One of the first outcomes of the Department of the Interior (DOI) Bison Conservation Initiative was the Bison Conservation Genetics Workshop held in Nebraska in September 2008. The workshop brought together scientists from government agencies and non-governmental organizations with professional population geneticists to develop guidance for the genetic management of the federal bison herds. The scientists agreed on the basic tenets of genetic management for the DOI herds and discussed different approaches to meeting those goals.

First, the 12 DOI herds are an irreplaceable resource for the long-term conservation of North American plains bison. Most of the herds show low levels of cattle introgression dating from the time when they were saved from extirpation; those herds should not be mixed without careful consideration as to their origin. Herds that show no evidence of cattle ancestry by the current molecular methods are the highest priority for protection from genetic mixing with any other bison herds.

Second, despite the fact that most of the herds now managed by the U.S. government were founded with very few bison and have been maintained for many generations at relatively low population sizes, they do not show obvious effects of inbreeding. They have retained significant amounts of genetic variation by the standard measures, heterozygosity and allelic diversity. This may be explained in part by the fact that most of these herds are not remnants of a single population.

Third, to preserve genetic variation in federal bison herds over decades and centuries, herds should be managed at a population or metapopulation level of 1,000 animals or more, with a sex ratio that enables competition between breeding bulls. The parks and refuges that currently have bison herds, with the exception of Yellowstone National Park, do not have enough land to support a population of this size. In the short term, it will be important to develop satellite herds to attain population targets, and develop a metapopulation structure between herds.

Fourth and finally, the current methods used to evaluate the DOI bison herds, using mitochondrial DNA and a suite of nuclear DNA microsatellites, are highly informative at the herd level. They have confirmed relatedness of herds that we know from historical records have a common origin. They have detected cattle ancestry in most of the herds where it was suspected and have shown some loss of rare alleles. However, they do not sample across the bison genome, and the use of neutral genetic markers as the basis for selection of individual bison—either to breed or move to other herds—would be better supported by more high-resolution molecular methods currently under development.

Introduction

Bison are an iconic animal of the American frontier, represented on both the Department of the Interior (DOI) seal and the National Park Service (NPS) arrowhead. The first principle of DOI Bison Conservation Initiative was to base management of its herds on the best available science. One of the priorities of the initiative was to convene a conservation genetics workshop focused on bison to develop genetic management guidelines, including the appropriate role in future conservation actions for bison with cattle ancestry. The NPS organized the workshop at the Lied Lodge on September 2–5, 2008, and brought together a diverse group of scientists to identify and recommend management actions and research needs important to the conservation genetics of DOI bison herds.

The DOI Bison Genetics Workshop came out of significant recent developments in North American bison conservation. Renewed public interest in bison, both as a natural food source and for their historic ecological role in western landscapes, underscored the importance of the DOI bison herds in conservation of the species. At the same time, recent published studies advanced understanding of the genetic status of these bison herds.

The workshop brought together population geneticists and other biologists from the Department of the Interior, Canadian Wildlife Service, Parks Canada, Texas Parks and Wildlife, academic institutions, and non-governmental organizations, including conservation organizations and zoos (see Appendix A for a participant list). The perspective of zoos was important, as most government herds, while roaming over large areas, are still captive populations facing fences and annual round-ups. The group heard presentations on the history of conservation of North American bison and the government role in these conservation efforts, reviewed the general principles for maintaining allelic diversity within a species, and received reports on the status of DOI bison herds addressing issues of allelic diversity and introgression of livestock genes in the North American bison genome (see Appendix B for the workshop agenda).

While there was agreement on the principles that should guide the management of DOI bison herds, consensus on the management practices that would best achieve those genetic principles was not achieved in the three-day meeting. To provide clear guidance, this report has been through multiple drafts. Workshop participants Peter Dratch, Eric Lonsdorf, and Peter Gogan and NPS writer-editor Virginia Reams all contributed to writing the final report, and most of those who attended the workshop have made substantial comments to the drafts. The recommendations primarily represent the views of the population geneticists that gave their time to address the challenge of conserving North American bison on the timescale of centuries.

The participants were asked to address three questions important to the public in developing the guidelines:

- 1) What criteria best describe a herd of wild bison?
- 2) How well do bison herds under DOI management authority meet the criteria for wild bison?

3) What steps can be taken to ensure that management of the DOI herds contributes to the future of wild bison in North America?

The participants established the criteria for a wild bison herd as one with a large enough population size to prevent loss of genetic variation and with low levels of cattle or subspecies introgression, and subject to some of the forces of natural selection, including competition for breeding opportunities. The desired minimum size of a population to maintain genetic variation in bison over two centuries is estimated at 1,000 individuals (Gross and Wang 2005, Gross et al. 2006, Boyd et al. 2010). This could be achieved through establishment of a single population or management of several smaller populations as a metapopulation. While recognizing that hybridization with cattle was not natural, and mixing between bison subspecies rare, participants discussed a threshold of cattle ancestry (all of the DOI herds have less than 2% cattle genes for currently used DNA markers) in evaluation of DOI bison herds. This definition of wild bison is more restrictive than that of a bison "conservation herd," which may be defined as any herd managed by a government or non-government organization with the primary mission of nature conservation (Gates and Ellison 2010).

While the group looked at the history of both plains bison and wood bison in North America, the recommendations focus on plains bison herds in the United States managed by DOI. Addressing the question of how well do DOI bison herds meet the criteria for wild bison, the participants noted that DOI herds meet the basic threshold for genetic integrity. However, most herds are managed at numbers well below a population size of 1,000, and there are no management plans in place to manage any group of spatially isolated herds as a metapopulation. In addition, the herds are not of equal value for long-term conservation of bison.

There was a consensus among workshop participants that herds with no evidence of cattle hybridization are particularly important resources that must be safeguarded from potential introgression of livestock genes. Lineages within all DOI herds that are representative of historical conservation efforts and confirmed by genetic analysis of herds should be preserved until issues of livestock introgression are resolved with DNA analysis at higher resolution. While no DOI herds are currently subject to the full range of historic natural selective forces that influence genetic variation, management actions should maximize population size, minimize selection for docility and other traits related to domestication, strive for an even sex ratio considering differential survival, and minimally interfere with social behavior.

Finally, the DOI bison herds have a crucially important role in long-term bison conservation. Almost all herds must be increased in size to avoid negative genetic effects on a decades-to-century time scale (Gross et al. 2006). Since DOI herds are generally at or near capacity within federal boundaries, establishing satellite herds that can contribute to metapopulations is an important first step. Further, managing bison herds across current jurisdictional boundaries is an important step to long-term bison conservation. The DOI herds also are valuable source bison with which to start new conservation herds proposed by other federal, state/provincial, or tribal governments/First Nations, and others. Any new efforts should move toward establishing satellite herds that can eventually serve as interbreeding populations or metapopulations with total herd sizes of 1,000 bison to sustain genetically healthy animals over time.

Background

Brief History of American Bison Conservation

The American bison (*Bison bison*) is an icon of the conservation movement in North America. It was one of the first animals that stirred citizens and governments to intervene on behalf of a species on the verge of extinction (Coder 1975, Lothian 1981). Due largely to commercial, sport, and subsistence hunting, as well as possibly exotic bovine diseases and forage competition with domestic stock (Flores 1991), plains bison (*B. b. bison*) were reduced from tens of millions at the time of European colonization (Shaw 1995) to a few hundred by the mid-1880s (Hornaday 1889, Isenberg 2000). The other subspecies of American bison, the wood bison (*B. b. athabascae*), an inhabitant of the woodlands of northern Canada and Alaska, was reduced to an estimated 250 animals by the end of the 19th century (Hornaday 1889, Soper 1941).

While there was sentiment in the 1800s to halt the destruction of bison in North America (Dary 1989), protective legislation in Canada and the United States was not enacted until bison were near extinction. In Canada, the 1877 Buffalo Protection Act was the first attempt to legislate protection (Hewitt 1921). This measure was ineffective, however, due to lack of enforcement. In 1894, the Dominion Government passed a law protecting the surviving wood bison (Soper 1941); by this time, wild plains bison were extirpated in Canada. Plains bison were extirpated from Mexico by the 1820s (List et al. 2007).

Plains bison disappeared from the wild in the United States except in Yellowstone National Park (NP). The states of Idaho, Wyoming, and Montana implemented statutes to reduce the killing of game, including bison, between 1864 and 1872, but—like the 1877 Canadian measure—these laws were largely ineffective due to limited enforcement. The Act to Protect the Birds and Animals in Yellowstone National Park and to Punish Crimes in Said Park was signed by President Grover Cleveland in 1894, halting the extirpation of the last free-ranging plains bison population in North America (Meagher 1973). By 1902, however, fewer than 50 wild bison were estimated to remain in the remote Pelican Valley of Yellowstone NP (Meagher 1973).

Plains bison were saved from extinction by the independent actions of private citizens (Dary 1989, Coder 1975). Between 1873 and 1889, several individuals in locations ranging from Manitoba to Texas captured the last of the wild plains bison, except for the few remaining in Yellowstone NP. William Hornaday, director of the New York Zoological Park, and other wildlife advocates concerned about the loss of this symbol of the American West formed the American Bison Society (ABS) in 1905. The ABS successfully lobbied for the creation of several public reserves in the United States, which the ABS then populated with bison from private herds and the Bronx Zoo (Coder 1975, Isenberg 2000).

In Canada, the national parks system first became involved in plains bison conservation in 1897 when three animals were purchased from Charles Goodnight in Texas. A more significant early contribution by the Canadian government occurred in 1907 when it purchased the privately owned Pablo-Allard herd in Montana. The herd was shipped first to Elk Island National Park, then on to a new park, Buffalo National Park, in the grasslands of east-central Alberta (Lothian 1981, Brower 2008). With protection, the numbers of plains bison increased rapidly, and the danger of extinction was averted in both countries (Hornaday 1927, Potter et al. 2010).

The early efforts to save the bison at a crucial time have rightfully been regarded as a conservation success story. The best current estimate is that about 430,000 plains and wood bison now exist in North America (Gates and Ellison 2010). Of these, only 20,500 plains bison and 11,000 wood bison are in publicly owned herds (Gates and Ellison 2010); the remainder are privately owned. Plains bison are classified as endangered in Mexico (Aune and Wallen 2010). Wood bison are classified as endangered under the U.S. Endangered Species Act and threatened under Canada's Species at Risk Act (Aune and Wallen 2010).

Many Indian tribes and First Nations maintain bison herds for cultural, nutritional, and commercial purposes. Some of these herds have the potential to contribute to species conservation. Most privately owned plains bison today are selected for meat production, protected from natural predators, and managed as small herds in fenced paddocks. More than 90% were founded with animals that have evidence of cattle ancestry and show significant amounts of cattle introgression. These herds are not considered wild and are not included in conservation planning for the species. Most publicly owned plains bison populations in North America are directly descended from only a few founders—an effective population size of fewer than 50 (Hedrick 2009). They constitute a critical resource for long-term bison conservation.

Department of the Interior agencies (the National Park Service and U.S. Fish and Wildlife Service [USFWS]) have a record of cooperation in bison management (see Appendix C for detailed histories of the DOI bison herds). Bison from the Pablo-Allard herd (now National Bison Range) and Goodnight herd (now Texas State Bison Herd) were provided to augment the remnant herd at Yellowstone NP in 1902 (Coder 1975, Meagher 1973). Yellowstone NP bison were provided to found a bison herd at Fort Niobrara National Wildlife Refuge (NWR) in 1913 (Coder 1975, Halbert 2003, Halbert and Derr 2007a). Similarly, in 1956 bison from Fort Niobrara NWR were the source stock used to establish bison herds within the North and South units of Theodore Roosevelt NP. This latter group of three herds constitutes a metapopulation (Halbert 2003, Halbert and Derr 2007a). The bison herd at Badlands NP was established with animals from Fort Niobrara NWR and the South Unit of Theodore NP in 1963 and augmented with bison from the former herd at Colorado National Monument in 1983 (Berger and Cunningham 1994).

The New York Zoological Park also cooperated extensively in the establishment of DOI bison herds: the bison herd at Wind Cave NP was established with bison from New York Zoological Park in 1913 and Yellowstone NP in 1916. The bison herd at Wichita Mountains NWR was established with bison from the New York Zoological Park in 1907 (Coder 1975, Halbert 2003, Halbert and Derr 2007a). The known genetic relatedness of contemporary DOI bison herds is depicted in Figure 1.

The Department of the Interior is the primary federal agency for management of bison within the United States. Currently, the Department of the Interior maintains exclusive management authority over 12 plains bison herds at 10 locations (Table 1). Two additional herds at two sites are managed under cooperative plans with the states of Montana and Wyoming, respectively (Gates and Ellison 2010, Aune and Wallen 2010). Of these, the National Park Service maintains exclusive management authority for bison within Yellowstone and Grand Teton national parks. Yellowstone bison are managed by the State of Montana beyond the park boundaries. The interagency management plan calls for more aggressive management of bison when they leave

the park when population estimates exceed 3,000 (USDI and USDA 2000, Plumb et al. 2009). Jackson bison are managed cooperatively by the National Park Service within Grand Teton NP, the U.S. Fish and Wildlife Service on the National Elk Refuge (NER), and the State of Wyoming on lands adjacent to Grand Teton NP and the NER. The target population objective for the Jackson herd is approximately 500 bison (USFWS and NPS 2007). Most herds managed by the Department of the Interior are relatively small, genetically isolated, and separated from natural predators. Some show evidence of cattle ancestry, and some do not (Table 1).

Management recommendations need to consider the consequences of small population size for genetic health as well as the prevention of further introgression of cattle genes, particularly into bison herds with no evidence of hybridization. For each major concern (genetic diversity and cattle ancestry), we present background and specific recommendations based upon our current knowledge and suggest research needs where additional information may be required. Current information on genetic variation in the DOI bison herds is summarized in Table 1. The U.S. Fish and Wildlife Service has implemented translocations of bison within herds under its management authority since completion of the assessment of genetic variation. The genetic status of the newly established herds is unknown.

General Principles for Maintaining Genetic Diversity in Bison

Effective population size (N_e) is an important measure used for the maintenance of genetic diversity. Genetic drift leads to the loss of genetic diversity, and the rate of loss is expected to correlate negatively with effective population size (Hartl and Clark 2007). Declining genetic diversity and increasing inbreeding depression may interact with the stochastic process of genetic drift (Hartl and Clark 2007) and demographic stochasticity to amplify extinction risk in small populations (Saccheri et al. 1998, Westemeier et al. 1998).

Genetic drift resulting in declining allelic diversity within populations along with reductions in gene flow between populations is of particular concern for species such as bison that evolved in large, outcrossing populations. Genetic drift leads to reduced performance in many fitness-related traits (Menges 1991, Keller and Waller 2002). Small and isolated populations are more prone to extinction than larger populations due to the consequences of demographic, genetic, and environmental stochasticity (Lande 1988).

Loss of genetic variation in bison herds is more likely when the number of breeding animals is small. Our best estimates are that bison populations can generally be considered of sufficient size for genetic purposes when the population size is 1,000 animals or more and the size of the population is stable over time. A population must have a sufficient number of mature bulls to enable breeding competition. In all populations, the expected loss of genetic diversity over time is directly related to how rapidly individuals in a population replace themselves (generation time) and to the effective population size. Most guidelines for genetic management can be understood in the context of just these two factors.

Biologists are concerned about the genetic health of bison herds because all North American herds were founded by a few individuals and have generally been maintained at small population sizes (Boyd et al. 2010). Most DOI herds were established from groups of 20–50 bison (Halbert 2003, Halbert and Derr 2008), and DOI herds have largely been managed to maintain a size of fewer than 500 animals. The relatively small size and isolation of most DOI bison herds has led

to concerns about their long-term genetic health. A summary provided by Halbert and Derr (Table 1) of the current state of bison genetic diversity indicates that genetic drift may already be causing a detectable loss of allelic diversity. For example, rare alleles present in bison at both units of Theodore Roosevelt NP are no longer present in the source population at Fort Niobrara NWR.

The status of the Texas State Bison Herd underscores the potential problems with maintaining small, isolated populations of bison. The interplay of a small number of founder animals, subsequent bottlenecks in population size, and long-term small population size with genetic drift has resulted in low levels of genetic diversity (Halbert 2003, Halbert et al. 2004). This contributed to high calf mortality and low recruitment rates. Population viability analysis predicted the demise of the herd within 50 years without the infusion of genetic material from another bison herd (Halbert 2003, Halbert et al. 2004). Bison bulls were brought in for breeding with an immediate positive effect (D. Sweptson, pers. comm., 2008)

Current Evidence of Cattle Ancestry

Bison and domestic cattle (*Bos taurus*) can produce fertile offspring from human-controlled crosses (Jones 1907; Boyd 1908, 1914; Goodnight 1914). The two species are not known to produce hybrids naturally, and even carefully controlled crosses result in a low birthrate of viable first-generation hybrid offspring (Boyd 1908, Steklenev and Yasinetskaya 1982). In addition, most viable offspring are female, as are first generation backcrosses (Boyd 1908, Hedrick 2009). This typically leads to higher levels of mtDNA than autosomal DNA in introgressed bison herds (Hedrick 2010).

Each of the ranchers involved in establishing the five plains 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 (Garretson 1938, Coder 1975, Brower 2008). Consequently, both mitochondrial (Polziehn et al. 1995, Ward et al. 1999) and nuclear (Halbert et al. 2005) evidence of domestic cattle ancestry has been identified in both public and private plains bison herds (Halbert and Derr 2007a). In a recent study, 14 unlinked microsatellite markers with non-overlapping allele size ranges between bison and domestic cattle were used to identify bison populations with evidence of nuclear domestic cattle introgression; regions of introgression were subsequently confirmed through analysis of microsatellites linked to the original diagnostic loci (Halbert et al. 2005). To date, evidence of mitochondrial or nuclear domestic cattle gene introgression has been identified in all but six of 14 U.S. and Canadian public bison populations (Ward et al. 1999, Halbert et al. 2005, Halbert and Derr 2007a). Only one of the more than 50 private bison herds examined to date showed no evidence of cattle gene introgression (J. N. Derr, pers. comm.).

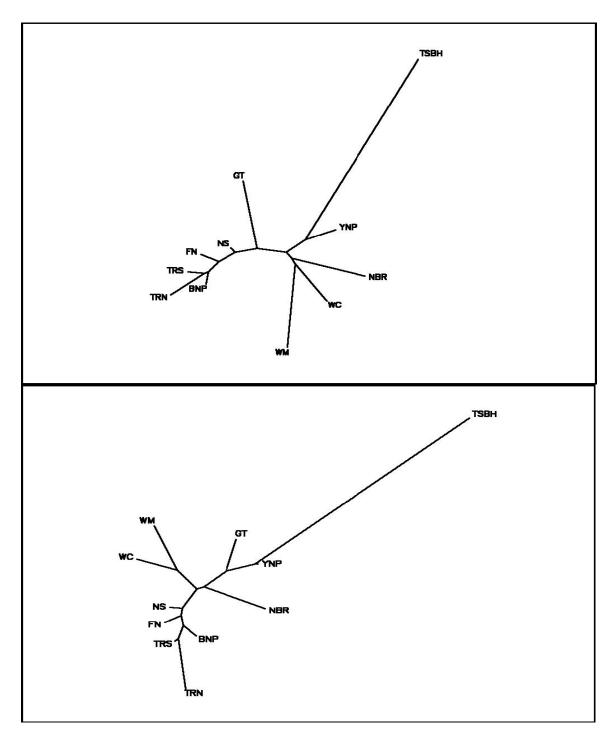


Figure 1. Neighbor-joining tree diagrams for DS (top) and $(\delta\mu)^2$ (bottom) distance measures for DOI bison herds as of 2003 (Halbert 2003:50). Herd abbreviations as in Table 1. TBSH is the Texas State Bison Herd; NS herd in these diagrams no longer exists.

Table 1. Summary of herd size and indicators of genetic diversity for U.S. Department of the Interior bison herds (after Halbert and Derr 2007a; Halbert et al. 2008; L. Jones, pers. comm. 2010, Robert Schnabel, pers. comm. 2010).

Herd name (abbreviation)	Estimated population size	Introgression present ^a	Allelic richness ^c	Expected heterozygosity ^d	Average F _{ST} ^e	Unreplicated conservation unit ^h
Fort Niobrara NWR (FN) – original herd	290	Yes	4.23	65.1	0.106	
Ft. Niobrara NWR (FNSH) – formerly located at Sullys Hill*	61	Suggested ^b	3.91	59.9	NA ^t	
Theodore Roosevelt NP – North (TRN)	312	Yes	3.16	52.2	0.139 ^g	
Theodore Roosevelt NP – South (TRS)	371	Yes	3.80	58.2	0.111	
National Bison Range (NBR)	350	Yes	4.51	66.4	0.133	Yes
Neal Smith NWR (NS)**	71	Suggested ^b	4.43	66.8		
Rocky Mountain Arsenal (RMA)***	44	Suggested ^b	4.44	64.2		
Wichita Mountains NWR (WM)	650	Yes	4.16	61.2	0.149	Yes
Badlands NP (BNP)	875	Yes	3.86	57.8	0.107	
Grand Teton NP (GT)	900	Suggested ^b	3.19	53.5	NA^{t}	
Wind Cave NP (WC)	350	Suggested ^b	4.29	65.2	0.123	Yes
Yellowstone NP (YNP)	3,000****	None detected	4.15	62.5	0.133	Yes

^a Based on mitochondrial DNA typing following Ward et al. 1999 and a panel of 14 nuclear microsatellites following Halbert et al. 2005.

^b Introgression was not directly detected in these herds using microsatellite markers, but it is highly suggested due to the source of the herd and/or initial testing using single nucleotide polymorphisms (Robert Schnabel, pers .comm.).

^c R_A, average of allelic richness values across markers; calculated based on a minimum sample size of 15 (El Mousadik and Petit 1996).

^d H_E, average expected heterozygosity (Nei 1987).

^e F_{ST} averaged across clusters assigned by STRUCTURE (Evanno et al. 2005) analysis.

^f These (composite) herds were assigned to multiple clusters. Average F_{ST} calculations not possible.

⁹ The TRN herd is directly descended from the TRS herd, which was in turn derived directly from the FN herd. It is well-established from other indices that these three herds (TRN, TRS, and FN) are closely related. Drift has likely acted to drive allele frequencies within this herd and differentiation of this herd such that inflated average F_{ST} values are detected.

^h Based on analysis of herd contribution to overall diversity, following Petit et al. 1998. These herds represent unique sources of bison diversity which is unreplicated among the DOI herds.

^{*} The entire Sullys Hill herd was moved to Fort Niobrara NWR in 2006. They are maintained separately from the original Fort Niobrara herd.

^{**} Based on genetic evaluation, in 2006, all bison at Neal Smith were donated to a local Native American tribe, and a new herd was established with 39 bison from the National Bison Range.

^{***} Established with bison from the National Bison Range in 2006–2007.

^{****} Yellowstone bison of are two distinct but closely related types (Halbert and Derr 2007b, Gardipee 2007).

Workshop Recommendations

Recommendations emerging from the Bison Genetics Workshop addressed the two long-term challenges facing DOI herds where genetic conservation is a primary management goal: actions to limit the effects of historical introgression and actions to maintain genetic diversity. Implementing the following actions will help sustain the genetic integrity of DOI bison herds. In addressing these challenges, research recommendations are made to resolve identified uncertainty and to allow for more informed decision-making in the future. These recommendations are summarized in Tables 2, 3, and 4.

Management to Limit Introgression

We recommend management actions that decrease or prevent the spread of cattle ancestry in any existing herds or new conservation herds.

Because of the cattle-bison hybridization that occurred in private herds when plains bison were saved from extinction in the 1800s and because animals from those herds were used to found or augment the DOI herds, no herd can be absolutely assured to have no cattle ancestry. That said, conservation herds, including those of the Department of the Interior, can be grouped into four classes: 1) those with no molecular evidence of cattle introgression; 2) those with molecular evidence of low levels of cattle introgression; 3) those with historical inference of cattle ancestry but no molecular evidence with the current DNA markers; and 4) those where molecular markers indicate high levels of cattle ancestry and/or recent hybridization with domestic cattle. We have specific recommendations for each of these classes, but all follow from the overarching recommendation to prevent the increase of bison with cattle ancestry in DOI herds.

- 1) No molecular evidence of cattle ancestry: Herds with no molecular evidence of cattle ancestry constitute a genetic resource that must be protected from inadvertent introgression. Yellowstone National Park has the only DOI herd where there is no suggestion of cattle introgression using all of the available molecular methods. The Yellowstone bison population requires further testing, as do non-DOI herds established with Yellowstone bison. There should be no introduction of bison to these herds from herds that show molecular evidence of cattle ancestry or for which the genetic status in unknown. High priority should be given to creating satellite herds for these herds on DOI-managed lands. Moreover, where the risk is great for inadvertent interbreeding with bison from adjacent herds that show high levels of cattle ancestry, herd boundaries should be secured by the appropriate means, trespass animals should be removed, and genetic testing should be conducted to confirm that the two herds are not mixing.
- 2) Molecular evidence of low-level cattle ancestry: Bison in DOI herds demonstrated to have detectable cattle ancestry at low levels have important genetic value and contain unique genetic variation that is absent from Yellowstone or other conservation herds with no molecular evidence of cattle ancestry. All DOI herds fall well below 2% of cattle genes at the current molecular markers and a threshold for conservation herds was suggested at the workshop. These herds should not be used to augment herds with no molecular evidence of cattle ancestry. While removal of individuals with cattle mtDNA haplotypes is warranted, selection on the basis of cattle alleles at nuclear loci could have unintended consequences of reducing overall variation. Herds with low levels of cattle ancestry that are not genetically unique should be the lowest

priority for herd expansion and transfer to other locations. The historical Fort Niobrara bison and the two bison herds at Theodore Roosevelt NP should be identified and managed as a metapopulation to ensure the persistence of rare alleles in all three herds.

The National Bison Range (NBR) herd is of interest because it represents a geographic lineage from the northern Montana region. An introduction of bison into this herd with molecular evidence of recent cattle introgression was reversed by DNA detection and swift management action (L. Garner, pers. comm. in Halbert 2003). Molecular evidence indicates that bison with introgressed cattle genes joined this herd prior to the 1980s (Halbert 2003, Halbert and Derr 2007a). Moreover, there are three state-owned plains bison herds in Alaska that may represent an unbranched lineage to the NBR herd that predates any introgression of cattle genes. If genetic testing identifies sufficient numbers of NBR-source bison free of cattle ancestry and with sufficient genetic variation, then the establishment of herds using these animals should be a high priority.

- 3) Historical suggestion of cattle ancestry: There is the possibility of cattle ancestry in all DOI herds, since those herds with no molecular evidence of cattle ancestry have Yellowstone origins and three male bison from the Goodnight herd (now Texas State Bison Herd) were introduced to Yellowstone in 1902 (Coder 1975, Meagher 1973). It is not clear whether cattle-bison breeding experiments had begun in the Goodnight herd prior to translocation of bull bison to Yellowstone NP, or whether he would have sent hybrids to Yellowstone NP. In some cases, the historical suggestion is stronger, such as with the Grand Teton/National Elk Refuge herd, which was augmented with 12 bison from Theodore Roosevelt NP, where cattle ancestry had been detected in 1964. To date there is no molecular evidence that these animals contributed to the current population (Halbert and Derr 2007a). In this case, as in others, higher resolution DNA testing may reveal traces of cattle ancestry, but the herds nonetheless have an important contribution to bison conservation.
- 4) Molecular evidence of higher levels of cattle ancestry: This category does not apply to any DOI herds but does apply to a number of other conservation herds that border DOI lands. Because the goal is for some DOI bison herds to move across landscapes and jurisdictions, evaluation of neighboring herds is important. When the level of cattle introgression is high, augmentation or systematic herd replacement should be considered, using animals made available from DOI herds or other sources that represent the same lineages. Genetic monitoring is a key part of management to determine the effectiveness of these efforts.

Management to Retain Genetic Diversity

We recommend that each DOI herd achieve a population size of 1,000 animals in the next 10 years. This can include identification of existing satellite and closely related herds, as well as the establishment of new satellite herds to achieve metapopulations of 1,000 bison.

With respect to the risk of losing genetic diversity, it is well understood that population size is a strong correlate of the rate of loss of genetic diversity. Therefore, we group DOI herds into three population size classes: 1) those with a population of greater than 1,000 bison; 2) those with between 500 and 1000 bison; and 3) those with fewer than 500 bison. We have specific

recommendations for each of these classes, but all follow from the overarching need to prevent the loss of genetic diversity by creating large herds. The last of these categories requires the most attention and additional research to resolve uncertainty regarding how best to slow the loss of genetic diversity.

- 1) Populations estimated at greater than 1,000: Yellowstone bison constitute the only DOI herd with a population size greater than 1,000, and even in this population the degree of genetic structure within the entire herd is unresolved (Halbert 2003, Gardipee 2007). In addition, the current practice of culling bison at the park's boundaries may lead to the removal of matrilineal groups and thereby allelic diversity (Halbert 2003). Further assessments of population substructure and the potential impacts of the current culling practices are recommended.
- 2) Populations estimated at 500–1,000: Three current herds—Wichita Mountains National Wildlife Refuge (WM), Badlands National Park (BNP), and Grand Teton/Elk Refuge (GT/NER)—have estimated population sizes greater than 500, and herd-specific management plans should be created for each within the next five years. The goal of these plans would be to manage each herd to approach 1,000 bison, either as a single herd or by creating metapopulations with formal plans for moving animals within metapopulations. The plans should ensure that there is no risk of interbreeding with other bison of uncertain genetic status or with known cattle introgression. These populations should be monitored for changes in heterozygosity and other measures of genetic diversity to ensure maintenance of genetic diversity and monitored for signs of demographic fitness changes (e.g., mating rates, reproduction, and survival).
- 3) Populations below 500: The remaining nine herds are at risk due to the loss of genetic diversity. We recommend immediate and aggressive actions to increase the size of these herds. A combination of actions may be needed to prevent rapid loss of diversity. Within this critical population size class, we have a set of recommended management actions and recommended research to support more effective small-population management.

Small-population management

First, because many of these small herds are limited by the size of their park or reserve, we recommend reviewing current unit management plans to explore the possibility of increasing the size of each bison herd to greater than 500. This may be achieved by establishing satellite herds to comprise a metapopulation, adjusting the abundance of other ungulate populations, and increasing bison carrying capacity by range expansion through identification of neighbors willing to have bison on their lands.

Second, intensive genetic and demographic management of the herds is vital to slowing the loss of genetic diversity. We recommend that several actions be taken until these populations can be increased:

• *Maintain stable population sizes*: Based on well-established genetic population theory, fluctuations in population size increase the rate of genetic loss. Any necessary population reductions should be small and frequent to create minor adjustments as opposed to large and infrequent adjustments.

- Maximize the number of breeding males: Observation has shown that there can be strong sexual selection in small bison herds. That is, the majority of offspring come from a small proportion of males, which reduces the effective population size and increases the loss of genetic diversity over time. As an initial step, we recommend using DNA methods to measure genetic contribution of individual males in small isolated herds. Restricting the breeding opportunity of successful bulls, however, should not be a routine practice.
- Approach a 1:1 sex ratio: We know from genetic theory that the loss of genetic diversity is slowest when the number of males approaches the number of females. In small herds, chance events (demographic stochasticity) can lead to uneven sex ratios. When the number of males drops below 40%, there is also the potential for reduced competition and loss of fitness. Culling and translocation plans should strive to approach an even sex ratio in herds, considering differential mortality.
- Remove young animals: When herd size is limited by carrying capacity and bison are removed annually (or every other year), more young bison should be removed to reflect natural predation mortality. In the smallest of herds, the loss of genetic diversity can be reduced by increasing the age of reproduction (Gross et al. 2006). It is suggested that herd demographics in small populations should be influenced by culling and providing young animals to establish new herds rather than through contraception.
- Increase genetic diversity: Finally, we recommend augmenting herds with additional animals if genetic testing for heterozygosity shows results below 0.5. No DOI herd currently approaches this threshold, but it has occurred in the Texas State Bison Herd when the herd also showed a substantial decline in reproduction. It is therefore important to also monitor fitness values and their possible decline. Augmentation with additional animals has increased genetic diversity and removed the manifestations of inbreeding depression in the Texas State Bison Herd and in other confined species. We recommend similar actions if any DOI herd experiences symptoms of poor genetic health, and we recommend following the guidelines in the introgression section whenever translocation is performed.

Research Recommendations

We recommend the development and application of more high-resolution molecular markers to identify the presence of cattle ancestry in existing herds, to prevent the spread of cattle ancestry to new conservation herds, and to monitor the genetic variation in DOI herds.

Continue to identify and develop a suite of molecular markers, including single nucleotide polymorphisms that are used for on-going genetic sampling of all DOI herds. Encourage other managers of conservation herds to apply the markers and protocols to their bison herds. New markers should be evaluated in peer-reviewed literature before they are added to herd genetic-sampling protocols.

Research to address uncertainty in small-population management

We know that the bison population sizes of 1,000 and 500, whether they represent survey, census, or breeding numbers, are significantly below the effective population size that many population geneticists see as necessary to secure genetic variation in bison over centuries. Theoretically the loss of genetic diversity is proportional to the effective population size (N_e , essentially, the number of individuals that contribute to breeding). We know that the effective population size of bison herds is lower than the breeding number and probably significantly lower than the estimated population size (N_e), but we do not know how much lower. To better manage small herds, we need more accurate estimates of the N_e/N ratio over time in existing populations and an analysis of the magnitude of the effect of factors that influence N_e/N (e.g., sex ratio, sexual selection, population age distribution, and other factors).

Intensive breeding management is being used in some of the smaller DOI herds, with all animals genetically screened and individuals selected so that all bison alleles are conserved in each generation. This strategy had support at the workshop for the elimination of cattle mitochondrial DNA haplotypes, where it is well established that selection could be occurring. Selection for particular alleles of neutral microsatellite loci would not eliminate cattle characters or change cattle ancestry and was not supported, as it could result in loss of the bison genetic variation it seeks to preserve.

Even with the existing data on bison, more informed management decisions could be made by using decision-support tools that use models to evaluate costs and benefits of management alternatives. For example, Halbert et al. (2005) created and used an individual-based model to evaluate management strategies for the Texas State Bison Herd that exhibited low genetic diversity and signs of low fitness, and Gross et al. (2006) evaluated a range of management alternatives and population targets to retain genetic diversity in bison herds. Incorporating extensive genetic data into a model would allow quantitative evaluation of a number of different strategies and provide transparency to the final decision. Other models have used stochastic simulation processes to determine which management strategies would result in the greatest genetic diversity over time for wood bison (Macfarlane et al 2006). In a structured decision process, models are essential.

Additional research to minimize potential introgression events

The risk of increasing the proportion of cattle ancestry in a herd is a major factor in selecting bison for movement between herds. It is important, therefore, to reduce uncertainty about the history of cattle ancestry in DOI and other conservation herds. The projects below are intended to provide the information necessary to minimize further introgression of livestock genes into DOI bison herds.

Develop and apply higher resolution molecular techniques to guide bison management: Molecular methods currently utilized in bison management (mtDNA and microsatellites) are only capable of resolving hybridization at the herd level. While these measurements can determine the presence of cattle genes, the absence of detectable cattle genes does not indicate unequivocally that hybridization has not occurred historically. The development and application of new molecular methods, such as single nucleotide polymorphic (SNP) markers, can provide much higher resolution, and these markers are already being developed for other ruminants (Van Tassel et al. 2008, Pertoldi et al. 2010, Decker et al. 2009). These markers could be used to

detect recent hybridization and to reduce its effect on conservation herds by removing specific individual bison from an existing herd, or for selecting non-introgressed individuals for translocation. These markers will also have value beyond detection of cattle ancestry. They can be used to monitor genetic variation in herds and to choose animals for transfer between closely related herds, and to better understand the relation between census and effective population size. New markers should be evaluated in peer-reviewed literature before they are added to genetic-sampling protocols.

Evaluate historic lineages and spatial genetic structure: The previous century of bison management (e.g., anthropogenic movement and re-establishment of herds) has likely wiped out the plains bison historical genetic structure. Reconstructing this history is likely to provide valuable insight into resolving and maintaining lineages to allow or prevent herd mixing. We recommend studies to analyze historical structure:

- Analyze bison samples that were collected before widespread introgression. Sources include museums, archeologists, and historic buffalo jumps. Extract DNA from teeth, bone, and untanned capes, in that order.
- Create mtDNA maps for historic herd structure and spatial structure by sampling contemporary bison herds.

Conclusions

The bison herds of the U.S. Department of the Interior constitute an invaluable resource and a keystone species in prairie and woodland ecosystems. By the efforts of citizens that saved the remnant bison and of the managers that have been entrusted with them, a remarkable amount of the North American bison genome has been preserved. No emergency actions are necessary to continue that preservation, but concerted actions by researchers and managers are needed if North American bison are to be conserved in their diversity for decades and centuries.

Herd sizes must be increased, and where there is not adequate land to support larger populations, satellite herds must be established with exchange of animals to constitute metapopulations. This requires close cooperation between government agencies, including the integration of management plans. Most importantly, management of bison must be refocused to the landscape scale, where natural selection can work to preserve variation.

Table 2. Recommendations to limit bison introgression in DOI bison herds.

	INTROGRESSION		
	Recommendation	Mechanism	Management
Maintain genetic integrity	Introduce individuals to a herd only when they do not increase overall levels of cattle ancestry	Test both donor and recipient herd for cattle markers before any translocation	Perform regular sampling and routine testing of DOI herds either during handling or by remote methods
	As a very high priority, maintain genetic isolation of herds that exhibit no DNA evidence of cattle ancestry	Secure boundaries by all appropriate means. Remove or eliminate trespass animals; test to confirm origin of trespass animals whenever possible	Install secondary fencing and perform regular testing
	Minimize historic cattle ancestry when establishing new herds, while maximizing preservation of existing genetic variation	Test herds to confirm that they do not have cattle mtDNA haplotypes and for the presence of bison with cattle microsatellite alleles	Perform genetic monitoring of satellite herd to test for drift as well trespass animals
	Separate wood and plains bison herds to avoid interbreeding and to maintain morphological and behavior differences that have a genetic basis	Use genetic analysis to evaluate the current distinctiveness of wood and plains bison herds	Support Wood Bison Recovery Strategy. As more bison markers are developed, test plains and wood bison for significant differences in marker frequency

Table 3. Recommendations to retain genetic diversity in DOI bison herds.

	PRESERVING VARIATION		
	Recommendation	Mechanism	Monitoring
Population size (loss of genetic variance over time)	Achieve herd size of 1,000 bison or more at a location whenever possible	If 1,000 or more, no action (herds with more than 1,000 bison do not require active genetic management under normal conditions) If fewer, attempt to increase size/capacity	Census or survey: The goal is to move conservation herds to a size where they do not require active genetic management
	Regularly test herds of 500 to 1,000 for heterozygosity and other measures of genetic diversity. Seek ways to increase effective herd size	Develop herd-specific management plan within (5) years	
	Actively manage herds of fewer than 500 bison to sustain adequate genetic variation	Occasionally supplement with additional genetic material, following guidelines for donor animals	
Demography – effective population size	In small(er) herds, minimize fluctuations in population size to maximize $N_{\rm e}$	For managed populations, conduct removals frequently, rather than less frequent large removals	
	In small herds, maintain a sex ratio approaching 1:1, but no more than 60% of either sex	Remove animals of relevant sex	Monitor demographics; measure genetic contribution of bulls
	In small herds, use management strategies that maintain generation interval	In the absence of predation, remove young animals in preference to old	Monitor lifetime reproductive success, particularly of bulls
Manage to minimize inbreeding	Supplement herds with additional genetic material if heterozygosity falls below 0.50 based on the 33 microsatellites	Move animals into herds based on guidelines for animal movements	Herds approaching threshold should be monitored for heterozygosity every year to avoid or alleviate signs of inbreeding depression
Facilitate adaptation and natural selection	When removing animals to control herd size, do not select for traits such as docility, body conformation, etc.	Randomly remove animals from within sex and age classes to achieve desired population structure	
	Maintain and allow the full range of natural selection pressures to operate where possible (e.g., predation, competition for mates)	Provide sufficient space for normal range of behaviors	

		To extent possible, retain spatial substructure of populations	Remove animals from all spatial segments of the population. Provide sufficient space for herds to naturally subdivide
		Maintain and allow the full range of natural selection pressures to operate where possible (e.g., predation, competition for mates)	Provide sufficient space for normal range of behaviors
		To extent possible, retain spatial substructure of populations	Remove animals from all spatial segments of the population. Provide sufficient space for herds to naturally subdivide
	Minimize risk among population of losing genetic diversity to drift	Establish multiple populations of highly valued herds	
		Create guidelines for prioritizing establishment of new populations	
1		When considering exchange between populations (lineages), use the best information (preferably results from historical genetic analyses) to determine and maintain historical genetic patterns and lineages of the species to the extent possible	
		If conserving lineages is important, the ideal donor herd should have a genetic, ecological, or historical link to the recipient herd	Examine genetic correspondence of potential donors and match to recipient, considering ability of donors to achieve other recommendations (e.g., achieve diversity goal)
		Attempt to replicate significant lineages (YELL, WM, WC) via satellite herd establishment	

Table 4. Recommendations for research priorities in bison genetics.

		RESEARCH	
Purpose	Recommendation	Mechanism	Monitoring
Resolving introgression	Identify and develop a suite of molecular markers, including Single Nucleotide Polymorphism (SNP) technology, for testing of all DOI herds	Transfer development of SNP technology from cattle to bison	Sample all DOI herds and conservation herds managed by other federal and state/provincial agencies, tribal/First Nation organizations, and NGOs in North America
	Develop models utilizing decision-support tools to evaluate costs/benefits of alternative management strategies for bison conservation	Fund model development	Use models to evaluate a range of specific management strategies prior to translocation of bison between herds and establishment of new herds
	Evaluate historic lineages and spatial genetic structure	Analyze historic samples utilizing advanced DNA methodologies, including SNPs when available	Include in decision-support models to assess bison translocations
	Estimate effective population size and N _e /N ratio in existing populations and evaluate sources of variation	Perform genetic testing and characterization of entire herds over a period of years to establish breeding success	Test all animals during management of small herds

Literature Cited

- Aune, K., and R. Wallen. 2010. Legal status, policy issues and listings. Pages 63–84 *in* C.C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. American bison: status survey and conservation guidelines. IUCN/SSC Bison Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.
- Berger, J. and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbian University Press, New York.
- Boyd, D. P., G. A. Willson, J. N. Derr and N. D. Halbert. 2010. Genetics. Pages 19–26 *in* C.C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. American bison: status survey and conservation guidelines 2010. IUCN/SSC Bison Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.
- Boyd, M. M. 1908. A short account of an experiment in crossing the American bison with domestic cattle. *Annual Report of American Breeders Association* 4:324–331.
- Boyd, M. M. 1914. Crossing bison and cattle. *Journal of Heredity* 5:189–197.
- Brower, J. 2008. Lost tracks: Buffalo National Park 1909–1939. Athabasca University Press, Edmonton, Alberta.
- Coder, G. D. 1975. The national movement to preserve the American buffalo in the United States and Canada between 1880 and 1920. Dissertation. The Ohio State University, Columbus, Ohio.
- Dary, D. A. 1989. The buffalo book: the full saga of the American animal. The Swallow Press Inc./Ohio University Press, Athens, Ohio.
- Decker J. E., Pires J. C., Conant G.C., McKay S.D., Heaton M. P., Vilkki J., Seabury C. M., Caetano A. R., Johnson G. S., Brenneman R.A., Hanotte O., Eggert L.S., Wiener P., Kim J.J., Kim K.-S., Sonstegard T. S., Van Tassell C. P., Neibergs H. L., Chen K., Cooper A., McEwan J. C., Brauning R., Coutinho L. L., Babar M. E., Wilson G.A., McClure M.C., Rolf M.M., Kim J.-W., Schnabel R.D., and Taylor J.F. 2009. High—Throughput Phylogenomics: From Ancient DNA to Signatures of Human Animal Husbandry. *Proc Natl Acad Sci USA* 106:18644-18649.
- Mousadik, A. and Petit, R. J. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. *Theoretical and Applied Genetics* 92:832-839.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* 14:2611–2620.
- Flores, D. 1991. Bison ecology and bison diplomacy: the southern plans from 1800 to 1850. *The Journal of American History* 78:465–485.

- Gardipee, F. M. 2007. Development of fecal DNA sampling methods to assess genetic population structure of Greater Yellowstone bison. Thesis. University of Montana, Missoula, Montana.
- Garretson, M.S. 1938. The American bison: the story of its extermination as a wild species and its restoration under federal protection. New York Zoological Society, New York, New York.
- Gates, C. C. and K. Ellison. 2010. Numerical and geographic status. Pages 55–62 *in* C.C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. American bison: status survey and conservation guidelines 2010. IUCN/SSC Bison Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.
- Goodnight, C. 1914. My experience with bison hybrids. *Journal of Heredity* 5:197–199.
- Gross, J. E., and G. Wang 2005. Effects of population control strategies on retention of genetic diversity in National Park Service bison (*Bison bison*) herds. Final Report Submitted to Yellowstone Research Group USGS-BRD, Bozeman, Montana.
- Gross, J. E., G. Wang, N. D. Halbert, P. J. Gogan, J. N. Derr, and J. W. Templeton. 2006. An evaluation of the effects of population control strategies on retention of genetic diversity in National Park Service bison (*Bison bison*) herds. Report to USGS-BRD, Bozeman, Montana, for the National Park Service.
- Halbert, N. D. 2003. The utilization of genetic markers to resolve modern management issues in historic bison populations: implications for species conservation. Dissertation. Texas A&M University, College Station, Texas.
- Halbert, N. D., T. Raudsepp, B. P. Chowdhary, and J. N. Derr. 2004. Conservation genetic analysis of the Texas state bison herd. Journal of Mammalogy 85:924-931.
- Halbert, N. D., Ward, T. J. Schnabel, R. D., Taylor, J. F., Derr, J. N. 2005. Conservation genomics: disequilibrium mapping of domestic cattle chromosomal segments in North American bison populations. *Molecular Ecology* 10:2343–2362.
- Halbert, N. D. and Derr, J. N. 2007a. A comprehensive evaluation of the introgression of cattle into the U.S. federal bison herds. *Journal of Heredity* 98:1–12.
- Halbert, N. D. and Derr, J. N. 2007b. Genetic subdivision in Yellowstone bison. Final project report to USGS BRD, Bozeman, Montana.
- Halbert, N. D. and Derr, J. N. 2008. Patterns of genetic variation in the U.S. federal bison herds. *Molecular Ecology* 17:4963–4977.
- Halbert, N. D., Gogan, P. J. P, Hiebert, R., Taylor, J. F., Derr, J. N. 2008. Where the buffalo roam: the role of history and genetics in the conservation of bison on U.S. federal lands. *Park Science* 24(2):22–29.

- Hartl, D. L. and A. G. Clark. 2007. Principles of Population Genetics, 4th ed. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Hedrick, P. W. 2005. Genetics of populations, 3rd ed. Jones and Bartlett, Boston, Massachusetts.
- 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. *Molecular Ecology* 19:3328–3335.
- Hewitt, C. G. 1921. The conservation of the wildlife of Canada. C. Scribner's Sons, New York, New York.
- Hornaday, W. T. 1889. The extermination of the American bison, with a sketch of its discovery and life history. Annual report of the Board of Regents of the Smithsonian Institution for the year 1887, part 2. Government Printing Office, Washington, D.C.
- Hornaday, W. T. 1927. Hornaday's American Natural History. Charles Scribner's Sons, New York, New York.
- Isenberg, A. C. 2000. The destruction of the bison: an environmental history, 1750–1920. Cambridge University Press, New York, New York.
- Jones, C.J. 1907. Breeding cattelo. Annual Report of American Breeders Association 3:161–165.
- Keller, L. F., and D. M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17:230–241.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- List, R., G. Ceballos, C. Curtin, P. J. P. Gogan, J. Pacheco, and J. Truett. 2007. Historic distribution and challenges to bison recovery in the northern Chihuahuan desert. Conservation Biology 21:1487-1494.
- Lothian, W. F. 1981. A history of Canada's national parks, vol. 4. Parks Canada, Minister of Supply and Services Canada, Ottawa, Ontario.
- Meagher, M. 1973. The bison of Yellowstone National Park. Government Printing Office, Scientific Monographs 1, National Park Service, Washington, D.C.
- Menges, E. S. 1991. Seed germination percentage increases with population size in a fragmented prairie species. *Conservation Biology* 5:158–164.
- Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, New York.
- Pertoldi C., J. M. Wo'jcik, M. Tokarska, A. Kawałko, T. N. Kristensen, V. Loeschcke, V. R. Gregersen, D. Coltman, G. A. Wilson, E. Randi, M. Henryon, C. Bendixen. 2010. Genome

- variability in European and American bison detected using the BovineSNP50 BeadChip. *Conservation Genetics* 11:627-634.
- Petit, R. J., A. Elmousadik, and O. Pons. 1998. Identifying populations for conservation on the basis of genetic markers. *Conservation Biology* 12:844–855.
- Potter, B. A., S. C. Gerlach, C. C. Gates. 2010. History of bison in North America. Pages 5–12 *in* C. C. Gates, C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors. American bison: status survey and conservation guidelines 2010. IUCN/SSC Bison Specialist Group. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- Plumb, G. E., P. J. White, M. B. Coughenour, R. L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation* 142:2377–2387.
- Polziehn, R. O., C. M. Strobeck, J. Sheraton, R. Beech. 1995. Bovine mtDNA discovered in North American bison populations. *Conservation Biology* 9:1638–1643.
- Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* 392:491–494.
- Shaw, J. H. 1995. How many bison originally populated western rangelands? *Rangelands* 17:148–150.
- Soper, J. D. 1941. History, range and home life of the northern bison. *Ecological Monographs* 11:347–412.
- Steklenev, E. P., and N. I. Yasinetskaya. 1982. Results of crossing of the bison (*Bison bison bison L.*) with the domestic cow (*Bos (Bos) taurus typicus*) and characteristics of the chromosome complexes of the hybrid progeny. *Tsitologiia i genetika* 16:28–33.
- USDI and USDA (U.S. Department of the Interior, National Park Service, and U.S. Department of Agriculture, Forest Service, Animal and Plant Health Inspection Service). 2000. Record of decision for final environmental impact statement and bison management plan for the State of Montana and Yellowstone National Park, Washington, D.C.
- USFWS and NPS (U. S. Fish and Wildlife Service and National Park Service). 2007. Final bison and elk management plan and environmental impacts statement for the National Elk Refuge/Grand Teton National Park/ John D. Rockefeller Jr. Memorial Parkway, Teton County, Wyoming, Volume 1. U. S. Government Printing Office, Washington, D. C.
- Van Tassell CP, Smith TPL, Matukumalli LK, Taylor JF, Schnabel RD, Lawley CT, Haudenchild CD, Moore SS, Warren WC and Sonstegard TS. 2008. Simultaneous SNP discovery and allele frequency estimation by high throughput sequencing of reduced representation genomic libraries. *Nature Methods* 5:247-252
- Ward T. J., J. P. Bielawski, S. K. Davis, J. W. Templeton, J. N. Derr. 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.

Westemeier, R. L., J. D. Brawn, S. A. Simpson, T. L. Esker, R. W. Jansen, J. W. Walk, E. L. Kershner, J. L. Bouzat, and K. N. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695–1698.

Appendix A. Participants in the Bison Conservation Genetics Workshop held in Nebraska City, Nebraska

Name	Affiliation	Position
Kaush Arha	Department of the Interior	Deputy Assistant Secretary Fish, Wildlife & Parks
Keith Aune	Wildlife Conservation Society	Senior Conservation Scientist
Scott Baker	Oregon State University	Associate Director, Marine Mammal Institute
James Derr	Texas A&M University	Professor of Genetics, College of Veterinary Medicine and Biomedical Sciences
Peter Dratch	National Park Service	Zoologist, Endangered Species Program Manager
Peter Gogan	U.S. Geological Survey	Research Wildlife Biologist, Northern Rocky Mountain Science Center
John Gross	National Park Service	Ecologist, Inventory and Monitoring Program
Natalie Halbert	Texas A&M University	Research Assistant Professor
Phil Hedrick	Arizona State University	Ullman Professor of Conservation Biology
Briar Howes	Parks Canada	Species at Risk Biologist
Lee Jones	U.S. Fish & Wildlife Service	Wildlife Health Biologist
Eric Lonsdorf	Lincoln Park Zoo	Director, Urban Wildlife Institute
Cecilia Penedo	University of California, Davis	Associate Director, Veterinary Genetics Laboratory
Kent Redford	Wildlife Conservation Society	Vice President, Conservation Strategies
Tom Roffe	U.S. Fish & Wildlife Service	Wildlife Disease Ecologist
Oliver Ryder	San Diego Zoo	Kleberg Associate Director, Head of Genetics Division
Danny Swepston	Texas Parks and Wildlife	Wildlife Biologist
Greg Wilson	Canadian Wildlife Service	Species at Risk Biologist

Appendix B. Workshop Agenda

Bison Genetics Workshop Lied Conference Center September 2–5, 2008

Tuesday, September 2

4:30 p.m. Gather – introductions and agreement on meeting objectives

Peter Dratch, Eric Lonsdorf

6:00 Dinner

7:00 Welcome and charge – Deputy Assistant Secretary Kaush Arha

A brief history of bison conservation – Kent Redford

Wednesday, September 3 Issue: Introgression and hybridization

6:30–8:30 a.m. Breakfast buffet

8:30 Gather and informal discussion

Genetic management plans that take a century view – Ollie Ryder The tools of the trade: molecular methods in use – Cecilia Penado

10:30 Break

11:00 Evidence of introgression in NA bison herds – Jim Derr

Hybridization of wood and plains bison – Greg Wilson

Noon Lunch

1:00 p.m. Establishing thresholds for cattle introgression – Eric Lonsdorf

Maintaining distinctness of NA bison subspecies

3:00 Break

Developing suggested guidelines on hybridization

Research priorities and their implications

6:00 Dinner

7:30 Subgroups working on introgression and research meet

Thursday, September 4 Issue: Maintaining variation in bison herds

6:30–8:30 a.m.	Breakfast buffet
8:30	Gather and report back of subgroups Maintaining intraspecific variation – John Gross Methods and measures for preserving variation – Tom Roffe Heterozygosity, allelic richness, etc. Remote biopsy sampling and genetic monitoring – Scott Baker
10:30	Break
11:00	Comparison of variation in conservation herds – Natalie Halbert Examining relationship between herds
Noon	Lunch
1:00 p.m.	Establishing targets for genetic variation – Eric Lonsdorf Minimum herd size; sex and age structure Methods of gene exchange in a conservation framework
3:00	Break
3:30	Developing guidelines for genetic health of NA bison Sample collection, storage and distribution
6:00	Dinner
7:30	Subgroups working on variation and sampling meet

Friday, September 5

6:30-8:30 a.m.	Breakfast buffet
8:30	Gather and report back of subgroups – Eric Lonsdorf Discussion of final recommendations on bison hybridization Discussion of final recommendations on bison variation
10:00	Break
10:30	Discussion of final recommendations on research and sampling Closing comments
11:30	Adjourn

Appendix C. U.S. Department of the Interior Herd Histories

Badlands National Park

Bison have continued to be the dominant large herbivore of Badlands National Park (BADL) since their establishment in 1963 through the restoration of 25 bison from Theodore Roosevelt National Park in North Dakota and three bison from Fort Niobrara National Wildlife Refuge in Nebraska. All of these animals originated from the Fort Niobrara herd. Twenty additional bison were restored to BADL in 1983 from Colorado National Monument (CNM), whose original lineage was from a 1925 Denver, Colorado, herd. All animals from both lineages have had the opportunity to interbreed since 1983.

The bison herd at BADL increased dramatically from these original bison restorations in 1963 and 1983. Between the years of 1983 and 1987, an extensive research effort was conducted at BADL. The population peaked at more than 1,000 animals, and annual recruitment rates were greater than 50%. The current population is regulated opportunistically when numbers exceed 600 animals. BADL conducted annual roundups from 2002 through 2007, and bison of different ages and sexes were given to the InterTribal Bison Cooperative (ITBC) and Ogalala Sioux Parks and Recreation Authority (OSPRA). The ITBC distributes bison to Native American tribes trying to establish bison populations on their lands. Donating the bison to the ITBC and OSPRA are the main avenues that BADL uses to regulate the current population that inhabits the 64,000-acre Sage Creek Unit of the BADL Wilderness Area.

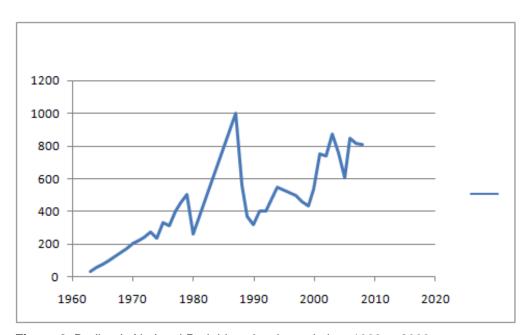


Figure 2. Badlands National Park bison herd population, 1963 to 2009.

Fort Niobrara National Wildlife Refuge

Fort Niobrara National Wildlife Refuge (NWR) consists of 19,131 acres located in north-central Nebraska along the Niobrara River. The refuge was established in 1912 as a "preserve and breeding ground for native birds." Later that same year, its purpose was expanded to include the conservation of bison and elk herds representative of those that once roamed the Great Plains. Prescribed fire and planned periods of rest, or non-disturbance, are used in combination with grazing by bison and elk in an effort to mimic historic processes that helped shape the native plant communities on the refuge. As many as 100,000 people visit Fort Niobrara NWR each year to see, appreciate, and learn about wildlife and their habitats.

The Fort Niobrara bison herd was founded in 1913 with the donation of six bison from J.W. Gilbert of Friend, Nebraska, and the transfer of two males from Yellowstone National Park. Additional introductions were made in 1935 (Custer State Park), 1937 (Custer State Park), and 1952 (National Bison Range).

Bison have been rounded up by refuge staff on horseback annually since the early 1930s to remove surplus animals, complete health testing, vaccinate, and/or mark animals. The entire bison herd tested negative for brucellosis in 1965 and was declared brucellosis-free in 1974 by the State of Nebraska. A comprehensive bison herd health monitoring program was initiated in 2003, and bison are no longer routinely vaccinated. The animals are individually identified with microchips.

Currently, both the Fort Niobrara and Sullys Hill bison herds are managed separately by fence on the refuge. In order to manage the refuge within carrying capacity (approximately 350 bison total), the Fort Niobrara herd will likely be reduced in future years to accommodate the growing Sullys Hill herd.

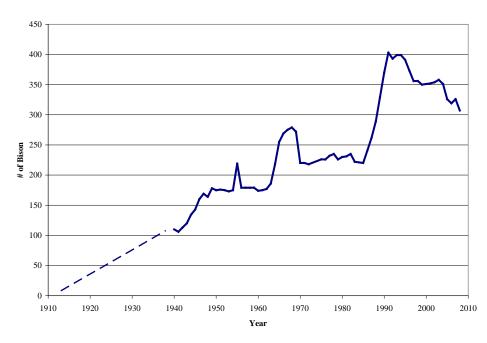


Figure C-2. Fort Niobrara National Wildlife Refuge bison herd population, 1913 to 2009.

Grand Teton National Park – National Elk Refuge (Jackson Bison Herd)

Bison were extirpated from Wyoming around Jackson Hole by the mid-1880s. In 1948, 20 bison from Yellowstone National Park were reintroduced to the 1,500-acre Jackson Hole Wildlife Park near Moran, Wyoming. A population of 15–30 bison was maintained there in a large exclosure until 1963, when brucellosis was discovered in the herd. All the adult animals were destroyed, but four vaccinated yearlings and five vaccinated calves were retained. Twelve certified brucellosis-free bison were added soon afterward from Theodore Roosevelt National Park. In 1968, the herd (down to 11 animals) escaped from the confines of the wildlife park, and a year later the decision was made to allow them to range freely. In 1975, the small Jackson Bison Herd began wintering on the National Elk Refuge, and the use of standing forage by bison on this winter range was viewed as a natural behavior and was not discouraged by managers. By 1980, however, the bison began eating supplemental feed provided for the elk, and they have continued to do so every winter since.

The discovery of supplemental feed by bison has had several consequences, including a decline in winter mortality and an increase in the population's growth rate. The Wyoming Game and Fish Department implemented a bison hunting season on lands outside Grand Teton National Park and the National Elk Refuge in 1997, but typically only 40 animals were harvested per year, and the effect on the population was minimal. The population increased approximately 10–14% per year between 1990 and 2007 and peaked at 1,059 animals in 2007. The Elk and Bison Management Plan and EIS was adopted in 2007. Under this plan the post-hunt objective is 500 bison, and the open hunting area was expanded to include the National Elk Refuge. During the 2007 harvest, 266 animals were removed, reducing the population to 920 during the 2008 winter count. The objective is to harvest 300 bison per year until the 500 objective is reached, at which time harvest levels will be reduced to maintain the population at 500.

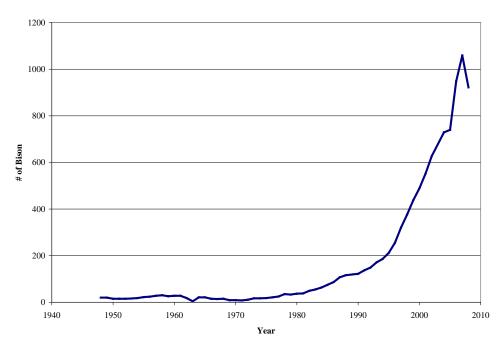


Figure C-3. Jackson Bison Herd (Grand Teton National Park/National Elk Refuge) population, 1948 to 2008.

National Bison Range

The National Bison Range, established in 1908 with the first Congressional appropriations ever made for the purchase of lands for a wildlife refuge, consists of 18,799 acres of Palouse prairie in northwest Montana. The refuge was established to provide "...for a permanent national bison range for the herd of bison..." Its purpose was expanded in 1921 to function "...as refuges and breeding grounds for birds," and again in 1958 "... to provide adequate pasture for the display of bison in their natural habitat at a location readily available to the public..." The refuge currently supports bison, elk, pronghorn antelope, Rocky Mountain bighorn sheep, mule deer and white-tailed deer, black bear, coyote, mountain lion, and more than 200 species of birds. As many as 250,000 visitors come to the refuge each year.

The herd was founded in 1909 from 34 northern plains bison purchased by the American Bison Society from the Conrad herd in Kalispell, Montana, plus two additional Conrad bison that were donated to the American Bison Society. One additional animal came from the Goodnight herd in Texas. In 1910, three additional northern plains bison were introduced from the Corbin herd. Subsequent additions include two bison in 1939 (7-Up Ranch, origin unknown); four in 1952 (Fort Niobrara); two in 1953 (Yellowstone National Park); and four in 1984 (Maxwell State Game Refuge).

The bison are rounded up annually by horseback to keep the population within the refuge carrying capacity, and a comprehensive herd health monitoring program has been in effect since 2000. The animals are individually identified with microchips, and the population is currently at approximately 320 bison.

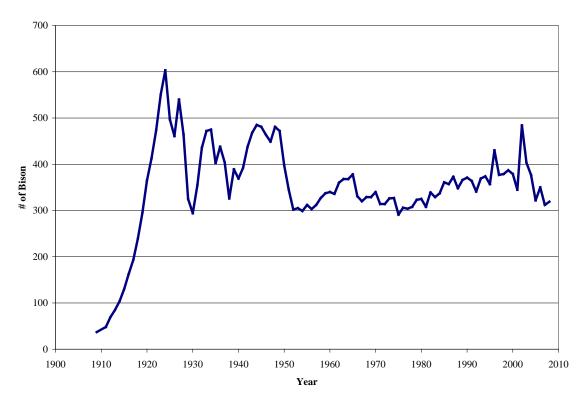


Figure C-4. National Bison Range bison herd population, 1909 to 2009.

Neal Smith National Wildlife Refuge

Neal Smith National Wildlife Refuge, located just east of Des Moines, Iowa, was established in 1991. Its mission is to re-construct tallgrass prairie and restore oak savanna on 8,654 acres of the Walnut Creek watershed and to provide a major environmental education facility focusing on prairie, oak savanna, and human interaction. Habitat management involves reclaiming agriculturally degraded land using grazing, prescribed fire, and other tools to restore tallgrass prairie and savanna habitat. Approximately 200,000 visitors come to the refuge every year. The refuge has been designated a U.S. Fish and Wildlife Service Land Management and Research Demonstration Area to facilitate development, testing, teaching, publishing, and demonstration of state-of-the-art management techniques for fish, wildlife, and plant conservation.

In 1996, bison were reintroduced from several other refuges around the country (not shown in graph below). However, recently completed genetics data suggested that the Neal Smith bison population contributed relatively little to national bison conservation efforts, and a new herd was established in 2006 with 39 animals transferred from the National Bison Range. The bison are rounded up annually to manage the population within refuge carrying capacity and to conduct health monitoring. The animals are individually identified with microchips, and the population is currently estimated at 71.

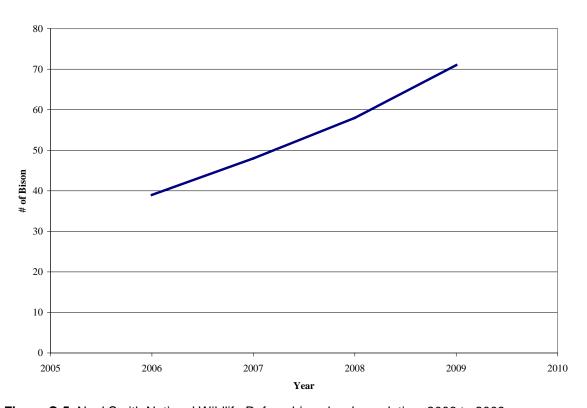


Figure C-5. Neal Smith National Wildlife Refuge bison herd population, 2006 to 2009.

Rocky Mountain Arsenal National Wildlife Refuge

In 1942, the U.S. Army bought thirty square miles of farmland to establish the Rocky Mountain Arsenal, a chemical weapons factory. After World War II, the army leased land to private companies that produced commercial pesticides. During the early Cold War of the 1950s, the U.S. Army again produced chemical weapons. While the industrial core of the site was contaminated, deer, prairie dogs, coyotes, and many species of hawks, owls, and other birds thrived in the abandoned fields, grasslands, and woodlots that had been protected from forty years of urban sprawl and development.

In 1992, Congress passed the Rocky Mountain Arsenal National Wildlife Refuge Act, designating the site as a future refuge. Since then, the U.S. Fish and Wildlife Service has managed the site "as if it were a refuge," monitoring wildlife health, restoring native prairie habitats, and providing opportunities for wildlife-dependent recreation. Located just northeast of downtown Denver, Colorado, the refuge is the largest contiguous open space in the Denver metropolitan area. The site is currently undergoing a major environmental restoration program and will become one of the largest urban national wildlife refuges in the United States.

The bison herd at the Rocky Mountain Arsenal was established in 2007 with 16 animals transferred from the National Bison Range as part of a pilot project. In spring 2008, two yearlings from Sullys Hill National Game Preserve, also of National Bison Range foundation, were added to the population. The population is currently estimated at 44, and the bison are individually identified with microchips. The refuge is planning to develop facilities to conduct annual roundups in an effort to manage the population within carrying capacity and complete herd health monitoring in future years.

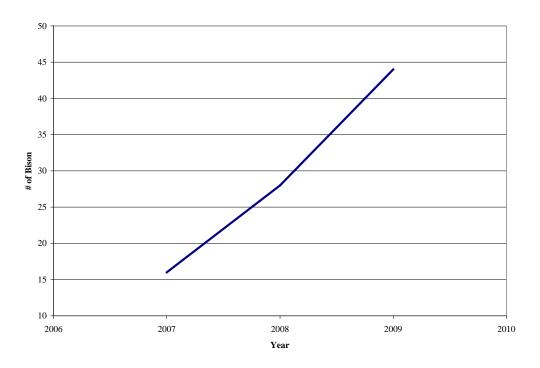


Figure C-6. Rocky Mountain Arsenal bison herd population, 2007 to 2009.

Sullys Hill National Game Preserve

Sullys Hill National Game Preserve, located on the south shore of Devils Lake, North Dakota, was established in 1904 by Teddy Roosevelt. In 1914, Sullys Hill was named a "Big Game Preserve" by Congress, and in 1921, President Warren Harding reserved the area as a refuge and breeding grounds for birds and all wildlife. Purposes include: "…a big game preserve, refuge, and breeding grounds for wild animals and birds…" and "…refuge and breeding grounds for birds." Sullys Hill National Game Preserve currently consists of 1,674 acres of wooded hills and open meadows.

Six bison were brought to Sullys Hill in October 1918 from the Portland City Park in Portland, Oregon, including the herd matriarch and her offspring. Based on historical documentation, it is believed that the herd matriarch was obtained by the Portland City Park from Ravalli, Montana, around 1906 through a trader named B.H. Denison. In 1932, the first addition to the herd, a bull from Wind Cave National Park, was made. Nine other introductions occurred between 1941 and 1997, including bison from the National Bison Range, Fort Niobrara NWR, and Theodore Roosevelt National Park.

Since 1980, average herd size has been approximately 30 animals at Sullys Hill, with about eight removed annually until 2006, when the entire herd was relocated to Fort Niobrara NWR to allow the population to expand. The population all currently contains 61 bison, and the animals are individually identified with microchips.

Seven bison from the National Bison Range were transported to Sullys Hill in 2006 to provide environmental education, outreach, and viewing opportunities for refuge visitors. This replacement herd is not included in the graph below.

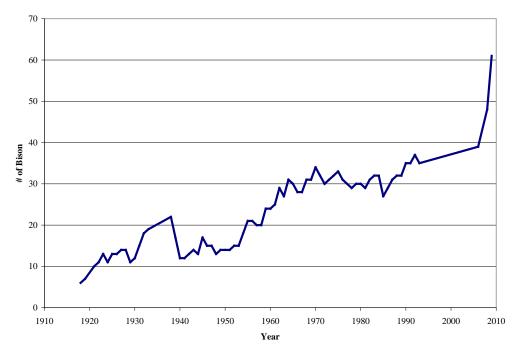


Figure C-7. Sullys Hill bison herd, 1918 to 2009 (relocated to Fort Niobrara in 2006).

Theodore Roosevelt National Park

Theodore Roosevelt National Park consists of three distinct areas totaling 70,446 acres (North Unit, 24,070; Elkhorn Ranch, 218; South Unit, 46,158). In 1956, 29 bison from Fort Niobrara NWR were reintroduced in the South Unit of the park, and in 1962, 20 bison from that population were released into the North Unit (there are no bison at the Elkhorn Ranch). Population objectives for bison in the North and South units were set at 100–300 and 200–500, respectively, using a park-specific forage allocation model, and since the initial releases, populations have ranged from 20 to 360 bison in the North Unit and from 29 to 472 in the South Unit.

Population monitoring prior to 1975 should be considered informal, and most estimates were made prior to roundups that occurred annually in the South Unit from 1962 through 1973. Records from 1975 to the present are more accurate and based on total-herd counts from complete park coverage by riders, aircraft, or both. During roundup years, the estimate reflects the population prior to culling the herd.

Each unit has its own wildlife-handling facility, holding and sorting pastures, a chute system, holding pens, and loading ramps. As bison are processed, morphometric and demographic data are collected, and each is identified with a micro-chip and federal identification tag in the right ear. Each bison is tested for brucellosis (*Brucella abortus*), and additional samples are archived for other studies (e.g., genetic purity, heterozygosity, etc.). No bison from either unit has tested positive for brucellosis.

The decision for culling an individual is based on population and demographic goals for that unit. Theodore Roosevelt National Park does not have sale authority for bison. Under a cooperative agreement, bison culled from the park are brokered through the Inter-Tribal Bison Cooperative, and other federal, state, and non-profit entities.

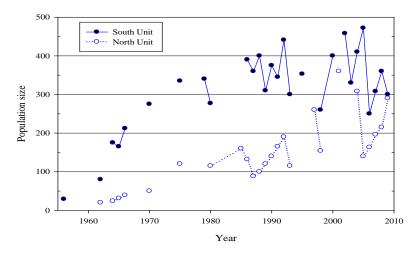


Figure C-8. Theodore Roosevelt National Park bison herd population, 1956 to 2009.

Wichita Mountains Wildlife Refuge

Wichita Mountains Wildlife Refuge, established in 1901, consists of 59,020 acres of mixed grass prairie in the Wichita Mountains of southwest Oklahoma. The refuge provides habitat for large native grazing animals such as bison, Rocky Mountain elk, and white-tailed deer. Texas longhorn cattle also share refuge rangelands as a cultural and historical legacy species. More than one million visitors come to the refuge each year.

Through the efforts of the American Bison Society and the New York Zoological Society, an offer was made to donate 15 bison to the Wichita National Forest and Game Preserve in the early 1900s. Congress set aside \$15,000 for this purpose, and on October 11, 1907, 15 bison from the New York Zoological Park were shipped by rail to the refuge. Four bison from the Fort Niobrara NWR were added to the herd in 1940.

The current population is approximately 650 bison, and an annual roundup is conducted to keep the population within refuge carrying capacity and to conduct herd health monitoring. The refuge began inserting microchips in 2007 to identify individuals, and approximately 90% of the bison herd has been microchipped to date.



Figure C-9. Witchita Mountains Wildlife Refuge bison herd population, 1907 to 2009.

Wind Cave National Park

The Wind Cave National Park bison herd was originally established in 1913 on the Wind Cave Game Preserve, administered by the U.S. Department of Agriculture (USDA) Bureau of Biological Survey. This initial group consisted of 14 bison (six bulls and eight cows) and was a gift from the New York Zoological Society through the American Bison Association. Six more bison (two bulls and four cows) were brought to the game preserve from Yellowstone in 1916. These 20 animals were the founders of the current Wind Cave bison herd. In 1935 the Wind Cave Game Preserve was transferred from administration by the USDA to the Department of the Interior, and became part of Wind Cave National Park. A 1938 law authorized the park to sell or otherwise dispose of surplus buffalo and elk, and until 1943 bison were sold live or culled. Under an agreement with South Dakota in 1952, bison were baited into Custer State Park (CSP). This was the major means of disposing of bison until 1961 when the agreement to bait the bison into CSP was terminated in 1964 due to the high incidence of brucellosis in the Wind Cave herd, and the initiation of a calf-hood vaccination program by CSP.

As the park was expanded from 10,500 to 28,295 acres, the bison herd was allowed to increase. In the mid-1960s, the park established a target bison management population of between 350 and 500 animals. In 1960, brucellosis test results revealed approximately 75% of 52 bison tested were reactors. This lead to the initiation of a brucellosis control program in 1964 in which 220 bison were shot in the field, reducing the herd from 440 to 220. The park was placed under quarantine by South Dakota from 1982 to 1986. There have been no positive brucellosis reactors from 1985 to the present.

When a roundup is conducted, as many bison as possible are captured, tested, and released back into the park or shipped to various Native American tribes, non-profit organizations, and state and federal agencies. From 1965 to 1987, the bison herd was reduced by sending to slaughter the first bison to be rounded up regardless of age or sex. Since then, the park primarily reduces the herd by live shipment of yearlings and sometimes two-year-olds, keeping 8–10 of each sex and age class. A total of 1,489 have been distributed live between 1987 and 2007. Bison are allowed to die naturally, and their remains are left on the landscape.

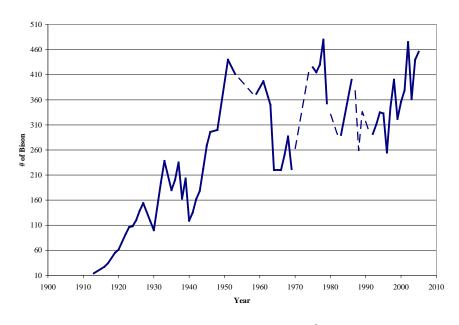


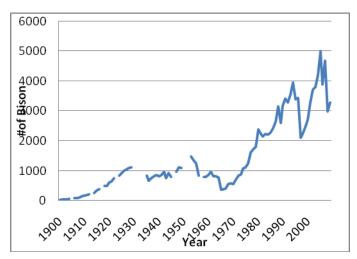
Figure C-10. Wind Cave National Park bison herd population, 1913 to 2009.

Yellowstone National Park

Yellowstone bison historically occupied approximately 20,000 km² in the headwaters of the Yellowstone and Madison rivers. Historical accounts of wild bison adjacent to and within the present-day Yellowstone National Park note that substantial numbers occupied the high plateaus in all seasons. When the park was established in 1872, the population of bison likely numbered in the several hundreds, but by 1900 the population had declined in abundance to less than 50 (actual count of 23) individuals located in the interior valley of Pelican Creek.

A restoration program on the northern range of Yellowstone was initiated in 1902 by translocating three adult males from Texas and 18 females from western Montana. This population was supplemented with a few calves from the Pelican Valley herd. The restoration program actively managed the bison by growing and feeding hay until the early 1950s and removing bison to manage abundance and sex ratio until the mid 1960s. Following a new 1968 management policy, the population increased to 4,000 by 1994 and to 5,000 bison in 2005. Conservation of Yellowstone bison is complicated by relatively high rates of *Brucella abortus* infection, their spring migratory behavior to low-elevation ranges along and outside the national park boundary, and especially with brucellosis detections in greater Yellowstone area livestock. The moderate to high population growth rate exacerbates the issue in the conflict zone at the conservation area boundary. The conservation area boundary was designated through negotiations with the State of Montana and does not include fencing to contain bison. Yellowstone bison occupy a range of about 2,300 km².

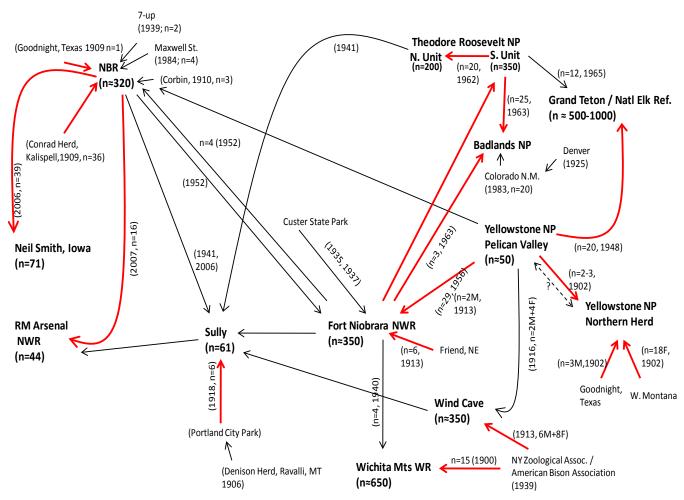
The current Yellowstone bison management program is a collaborative effort with four other state and federal management agencies, directed by a long-term management plan signed by the Secretary of the Interior in 2002. The program uses a conservation strategy to manage for fluctuations in population abundance between 2,500 and 4,500 bison in order to balance the influence bison have on the park's forage base, conservation of the genetic integrity of the bison population, protection of migratory tendencies that wild bison exhibit, meeting brucellosis risk management responsibilities negotiated with state wildlife managers, and other constraints that influence human tolerance for wild bison outside Yellowstone National Park. An active surveillance program includes annual monitoring of the population to track demographic rates, brucellosis exposure, and brucellosis sero-conversion rates by maintaining a cohort of radio-



marked individuals. Periodic roundups of bison at capture pens at the perimeter of the conservation area occur in which a few to more than 1,000 bison are removed per year depending on the population abundance and the prevailing weather conditions. Removals are focused on migrants to the boundary ranges, and in some years bison that are found to be brucellosis sero-negative are released after testing.

Figure C-11. Yellowstone National Park bison herd population, ca. 1900 to 2009.

Appendix D. Sources and Movement of DOI Bison (M. Schwartz 2010)



Bold Locations are Existing DOI Herds

Animals Used to Found Herd

Animals Used to Augment Herd

Natural Migration ---->



National Park Service U.S. Department of the Interior



Natural Resource Program Center 1201 Oakridge Drive, Suite 150 Fort Collins, CO 80525

www.nature.nps.gov