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IN LIGHT OF HERD HISTORY AND GENETICS STUDIES

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UNITED STATES DEPARTMENT OF THE INTERIOR NATIONAL PARK SERVICE

ON THE COVER

Coated in frost on a cold, fall evening, a bison cow traverses snowy terrain of its northern range in Yellowstone National Park, Wyoming. Recent genetics studies and analysis of herd histories of bison on federal lands, including five national parks, are helping wildlife managers understand the many interrelated factors affecting the long-term conservation of this beloved North American species. For more of the story see our cover article on page 22.

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Where the buffalo roam:

Figure 1. Bison in Wind Cave National Park, South Dakota.
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THE ROLE OF HISTORY AND GENETICS IN THE CONSERVATION OF BISON ON U.S. FEDERAL LANDS

By Natalie D. Halbert, Peter J. P. Gogan, Ronald Hiebert, and James N. Derr

History of bison

As an emblem of the Great Plains, American Indians, and wildlife conservation, the American bison (*Bison bison*) is one of the most visible and well-known of wildlife species in North America (fig. 1). Species of the genus *Bison* originally entered the continent via the Bering land bridge from northern Eurasia in the Illinoian glacial period of the Pleistocene epoch (125,000–500,000 years ago). Bison are the largest species in North America to have survived the late Pleistocene–early Holocene megafauna extinction period (around 9,000–11,000 years ago), but likely experienced a dramatic population reduction triggered by environmental changes and increased human hunting pressures around this time (Dary 1989; McDonald 1981). The modern American bison species (*Bison bison*) emerged and expanded across the grasslands of North America around 4,000–5,000 years ago (McDonald 1981).

As the major grazer of the continent, bison populations ranged from central Mexico to northern Canada and nearly from the east to west coasts (fig. 2; McDonald 1981), with 25–40 million bison estimated to have roamed the Great Plains prior to the 19th century (Flores 1991; McHugh 1972; Shaw 1995).

By the 1820s, bison in North America were already in a state of continuous decline, especially in the South and East (Flores 1991; Garretson 1938). Evidence on many fronts indicates the initial decline was due to both natural and anthropogenic (human-induced) forces (Flores 1991; Isenberg 2000). For example, the introduction of nonnative animal species led to increased hunting efficiency by aboriginal peoples with the proliferation of the horse culture, spread of exotic diseases (e.g., tuberculosis and brucellosis from cattle), and competition for grazing and water sources with growing populations of cattle, horses, and sheep. Natural pressures including fire, predation by wolves, and severe weather events such as droughts, floods, and blizzards also served to limit historical bison population sizes (Isenberg 2000). Uncontrolled hide hunting by both aboriginal and Euro-American hunters, facilitated by advances in firearms and transcontinental rail transportation, advanced the rapid decline leading to the well-documented, precipitous population crash of the late 1800s (Coder 1975; Garretson 1938). A preference for young female bison hides likely added to the population decline by disrupting herd social structure and natality (birth) rates. Fewer than 1,000 American bison—including both the plains and wood bison types—existed in the world by the late 1880s, and the species appeared to be at risk of extinction (Coder 1975; Soper 1941). The timely formation of six captive herds from 1873 to 1904 by private individuals and governmental protection of two remnant wild herds in the United States (Yellowstone National Park, established in 1872) and Canada (Wood Buffalo National Park, federally protected from 1893, park established in 1922) effectively served to save the species from extinction (table 1, page 25; locations indicated on fig. 2). The individuals involved in the early bison conservation movement were primarily cattle ranchers concerned with the disappearance of large, free-roaming bison herds. For example, the Texas cattle rancher Charles Goodnight (fig. 3, page 24), at the behest of his wife (Haley 1949), captured bison in the panhandle of Texas during the late 1870s and early 1880s to form a small captive herd. From these few herds, a combined total of fewer than 500 bison served as the foundation stock from which all bison in existence today are derived (Coder 1975; Soper 1941).

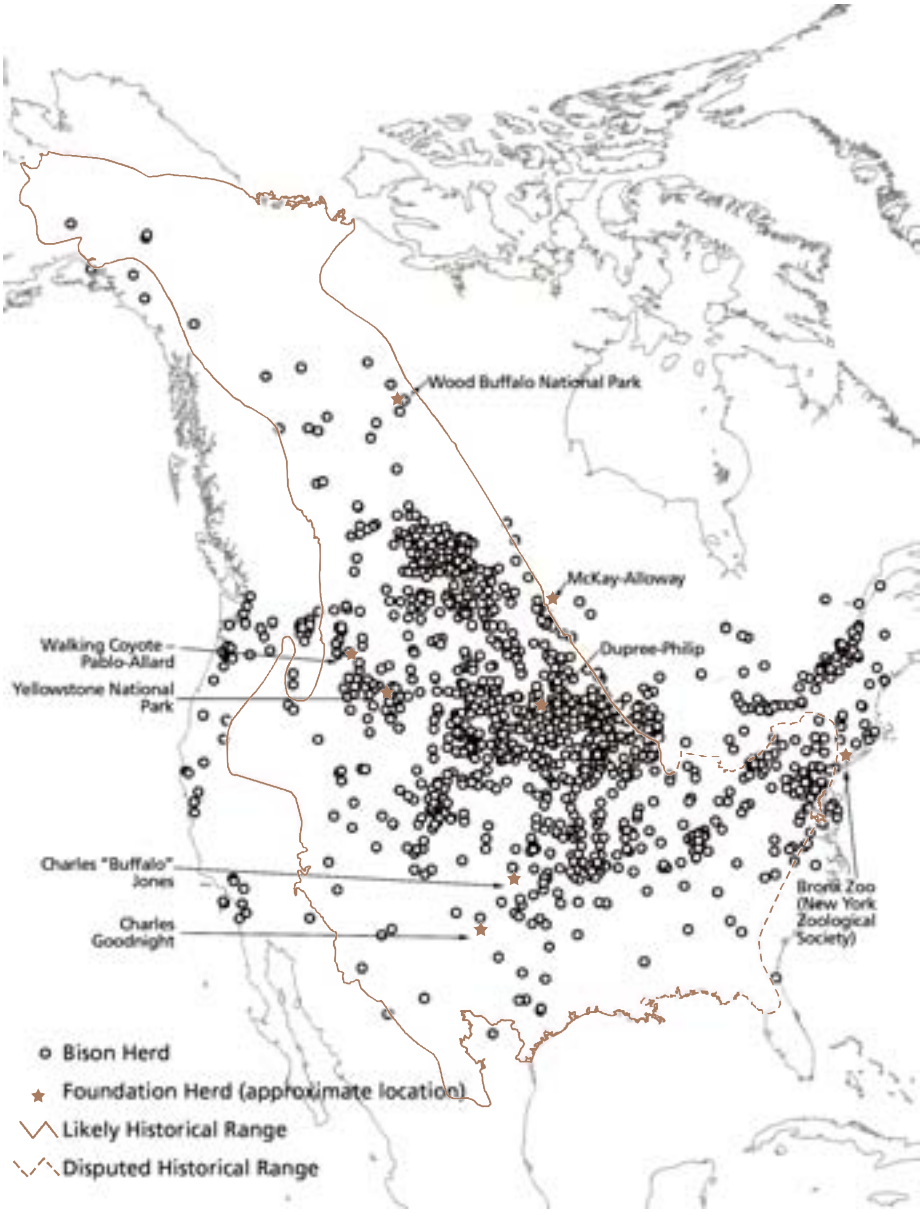

Figure 2. Historical distribution of Bison bison, with locations of foundation herds indicated (see table 1 for foundation herd histories). WILDLIFE CONSERVATION SOCIETY

Fewer than 500 bison served as the foundation stock from which all bison in existence today are derived.

Establishment of federal bison herds

Despite the significant population crash experienced in the late 1880s, bison in captivity thrived and by the turn of the 20th century, surplus bison were being sold off by private owners (Coder 1975). In contrast, the bison herd in Yellowstone National Park, representing the only continuously wild herd in the United States, was declining during this period due to unabated poaching; by 1902 only 30–50 bison persisted in the park (Garretson 1938; Meagher 1973). A critical shift in the bison conservation movement would occur, however, with new legislation in the United States and Canada providing for the protection of wildlife and the formation of additional federal bison herds (Coder 1975). The famous naturalist, William Hornaday, and the American Bison Society, founded in 1905, were instrumental in lobbying the U.S. government for such protective legislation and in procuring bison through the New York Zoological Park (see table 1) to establish new federal herds. At present, approximately 8,500 bison are maintained in five units administered by the National Park Service (NPS) and six units administered by the U.S. Fish and Wildlife Service (USFWS) (table 2). The bison in these 11 herds were derived almost exclusively from the 6 foundation herds and the continuously wild herd in Yellowstone National Park and, therefore, serve as an important reservoir of bison germplasm (genetic content).

Figure 3. The famous Texas cattle rancher Charles Goodnight, who captured wild bison in the panhandle of the state to form one of the six foundation herds (see table 1) from which many extant bison are derived. In 1902, Goodnight gave three bison bulls to the U.S. federal government to supplement the small, wild herd in Yellowstone National Park (see table 2).

PANHANDLE-PLAINS HISTORICAL MUSEUM AND THE TEXAS STATE BISON HERD ARCHIVE PROJECT

Need for genetic information for bison management

The U.S. Department of the Interior (DOI) Bison Conservation Management Working Group has met annually since 1997 to gather and share information on bison management techniques, policy issues, animal health, genetics, and demographics. Early on, the group recognized the need for genetic information to guide management and specifically wanted to know: (1) the present levels and patterns of genetic variation within and among herds; (2) if it is more appropriate to manage DOI bison herds as separate populations or as a meta-population; (3) the effects of various culling practices on the maintenance of genetic variation; and (4) levels of domestic cattle (*Bos taurus*) introgression (introduction of foreign DNA fragments into a genome) in the DOI bison herds.

With funding from the U.S. Geological Survey Natural Resource Preservation Program and the U.S. Fish and Wildlife Service, a cooperative project was initiated with Texas A&M University. A summary of the results of this project and management implications follows.

Genetic architecture of bison herds

Knowledge of the genetic architecture of federal bison herds is critical to proper management, long-term maintenance of genetic diversity (that is, for the next 100+ years), and species conservation. For instance, genetic technologies can be used to assess the effects of the historic 19th century population crash (genetic bottleneck) and foundation of herds with few individuals (founder effect), levels of inbreeding and diversity in herds, subpopulation structure within herds (nonrandom mating), and genetic relationships among herds. Such information is of great value to managers in determining appropriate herd sizes, sex ratios, and culling strategies.

To address these issues, polymorphic DNA markers—those having more than one allele or "form" of a gene/DNA sequence—are commonly employed to obtain genotypic information on individuals from populations. One such polymorphic marker is called a microsatellite, which is a type of simple sequence repeat (SSR). Microsatellites have several advantages in population genetic studies in that they are relatively inexpensive to use, simple and reliable to score (i.e., obtain genotypes), highly polymorphic, and abundant throughout the genomes of mammals.

Using a panel of 49 microsatellites dispersed throughout the bison genome, we recently completed an evaluation of the genetic structure of the 11 U.S. federal bison herds. (For complete study details, see Halbert (2003); Sully's Hill National Game Preserve herd data is from

Halbert and Derr, unpublished data.) Blood, hair, or tissue samples collected by DOI personnel from 2,260 individual bison were shipped to Texas A&M University for DNA isolation and genetic evaluation. From these analyses we identified differences among herds in the average number of alleles per microsatellite (a measure of diversity) and calculated an average across all herds of 4.36 and a range from 4.96 (National Bison Range herd) to 3.55 (Theodore Roosevelt National Park, north unit herd) alleles per microsatellite. Herds also differed in levels of heterozygosity (an indicator of the breeding history of a herd), with an average across all herds of 59.1% and range from 65.7% (Wind Cave National Park herd) to 51.9% (Theodore Roosevelt National Park, north unit herd) heterozogosity. In general, higher levels of both heterozygosity and genetic diversity (alleles per microsatellite) are desirable, as these measures correlate with population stability and viability. The U.S. federal bison herds appear to have relatively high levels of both heterozygosity and genetic diversity, especially considering the significant population bottleneck experienced in the late 1800s and small numbers of founders used to establish the herds. In comparison, the Texas State Bison Herd, which is directly descended from the original Goodnight herd (table 1) and has remained a small, closed population for many generations, has an average of 2.61 alleles/marker and 38.5% heterozygosity (Halbert et al. 2004). As is often found in populations suffering from low levels of genetic diversity, the Texas State Bison Herd has a history of inbreeding, low natality rates, and high juvenile mortality rates compared with other bison herds (Halbert et al. 2005a).

The genotypic information obtained in this study was used to evaluate relationships among herds (fig. 4, page 27). While some herds are closely related, such as those in Fort Niobrara National Wildlife Refuge, Badlands National Park, and Theodore Roosevelt National Park (south and north unit herds), others are more distantly related, such as those in Wichita Mountains National Wildlife Refuge and Grand Teton National Park. Overall, the identified genetic relationships follow closely the history of establishment of these herds (table 2, page 26). For example, the Wichita Mountains National Wildlife Refuge and Wind Cave National Park herds share a historical link through their establishment (at least in part) from New York Zoological Park herd bison (table 2), and the genetic data indicate that this relationship persists, as the two modern derivatives of these herds are more closely related to each other than either is to any other herd examined (fig. 4). As another example, the Badlands National Park and Theodore Roosevelt National Park north unit herds were both established with bison from the south unit herd of Theodore Roosevelt National Park, which was in turn derived from Fort Niobrara National Wildlife Refuge stock (table 2); this relationship is also evident based on the genetic data (fig. 4).

In other cases, genetic analyses shed new light on the relative contributions of various founder sources. For instance, the Grand Teton National Park herd was originally established with bison from Yellowstone National

Table 1. Captive bison herds providing founding stock for U.S. and Canadian federal herds

Herd	Source	Year	Number of bison
James McKay-Charles Alloway	Saskatchewan	1873–1874	5
Charles Goodnight	Texas	1878	5
Frederick Dupree	Montana	1882	6–7
Michel Pablo-Charles Allard	Montana	1879	4[a]
	Jones herd	1893	44
Charles Jones	Texas	1886–1889	56
	McKay-Alloway herd (through Samuel Bedson)	1888	86
	Kansas, Nebraska (various)	unknown, prior to 1893	10
New York Zoological Park[b]	Nebraska	1888	2
	South Dakota	1889	4
	Pablo-Allard herd	1897	3
	Mix[c]	1904	4

Source: Derived from Coder 1975, Garretson 1938, and Seton 1937.

Note: Wild bison captured within their native range were used as initial stock for each captive herd and were later pivotal in providing founding stock for U.S. and Canadian federal herds. In addition to these herds, remnant wild herds existed in Yellowstone National Park (reaching a low of 30–50 bison in 1902; Garretson 1938; Meagher 1973) and the area now protected as Wood Buffalo National Park (with a low of 300 bison around 1891; Soper 1941).

[a]Wild bison originally captured by Walking Coyote (Samuel Wells), a Pend d'Oreille Indian in 1879; the herd grew and 12 head were sold to Pablo and Allard in 1883.

[b]Herd formation largely due to efforts of William Hornaday and the American Bison Society (Coder 1975).

[c]Derived from Wyoming, Manitoba, and the Jones herd.

Park in 1948. In 1963, the infectious disease brucellosis was discovered in the herd and all 13 adults were killed (National Park Service 1996). To the remaining 4 yearlings and 5 calves, 12 adult (6 male and 6 female) bison from the Theodore Roosevelt National Park south unit herd were added in 1964 (National Park Service 1996). The modern Grand Teton National Park herd appears to be more closely related to the Theodore Roosevelt National Park south unit herd than the Yellowstone National Park herd (fig. 4), most likely as a result of preferential breeding for a number of years by the adult Theodore Roosevelt National Park south unit bison while the herd was small. Genetic drift, or random changes in allele frequencies, which is especially powerful in small populations, might also have played a part in shaping the modern genetic structure of the Grand Teton National Park herd. Regardless, the genetic data in this case reveal relationships not clearly apparent from herd history alone.

A common concern in wildlife management is inbreeding, which can lead to decreased heterozygosity, adaptive response (ability of a population to adapt to environmental changes), and population viability (Franklin 1980). Indeed, the history of formation of these herds from a handful of individuals (table 2) and continued maintenance of federal bison in relatively small (with the

Table 2. Establishment of U.S. federal bison herds

Herd	Location	Year	Founding Stock Number – Source[a]
Badlands NP	South Dakota	1963	3 – Fort Niobrara NWR; 50 – Theodore Roosevelt NP south unit
		1983	20 – Colorado National Monument (unknown origin)
Fort Niobrara NWR	Nebraska	1913	6 – private ranch, Nebraska; 2 – Yellowstone NP
		1935	4 – Custer State Park, South Dakota
		1937	4 – Custer State Park, South Dakota
		1952	5 – National Bison Range
Grand Teton NP	Wyoming	1948	20 – Yellowstone NP
		1964	12 – Theodore Roosevelt NP
National Bison Range	Montana	1908	1 – Goodnight herd; 3 – Corbin (McKay-Alloway); 34 – Conrad (Pablo
		1939	2 – 7-Up Ranch (unknown origin)
		1952	4 – Fort Niobrara NWR
		1953	2 – Yellowstone NP
		1984	4 – Maxwell State Game Refuge, Kansas (Jones)
Neal Smith NWR	Iowa	1996	8 – Fort Niobrara NWR; 8 – Wichita Mountains NWR
		1997	6 – Fort Niobrara NWR; 8 – National Bison Range
		1998	3 – Fort Niobrara NWR
Sully's Hill National GamePreserve[b]	North Dakota	1919	6 – Portland City Park, Oregon (unknown origin)
		1932	1 – Wind Cave NP
		1941–1979	7 – Fort Niobrara NWR
		1987	3 – National Bison Range
		1994–1997	2 – Theodore Roosevelt NP
Theodore Roosevelt NP[c]	North Dakota	1956	29 – Fort Niobrara NWR to found Theodore Roosevelt south unit herd
		[1962]	[20 – Theodore Roosevelt south unit bison to establish north unit herd]
Wichita Mountains NWR	Oklahoma	1907	15 – New York Zoological Park
		1940	2 – Fort Niobrara NWR
Wind Cave NP	South Dakota	1913	14 – New York Zoological Park
		1916	6 – Yellowstone NP
Yellowstone NP	Wyoming, Idaho, Montana	1902	approximately 30 indigenous; 18 – Pablo-Allard herd; 3 – Goodnight herd

Source: Halbert and Derr 2007; copyright 2007 by the America Genetic Association.
[a]See table 1 for description of six foundation herds.
[b]History of introductions provided by C. Dixon, personal communication.
[c]Theodore Roosevelt National Park hosts two herds: south unit and north unit.

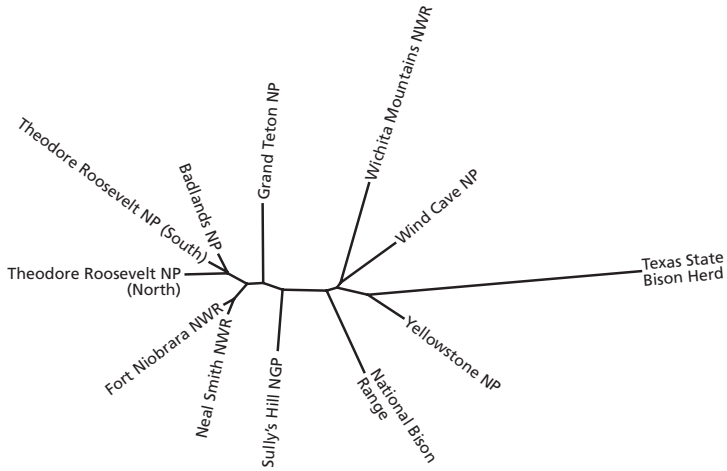

Figure 4. Genetic relationship tree based on 49 polymorphic microsatellites. Populations and sample sizes indicated in table 2. Figure derived from DS genetic distances (Nei 1972), which is based on the infinite alleles model of evolution. Branch lengths correlate with the amount of genetic similarity identified between herds.

exception of Yellowstone National Park), closed herds (table 3) would suggest that inbreeding may be adversely impacting the genetic architecture and trajectory of these herds. However, the genetic data described herein do not indicate inbreeding (Halbert 2003), and phenotypic indicators of inbreeding depression (e.g., decreased birth rates, abnormal physical characteristics, increased mortality) have not been observed in these herds. Although genetic data from pre-bottleneck bison herds are currently not available to make direct measurements of changes in genetic diversity over time, these herds appear to have maintained moderate levels of genetic diversity despite the bottleneck event of the late 1800s and subsequent small founding population sizes. In fact, compared with cattle and related species, bison in general appear to have levels of genetic diversity and heterozygosity similar to other nondomesticated bovids (e.g., MacHugh et al. 1997; Navani et al. 2002; Rendo et al. 2004).

The genetic data ... do not indicate inbreeding.

Historical—and in some private herds, recent—hybridization between bison and their close relative, domestic cattle, has complicated bison conservation efforts due to introgression of domestic cattle DNA into the bison genome. The two species do not naturally interbreed, and, in fact, viable first-generation hybrids are somewhat difficult to produce (Boyd 1914; Goodnight 1914). However, most of the people involved in saving bison from near-extinction in the 1880s were cattle ranchers interested in producing hardier breeds of cattle. Various records of successful attempts by ranchers to hybridize the two species exist (e.g., Coder 1975; Jones 1907), and the remnants of these crosses are evident today. Domestic cattle DNA has been detected in both the mitochondrial (Polziehn et al. 1995; Ward et al. 1999) and nuclear (Halbert and Derr 2007; Halbert et al. 2005b) genomes of bison in state, federal, and private herds in the United States. In U.S. federal bison herds, levels of detected introgression are low, and probably constitute less than 1% of the total nuclear DNA (Halbert and Derr 2007). No evidence of introgression has been detected in the Yellowstone and Wind Cave national park herds, where several hundred bison have been tested (Halbert and Derr 2007). Conversely, some private and state herds have substantially higher levels of introgression, with up to 100% of the bison in one private herd harboring domestic cattle mitochondrial DNA (Halbert and Derr, unpublished data).

Table 3. Nuclear microsatellite sampling regimen for federal bison herds

Population	Collection year(s)	Census[a]	Total sampled
Badlands NP	2002	875	312
Fort Niobrara NWR	2001–2002	380	167
Grand Teton NP	1999–2000	600	39
National Bison Range	1999–2002	350	152
Neal Smith NWR	2001	63	49
Sully's Hill National Game Preserve	2004	35	31
Theodore Roosevelt National Park, north unit	2000	312	270
Theodore Roosevelt National Park, south unit	2001	371	324
Wichita Mountains NWR	1999, 2002	600	35
Wind Cave National Park	1999–2001	350	293
Yellowstone National Park	1997, 1999–2002	3,000	488
Sum		6,936	2,160

Note: A total of 2,160 bison were scored for 49 nuclear microsatellites.
[a]Approximate census population size, as estimated by individual herd managers. When possible, estimates are given of total census population size at time of collection for this study (or average across collection years).

Implications for future management

The human-aided recovery of bison from the brink of extermination in the late 1800s is among the first and best known conservation success stories. With more than 500,000 American bison in the world today, the recovery of the species would indeed seem secure. However, only 5% of these bison are in conservation herds (maintained by federal, state, or private conservation groups); all other bison are maintained on private ranches (Boyd 2003). While some ranchers with private bison herds are interested in and committed to conservation, others raise bison as semidomesticated livestock subjected to intensive management, handling, herd structure manipulation, and artificial selection. Artificial selection on phenotypes (traits), such as weight or hump size, effectively selects for or against alleles at one or more genes in the genome that control the trait; this type of selection leads to changes in the genetic architecture of a herd that are difficult to predict, alter the genome (in many cases irreversibly) from its "natural" state, and can lead to reduced fitness due to decreased genetic variation or inadvertent selection on nearby "fitness-related" genes. Arguably, therefore, the primary—though possibly not exclusive—burden of the long-term preservation of bison as a distinct species falls on the managers of conservation herds. Before a complete picture of the modern bison germplasm can be understood and most effectively conserved, however, further evaluation using methods such as those presented here is needed to assess the genetic architecture of several conservation herds in both the United States and Canada for which such information is poorly understood or altogether unknown.

The current and future management of U.S. federal bison herds has been debated and scrutinized from many perspectives. As is the case with many other wildlife species, anthropogenic changes to the environment and landscape have forced the primary existence of bison into fragmented herds of relatively small size (<1,000 individuals). Small populations are prone to losses of genetic diversity, or genetic erosion, which in turn can lead to decreased fitness and adaptive response. Migration among populations is the principle process that can counteract genetic erosion. For modern bison, opportunities for natural migration do not exist. Movement of bison among herds only occurs artificially. Extreme caution must be practiced when moving animals in this way, however, to prevent the inadvertent transmission of disease and further dilution of the bison genome with introgressed domestic cattle DNA.

Small populations are prone to losses of genetic diversity, or genetic erosion, which in turn can lead to decreased fitness and adaptive response.

Probably the most pressing genetic issue facing U.S. federal bison herd management today is the general need for increased herd sizes. Recent simulation modeling based on the genetic data presented herein indicates that effective population sizes of at least 1,000 individuals are necessary for the long-term maintenance of both genetic diversity and heterozygosity (Gross and Wang 2005). Effective population sizes reflect the effective number of breeding individuals and are generally only a fraction of the census population sizes. A "population" need not be contiguous, and several herds from the same genetic stock might be considered in the effective population size calculation. In fact, the creation and maintenance of such herds is recommended to prevent genetic erosion and decrease chances of catastrophe (e.g., devastating disease, flood, fire) leading to the loss of irreplaceable germplasm. The Yellowstone National Park herd is the only U.S. federal herd that likely meets the effective population size criteria directly, although the continued presence of brucellosis in the herd greatly complicates efforts to create satellite herds outside of the park boundaries. The Fort Niobrara National Wildlife Refuge herd and direct satellite herds in Theodore Roosevelt National Park (south and north units) combined likely also meet the effective population size criteria. The establishment and proper management of disease-free satellite herds from various U.S. federal bison herds, especially those with unique lineages and no historic or genetic evidence of introgression (e.g., Wind Cave and Yellowstone National Park herds), will serve to not only decrease genetic erosion, but also support long-term species conservation efforts.

More genetic information has been gathered, analyzed, and utilized for the study and conservation of American bison than for any other wildlife species. Collectively, genetic technologies have given us a detailed snapshot of the current architecture of both public and, to a lesser degree, private bison herds. Conservation herd data gaps still exist, especially with regard to largely unexamined herds (e.g., private conservation herds, Canadian public herds) and to intrapopulation dynamics (e.g., subpopulation division, effects of age and sex structure on genetic diversity). The long-term preservation of the bison genome will depend upon the responsible use of available data in the management of conservation herds. Like bison, many other species currently exist in fragmented populations, in limited habitats, and with continuous anthropogenic pressures. Genetic technologies such as those described here should be considered in the assessment of population structure and relationships as tools to assist management efforts and promote long-term species conservation.

Literature cited

Boyd, D. P. 2003. Conservation of North American bison: Status and recommendations. University of Calgary, Calgary, Alberta, Canada.

Boyd, M. M. 1914. Crossing bison and cattle. Journal of Heredity 5:189–197.

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

Dary, D. A. 1989. The buffalo book: The full saga of the American animal. Swallow Press, Chicago, Illinois, USA.

Flores, D., 1991. Bison ecology and bison diplomacy: The southern plains from 1800 to 1850. Journal of American History 78(2):465–485.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–149 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation biology: An evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts, USA.

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, USA.

Goodnight, C. 1914. My experience with bison hybrids. Journal of Heredity 5:197–99.

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. Yellowstone Research Group, USGS-BRD, United States Geological Survey, Bozeman, Montana, USA.

Halbert, N. D. 2003. The utilization of genetic markers to resolve modern management issues in historic bison populations: Implications for species conservation. PhD dissertation. Texas A&M University, College Station, Texas, USA.

Halbert, N. D., and J. N. Derr. 2007. A comprehensive evaluation of cattle introgression into U.S. federal bison herds. Journal of Heredity 98:1–12.

Halbert, N. D., W. E. Grant, and J. N. Derr. 2005a. Genetic and demographic consequences of importing animals into a small population: A simulation model of the Texas State Bison Herd (USA). Ecological Modelling 181:263–276.

Halbert, N. D., T. J. Ward, R. D. Schnabel, J. F. Taylor, and J. N. Derr. 2005b. Conservation genomics: Disequilibrium mapping of domestic cattle chromosomal segments in North American bison populations. Molecular Ecology 14:2343–2362.

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(5):924–931.

Haley, J. E. 1949. Charles Goodnight: Cowman and Plainsman. University of Oklahoma Press, Norman, USA.

Isenberg, A. C., 2000. The destruction of the bison: An environmental history, 1750–1920. Cambridge University Press, New York, USA.

Jones, C. J. 1907. Breeding cattle. Annual report of the American Breeders' Association 3:161–165.

MacHugh, D. E., M. D. Shriver, R. T. Loftus, P. Cunningham, and D. G. Bradley. 1997. Microsatellite DNA variation and the evolution, domestication and phylogeography of taurine and zebu cattle (*Bos taurus* and *Bos indicus*). Genetics 146:1071–1086.

McDonald, J. N., 1981. North American bison: Their classification and evolution. University of California Press, Berkeley, California, USA.

McHugh, T., 1972. The time of the buffalo. University of Nebraska Press, Lincoln, Nebraska, USA.

Meagher, M. M. 1973. The bison of Yellowstone National Park. Scientific Monograph Series. National Park Service, Washington, DC, USA.

National Park Service. 1996. The Jackson Bison Herd: Long-term management plan and environmental assessment. National Park Service, Washington, DC, USA.

Navani, N., P. K. Jain, S. Gupta, B. S. Sisodia, and S. Kuman. 2002. A set of cattle microsatellite DNA markers for genome analysis of riverine buffalo (*Bubalus bubalis*). Animal Genetics 33:149–154.

Nei, M., 1972. Genetic distance between populations. American Naturalist 106(949):283–292.

Polziehn, R. O., C. M. Strobeck, J. Sheraton, and R. Beech. 1995. Bovine mtDNA discovered in North American bison populations. Conservation Biology 9(6):1638–1643.

Rendo, F., M. Iriondo, B. M. Jugo, A. Aguirre, L. I. Mazón, A. Vicario, M. Gómez, and A. Estonba. 2004. Analysis of the genetic structure of endangered bovine breeds from the western Pyrenees using DNA microsatellite markers. Biochemical Genetics 42(3–4):99-108.

Seton, E. T. 1937. Lives of game animals. Volume 3. Literary Guild of America, New York, USA.

Shaw, J. H. 1995. How many bison originally populated western rangelands? Rangelands, 17(5):148–150.

Soper, J. D. 1941. History, range, and home life of the northern bison. Ecological Monographs 11(4):349–412.

Ward, T. J., J. P. Bielawski, S. K. Davis, J. W. Templeton, and 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(1):51–57.

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