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Review

Second chance for the plains bison

Curtis H. Freese[a,*], *Keith E. Aune*[b], *Delaney P. Boyd*[c], *James N. Derr*[d], *Steve C. Forrest*[a], *C. Cormack Gates*[e], *Peter J.P. Gogan*[f], *Shaun M. Grassel*[g], *Natalie D. Halbert*[d], *Kyran Kunkel*[h], *Kent H. Redford*[i]

[a]Northern Great Plains Program, World Wildlife Fund, P.O. Box 7276, Bozeman, MT 59771, USA
[b]Montana Fish, Wildlife & Parks, 1420 E 6th Avenue, Helena, MT 59620, USA
[c]P.O. Box 1101, Redcliff, AB, Canada T0J 2P0
[d]Department of Veterinary Pathobiology, Texas A&M University, College Station, TX 77843-4467, USA
[e]Faculty of Environmental Design, University of Calgary, Calgary, AB, Canada T6G 2E1
[f]USGS Northern Rocky Mountain Science Center, P.O. Box 173492, Bozeman, MT 59717-3492, USA
[g]Lower Brule Sioux Tribe, Department of Wildlife, Fish and Recreation, P.O. Box 246, Lower Brule, SD 57548, USA
[h]Northern Great Plains Program, World Wildlife Fund, 1875 Gateway South, Gallatin Gateway, MT 59730, USA
[i]WCS Institute, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460, USA

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ABSTRACT

Before European settlement the plains bison (*Bison bison bison*) numbered in the tens of millions across most of the temperate region of North America. Within the span of a few decades during the mid- to late-1800s its numbers were reduced by hunting and other factors to a few hundred. The plight of the plains bison led to one of the first major movements in North America to save an endangered species. A few individuals and the American Bison Society rescued the remaining animals. Attempts to hybridize cattle and bison when bison numbers were low resulted in extensive cattle gene introgression in bison. Today, though approximately 500,000 plains bison exist in North America, few are free of cattle gene introgression, 96% are subject to anthropogenic selection for commodity production, and only 4% are in herds managed primarily for conservation purposes. Small herd size, artificial selection, cattle-gene introgression, and other factors threaten the diversity and integrity of the bison genome. In addition, the bison is for all practical purposes ecologically extinct across its former range, with multiple consequences for grassland biodiversity. Urgent measures are needed to conserve the wild bison genome and to restore the ecological role of bison in grassland ecosystems. Socioeconomic trends in the Great Plains, combined with new information about bison conservation needs and new conservation initiatives by both the public and public sectors, have set the stage for significant progress in bison conservation over the next few years.

* *Corresponding author:* Tel.: +1 406 582 0235; fax: +1 406 585 7910.
E-mail addresses: curt.freese@wwfus.org (C.H. Freese), kaune@mt.gov (K.E. Aune), delaneyboyd@shaw.ca (D.P. Boyd), jderr@cvm.tamu.edu (J.N. Derr), steve.forrest@wwfus.org (S.C. Forrest), ccgates@nucleus.com (C. Cormack Gates), peter_gogan@usgs.gov (P.J.P. Gogan), smgrassel@gmail.com (S.M. Grassel), kredford@wcs.org (K.H. Redford).
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Contents

1. Introduction

Perhaps no species is as emblematic of the Great Plains of North America as the American bison (*Bison bison*). The explorers Meriwether Lewis and William Clark often commented on the "immence" herds and more than once estimated 10,000–20,000 were within view while traversing the Great Plains from 1804–1806 (Ambrose Tubbs, 2003). The range of the plains bison (*B. bison bison*) before European settlement extended from nearly coast-to-coast in the US and from the Great Plains of southern Canada to northern Mexico (Hornaday, 1889).

The bison was also an early icon of the conservation movement in the US and Canada, being one of the first species that stirred citizens and governments in North America to intervene on behalf of a species that seemed destined for extinction (Coder, 1975; Lothian, 1981). Due largely to commercial and subsistence hunting, as well as probably exotic bovine diseases and forage competition with domestic stock (Flores, 1991), plains 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 sub-species of American bison, the wood bison (*B. bison athabascae*) which inhabited woodlands of northern Canada and Alaska, was reduced to perhaps 250 animals (Hornaday, 1889; Soper, 1941).

Pleas in the early 1800s to halt the destruction of bison in North America were largely ignored (Dary, 1989). Protective legislation in Canada and the United States was not enacted until much later when bison were near extinction. In Canada, the 1877 Buffalo Protection Act was the first attempt to legislate protection (Hewitt, 1921). However, this measure was ineffective because of a lack of enforcement. It was reinforced in 1894 when the Dominion Government passed a law protecting the surviving wood bison (Soper, 1941). By this time, plains bison had been extirpated from the wild in Canada. In the absence of protective legislation the plains bison disappeared from the wild in the United States except in Yellowstone National Park. The states of Idaho, Wyoming, and Montana implemented statutes to reduce the killing of game, including bison, between 1864 and 1872, but these 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, thereby halting the extirpation of the last free-ranging plains bison population in North America (Gates et al., 2005). In 1902, fewer than 25 bison remained in the remote Pelican Valley in Yellowstone National Park (Meagher, 1973).

The independent actions of private citizens, taken long before national governments reacted, were responsible for saving the plains bison (Dary, 1989; Coder, 1975). Between 1873 and 1889 several individuals in areas ranging from Manitoba to Texas captured the last of the wild plains bison, except for the few remaining in Yellowstone National Park. Concerned about the fate of the bison, William Hornaday, Director of the New York Zoological Park, and other wildlife advocates formed the American Bison Society in 1905, which successfully lobbied for the creation of several public conservation herds in the United States (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. However, the most significant early contribution by the Government of Canada was made 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 in the grasslands of east-central Alberta (Lothian, 1981). With protection, numbers of both the plains and wood bison increased quickly and a close brush with extinction was averted (Hornaday, 1927; Boyd, 2003). Although the wood bison also faces conservation challenges today, it is not considered further here. (We also note that the European bison [*Bison bonasus*] faces similar conservation problems as well as opportunities for significant restoration (Olech and Perzanowski, 2002; Perzanowski et al., 2004), and that closer collaboration between North American and European bison conservation efforts may be fruitful.)

These early efforts to save the plains bison have rightfully been regarded as a conservation success story. With roughly 500,000 plains bison now in North America (Boyd, 2003), their future would seem secure. A new body of knowledge, however, exposes major problems that give urgency to a second effort a century later to conserve this icon of the Great Plains.

2. Current problems facing conservation of the plains bison

Species extinctions occur in two basic ways: (1) the last individuals of a species die, bringing the genetic lineage of that species to an end; (2) the genetic makeup of a species changes substantially over time, whether through natural evolutionary processes, anthropogenic selection, or hybridization, resulting in genomic extinction (Rhymer and Simberloff, 1996; Allendorf et al., 2001). A new species need not emerge before we can label this genetic transformation an "extinction." For example, though domestic cattle (*Bos primigenius taurus*) belong to the same species as their extinct wild ancestor, the aurochs, it is not justifiable to claim that the Heck breed of cattle, the attempted re-creation of the aurochs, is a suitable substitute for aurochs conservation, despite having distinctly aurochs-like characteristics.

Bison barely escaped the first type of extinction in the late 1800s. Now, more than a century later, the plains bison is confronting the second form of extinction due to two major problems: (1) domestication and anthropogenic selection and (2) cattle gene introgression. In addition, we can now add ecological extinction to our concerns, a concept not generally considered by conservationists a century ago.

2.1. *Anthropogenic selection and small herd size*

There is a disconnect, if not antagonism, between bison conservation and intensive anthropogenic selection for domestication of bison. Domestication may not only be irreversibly altering the bison gene pool and its morphology, physiology and behavior (Price, 1999; O'Regan et al., 2005), but the large and growing number of commercial bison herds one sees while traveling around the continent may create complacency and weak support among the public for bison conservation.

A continent-wide survey in 2002 by Boyd (2003), conducted on behalf of the World Conservation Union's North American Bison Specialist Group (IUCN Bison Specialist Group), found that of the roughly 500,000 plains bison in North America, fewer than 20,000 are in herds managed principally for conservation purposes. The rest (96%) are being bred for commodity-production purposes such as ease of handling and meat production. In fact, the number of bison in conservation herds has stayed relatively constant since it peaked in the 1930s, while the number of bison in private, commercial herds has exploded since around 1970, when the number of bison in commercial herds surpassed those in conservation herds for the first time (Fig. 1) (McHugh, 1972). Apart from the potential problems posed by domestication of such a large portion of the bison population of North America, conservation of the wild bison genome is further compromised by problems confronting conservation herds, such as small herd size, confinement to fenced areas, introgression of cattle genes, intensive management and culling practices, absence of major predators, and non-native diseases.

The largest conservation herds of plains bison within their original range are in Yellowstone National Park (4000–5000 animals) and Grand Teton National Park (approximately 800), referred to as the Greater Yellowstone Area. These herds are free-ranging within the boundaries of the parks and nearby areas. With the successful reintroduction of wolves in 1995, they are subject to the full suite of native predators and other natural selection factors. Both herds, however, are infected with *Brucella abortus*, a non-native pathogen that causes brucellosis, a disease that causes abortion in many ungulate species, though it appears to have limited direct effect on these bison populations (Meyer and Meagher, 1995; Berger and Cain, 1999). The primary problem with brucellosis is the management conflict it creates because of fears that domestic cattle will be infected by bison wandering outside

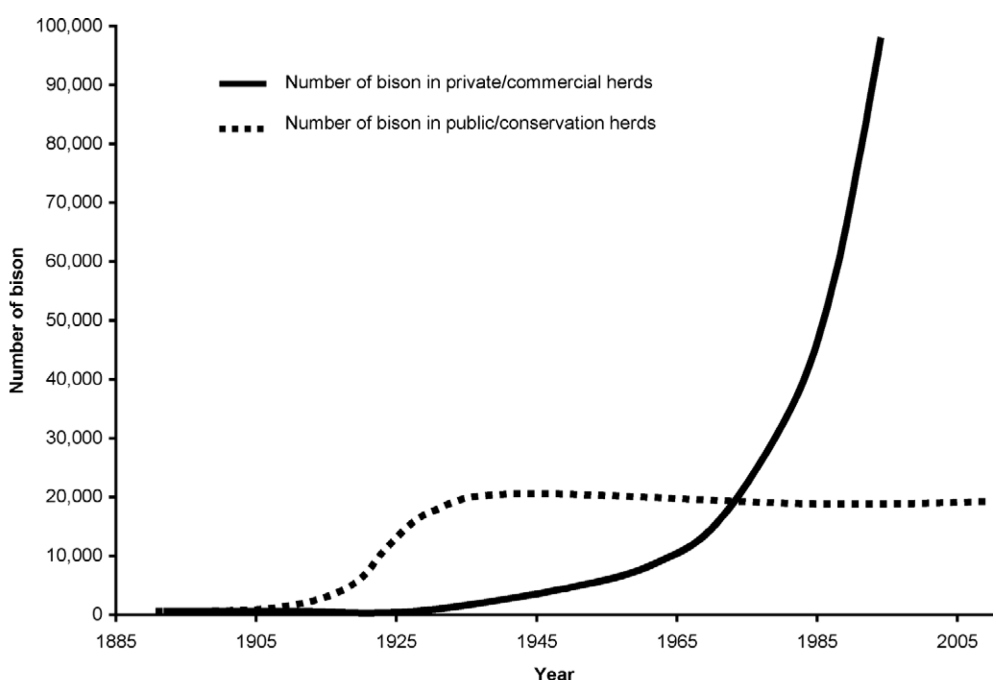

Fig. 1 – A comparison of bison numbers estimated to occur in public/conservation herds (sensu Boyd, 2003) and in private/commercial herds from 1883 to 2003; private/commercial animals totaled around 500,000 by 2003. (*Sources*: Hornaday, 1889; Seton, 1906; American Bison Society, 1908, 1911, 1914, 1918, 1923, 1930; Garretson, 1934, 1938; Dary, 1989; Callenbach, 1996; Boyd, 2003).

the park (Gates et al., 2005). Free-ranging, disease-free (i.e., free of non-native regulated diseases such as brucellosis) populations that are potentially influenced by natural regulating factors in the original range of plains bison accounted for, at the time of Boyd's (2003) survey, only 1289 bison (6.7% of the total conservation population). No herd among this latter group numbers more than 400 animals, which is probably well below the minimum number of animals needed to maintain the long-term genetic health of the herd (see below). Thus, no viable population that is free of regulated diseases such as brucellosis exists under natural conditions within the original range of the plains bison.

2.2. *Introgression of cattle genes*

Hybridization, with or without introgression, has caused the extinction of many plant and animal taxa, and is of growing concern in the conservation community (Rhymer and Simberloff, 1996; Allendorf et al., 2001). In the United States, considerable uncertainty exists concerning if and how the US Endangered Species Act should be applied to hybrids (Allendorf et al., 2004; Campton and Kaeding, 2005). The legacy of extensive efforts to create "cattalo" by cross-breeding bison and domestic cattle during the period when bison numbers were very low in the late 1800s and early 1900s (Garretson, 1938; Coder, 1975) is evident today by widespread domestic cattle gene introgression in both the mitochondrial (Polziehn et al., 1995; Ward et al., 1999) and nuclear (Halbert et al., 2005; Halbert and Derr, in press) genomes of bison herds across North America. While many public bison herds harbor evidence of domestic cattle nuclear gene introgression, the amount of introgression across the genome of each individual herd appears to be fairly low, with introgression rates ranging from 0.56% to 1.80% (Halbert et al., 2005; Halbert and Derr, in press).

All significant public herds of plains bison in the US and Canada have been tested and all but six show domestic cattle gene introgression. Of these six, sufficient numbers of individuals have been examined from only two herds to allow statistical confidence (>95%) in the lack of detection of domestic cattle introgression (i.e., low probability of type II error): Wind Cave National Park in South Dakota and Yellowstone National Park (Halbert et al., 2005; Halbert and Derr, in press). Four other public herds show no evidence of cattle introgression but the sample size is too small for statistical inference: Henry Mountains State Park in Utah, Teton National Park in Wyoming, Sully's Hill National Game Preserve in North Dakota, and Elk Island National Park in Alberta (Polziehn et al., 1995; Ward et al., 1999; Halbert and Derr, in press).

Four of these six herds contain fewer than 400 animals and, as noted previously, the two larger herds of Yellowstone and Grand Teton National Parks carry brucellosis and face troubling management issues (Gates et al., 2005). The only known private herd (of more than 100 tested; J.N.D., unpublished data) that has a high probability of being free of cattle genes based on known history and number of animals examined is the Castle Rock herd on the Turner Enterprise's Vermejo Park Ranch in New Mexico. At best, therefore, less than 1.5% of the 500,000 plains bison in existence today can be classified as likely free of domestic cattle gene introgression.

Intentional translocations or unintentional immigration of cattle-gene-introgressed bison into bison herds of conservation importance is a threat, particularly for herds that are cattle-gene free. The Wind Cave herd is separated from the cattle-gene-introgressed herd of Custer State Park by a single fence, and Custer bison have recently crossed this divide into Wind Cave (S.C.F., C.H.F and K.K., unpublished data). At least one private bison herd with cattle gene introgression (J.N.D. and C.H.F., unpublished data) and other herds that have not been tested for cattle gene introgression occur in the region around Yellowstone and Grand Teton National Parks, raising the possibility of cross-breeding with these valuable conservation herds. In spring 2006, a young male bison that escaped from a private herd was shot inside Yellowstone National Park's north boundary (R. Wallen, personal communication). As the popularity of private bison breeding increases without restrictions on bison that can inhabit lands near these conservation herds, the potential for interbreeding between conservation herds and cattle-gene-introgressed herds that are also undergoing selection for domestication will increase.

2.3. *Ecological extinction*

A primary mission of conservation should be to restore interactive species, species whose "virtual or effective absence leads to significant changes in some feature of its ecosystem(s)" (Soule et al., 2003, p. 1239). As an interactive species that was also highly abundant on the Great Plains, the plains bison was almost certainly a foundation species (Soule et al., 2003). Today, the plains bison is for all practical purposes ecologically extinct within its original range. Even in the few areas of the Great Plains where bison occur, they contribute less to food chains and landscape heterogeneity than they once did. Lost is the large influence of bison as a grazer that once roamed over large areas creating a mosaic of grazing intensities, as a major converter of grass to animal biomass that provided food for Native Americans, predators, scavengers and decomposers, as a key link in nutrient recycling, and as a maker of wallows and mini-wetlands, among other factors (Knapp et al., 1999; Truett et al., 2001). Heavily grazed areas also may have acted as fire breaks which further influenced habitat heterogeneity. Bison grazing has been shown to increase plant species diversity and structural heterogeneity in tall grass prairie (Hartnett et al., 1996). Bison were probably important in enabling the establishment of prairie dogs (*Cynomys* spp.), especially in the tallgrass prairie, by creating heavily grazed areas which are preferred by prairie dogs (Truett et al., 2001). As a keystone species, prairie dogs in turn affect multiple ecosystem processes and species, including bison (Kotliar et al., 2006). Although more research is needed to understand the relationship, one reason that grassland birds have experienced steeper declines than any other guild of birds in North America may be the loss of habitat heterogeneity that bison grazing patterns once created (Knopf, 1996).

Restoring the ecological role of bison is a prerequisite to large-scale and comprehensive restoration of biodiversity in the Great Plains and other grassland regions of North America that bison once inhabited. Although cattle, if managed to create heterogeneous grazing intensities (which is rarely done), are often proposed as surrogates for bison, the ecological effects of the two species are substantially different. Research at Konza Prairie in Kansas and in Utah indicates that the abundance and richness of annual forbs and the spatial heterogeneity of biomass and cover are higher in sites with bison than in sites with cattle. Plumb and Dodd (1993) reported a difference in diet of the two species, with bison demonstrating a stronger preference for graminoids over forbs compared to cattle. Cattle do not create wallows and generally stay closer to bodies of water, which causes different grazing patterns and impacts on streams and riparian areas. Bison grazing, especially in combination with burning, has the potential for inducing a much more complex set of local interactions and spatial and temporal patterns of vegetation than cattle grazing (Steuter, 1997). Apart from the ecological differences between bison and cattle, perhaps the most important constraint is that cattle are invariably managed for commodity production. In addition to the truncation of the food web caused by removal of livestock for human consumption, large prairie dog populations are generally not tolerated by livestock producers, nor are large numbers of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) (Freilich et al., 2003). Particularly in the Great Plains, large reserves with abundant bison will be needed if these ecologically important species are to be restored.

3. Restoration issues and potential

Unlike many endangered species restoration efforts, there are no significant biological challenges to building bison populations, as evidenced by the success of commercial bison breeders across North America and successful reintroductions of plains bison to the wild in Yellowstone National Park's northern range, the Henry Mountains of Utah, four areas in Alaska (Boyd, 2003), and wood bison in several locations in Canada (Gates et al., 2001). Millions of acres of bison habitat, particularly native grasslands of the Great Plains, remain largely intact. Rebuilding a population is biologically relatively simple: give a suitable founder herd lots of land to roam and grass to eat and watch their numbers double every 4 or 5 years (Fredin, 1984). The major challenge is primarily a socioeconomic one of securing sufficiently large areas of land.

The primary biological questions regarding bison restoration are genetic, including providing for natural selection. The amount of genetic diversity within and between historic populations of plains bison across pre-European North America is largely unknown; individuals were routinely traded among the founding herds thereby largely precluding any attempt today to reconstruct historic genetic patterns. If there was significant genetic variation across their range, we were lucky that the half dozen or so herds rescued in the late 1800s sampled a relatively broad cross-section of the North American distribution of the sub-species (Halbert, 2003). Though the bison went through a severe population bottleneck, this was short-lived as herds quickly grew in the early 1900s. The brevity of the bottleneck may have served to prevent significant genetic erosion as the nuclear genetic variation of bison today is generally much greater than other mammal species that have gone through population bottlenecks (McCleneghan et al., 1990; Stormont, 1993) and is similar to other wild ungulates (Wilson and Strobeck, 1999; Halbert, 2003).

Genetic differences exist among the conservation herds of plains bison in North America. Some herds, including those with cattle gene introgression, have a distinct genetic composition compared with other bison populations due to unique bison alleles and allelic distributions (Halbert, 2003). Development of a North American bison conservation strategy needs to address the resulting questions: Do these differences reflect local adaptations or simply represent the random effect of a small number of founders? Should we strive to create several populations replicating each of the herds without detectable domestic cattle introgression, such as those of Wind Cave and Yellowstone National Parks, as well as those cattle-gene-introgressed herds that have a unique genetic constitution and historical significance, such as the National Bison Range herd in Montana? Or, given limited resources and land, is the best strategy to found new herds that incorporate the genetic diversity of all these herds and manage all or most conservation herds as one metapopulation?

Given the option, we agree with Allendorf et al. (2001) that in cases where widespread introgression has occurred in a species, highest priority should be given to conserving populations that are genetically pure. However, some bison populations with low levels of domestic cattle introgression might also be valuable conservation targets due to their historical importance and unique genetic constitution, and because they can presumably fulfill the ecological role of bison. We say "presumably" because we do not know what effects, if any, cattle DNA may have on bison physiology, behavior and fitness. For example, given the distinct metabolisms of cattle and bison (e.g., bison, unlike cattle, greatly reduce their metabolic rate in winter [Rutley and Hudson, 2000]), the presence of a domestic cattle mitochondrial genome in bison might affect bison energetics, growth, and seasonal foraging behavior. The potential for selectively removing bison with cattle mitochondrial DNA from these important introgressed herds emerges as a possibility with new DNA screening methods under development. Domestic cattle nuclear fragments have been widely dispersed throughout the bison genome over a long enough period of time (hybrid swarm), however, that recapitulation of the parental bison nuclear germplasm through similar selective removal and breeding is highly cost- and labor-prohibitive at this point.

The goals of conserving the bison gene pool and ensuring the viability of bison populations pose questions about what herd sizes must be maintained and how these herds must be managed, both individually and collectively. Inbreeding depression appears to significantly increase the risk of extinction for small populations (Frankham, 2005), including many mammalian taxa at populations of less than a few thousand individuals (O'Grady et al., 2006). Population viability analysis for vertebrates has similarly suggested that adult population sizes of several thousand are needed for long-term persistence (Reed et al., 2003).

One important bison conservation herd has already exhibited problems of inbreeding depression. The Texas State Bison Herd, which has a distinct genetic composition and history, suffers from dangerously low levels of genetic diversity resulting from a small number of founders, chronically small herd size, and inbreeding which has resulted in fertility and recruitment problems (Halbert et al., 2004).

Although the National Park Service, the United States Fish and Wildlife Service, and Parks Canada manage a large proportion of public herds and the most important conservation herds on the continent, none of the agencies has science-based quantitative management objectives for conserving the genetic diversity of bison, nor is there a policy for coordination of bison conservation among agency units. Recent computer models aimed at informing National Park Service decisions about this question suggest that an actual population size of about 400 animals is likely to achieve a goal of retaining 90% of currently existing herd heterozygosity if management closely follows simulated management actions and if assumptions on (poorly known) bison breeding behavior are approximately correct (Gross and Wang, 2005). Because management practices are seldom as precise as models and our knowledge of bison behavior is limited, a larger population may well be needed to meet this goal.

Gross and Wang (2005) estimate that to retain 90% of existing alleles over 200 years an actual population size of 1000 bison is required. However, to meet the need for bison to adapt to new areas where they are reintroduced and to adapt to large current (e.g., exotic diseases) and future (e.g., climate change) alterations in their habitats, as well as for the intrinsic value of conserving genetic diversity, a more prudent goal would be retention of at least 95% of allelic diversity over 200 years. Their analysis suggests a herd size of at least 2000 animals is required to meet this goal. As Gross and Wang (2005, p. 11) state: "High allelic diversity will virtually always be correlated with the occurrence of many alleles that have a low frequency in the population. These rare alleles are unlikely to contribute substantially to short-term population responses to selection, but they can be a very important limit to the response to selection over many generations. Allelic diversity is thus considered important for the long-term survival of a species, especially where there may be substantial environmental changes, range expansions, or (re)introduction into new sites."

No federal or state conservation area that currently harbors bison in the Great Plains maintains even one half of a herd goal of 2000 animals. However, The Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma harbors a herd of around 2000 animals (The Nature Conservancy, 2006). Within the original range of the plains bison, the only federal or state herd that currently meets the 2000 goal is in the Rocky Mountains of Yellowstone National Park. Managing the genetic diversity of these small herds is compounded by the fact that all of them, including the Yellowstone National Park herd, are currently subject to culling practices that may inadvertently affect genetic diversity.

Although the genetic questions are complex, probably the most difficult question to answer with any certainty is: How many bison over how large an area are needed to restore the ecological role of the bison on a meaningful scale for biodiversity conservation in the Great Plains? We can develop some reasonably sound estimates for how many thousands of bison over several hundred thousand hectares, combined with other native ungulates, would be needed to support viable populations of wolves and perhaps grizzly bears. But questions of scale become much more difficult to answer as we try to envision how, for example, bison and prairie dogs, as two ecologically important species of the Great Plains, historically interacted to create a mosaic of grassland habitats. Our understanding of how habitat features and patch size were influenced by bison carcasses and grazing patterns, and how these in turn affect grassland bird distribution and nesting success, is still too rudimentary for the formulation of sound management recommendations (Truett et al., 2001).

The late bison biologist and conservationist Dale Lott proposed that "A Great Plains Park must be very large—at least 5000 square miles (1.3 million hectares)—and must include both upland and river bottom habitat" (Lott, 2002, p. 203). Only 1.5% of the Northern Great Plains Ecoregion is in parks, reserves and similar protected areas (Forrest et al., 2004), a figure probably representative of the Great Plains as a whole. No protected area in the Great Plains is close to 13,000 square kilometers in size. Nevertheless, roughly 50% of the Northern Great Plains ecoregion remains in largely native prairie, with 10 areas recently identified that have several hundred thousand to more than a million hectares of public lands in primarily native prairie, often interspersed with private land that also contains substantial intact prairie (Forrest et al., 2004). Thus, several areas in the Northern Great Plains alone appear to have suitable habitat for supporting populations of 10,000–30,000 or more bison. Ecosystem restoration at such a scale is challenging, given that much of the landscape is privately owned or managed for a multitude of other uses, some of which are incompatible with bison restoration.

4. The social context

Large-scale biodiversity restoration always involves various layers of social complexity. Clewell and Aronson (2006) discuss the five major motivations or rationales for the restoration of ecosystems (and their associated species). These include technocratic, biotic, heuristic, idealistic, and pragmatic rationales and often result in apparent social conflicts. Restoration of bison and their native ecosystems is no exception, as a diversity of socioeconomic factors, from local to regional to international scales, are involved. Some of these factors are largely unique to bison conservation because bison occupy a rather distinct spiritual, iconic, and legal status among wildlife of the Great Plains, if not more broadly across much of North America, and because they are particularly important culturally and economically for many Great Plains Indians (Wyckoff and Dalquest, 1997).

The cattle ranching culture and economy, occupying more than 95% of the Great Plains grasslands, is the successor to the bison economy of Native Americans that previously dominated the region. The potential for restoring bison at a meaningful ecological scale is therefore inextricably linked to the existing cattle industry. The Buffalo Commons concept for 're-bisoning' the Great Plains proposed by geographers Frank and Deborah Popper in the 1980s (Popper and Popper, 1987) created a firestorm of protest among communities of the region that continues to taint discussions about present-day bison conservation. Nevertheless, the Popper's predictions have withstood the test of time as the economic tailspin and human population decline, with the exception of the Native

American population, continues unabated in the Great Plains (Forrest et al., 2004).

These conditions create both a socioeconomic need and an opportunity for large-scale conservation of bison and native grasslands. The economic revitalization of many rural communities may be possible through the development of a natural-amenity economy based on grassland reserves and abundant wildlife, whether done through privately or publicly funded initiatives. Abundant wildlife and wildlands brought the wealthy from the east coast and Europe on safari to the Great Plains in the 1800s, and the Rocky Mountain West provides many examples of the positive effect today that wildlife and wildlands have on the economic vitality of local communities (Rudzitis and Johansen, 1991; Rudzitis, 1999; Rasker and Hansen, 2000). The depopulation of rural areas, an ageing population of current ranch owners, and relatively low land prices in much of the Great Plains provide the conditions for large-scale changes in land ownership, in the subsequent management of those lands, and in the rural economy over the next decade. How these changes will unfold remains to be seen, but conservationists, Native American tribes, and ranching communities have perhaps an unparalleled opportunity over the next few years to restore ecological relationships, structure, and function at a regional scale in a manner that is sensitive to cultural history and heritage while providing economic opportunities.

Bison also fall into an unusual legal framework that greatly complicates conservation efforts. Unlike any other native animal species in North America, bison are commonly not classified or managed as "wildlife," but rather, with some exceptions, as "livestock" by state and provincial agencies, although they are considered wildlife in federal refuges and parks (Forrest et al., 2004) and on some state and provincial lands (Gates et al., 2001; Boyd, 2003). This leaves one of North America's most majestic and adaptable native grassland species, legally and in the public's mind, straddling the fence between being wild and domestic (Cahalane, 1944).

This dual status complicates management, as indicated by recent events in Canada. In May 2004, Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommended to list plains bison as a threatened species (COSEWIC, 2004). Following a review of public commentary, the Governor General in Council, on the recommendation of the Minister of the Environment, decided to not list the plains bison "because of potential economic implications for the Canadian bison industry" (Canada Gazette, 2005). Instead of listing, the federal government committed to "working with provincial governments, the bison industry and other stakeholders to develop an approach for the recovery of wild plains bison."

Although bison conservation is not a priority for most states, Montana lists free-ranging herds as a species of concern with an S2 status: "imperiled because of rarity or because other factors demonstrably making it very vulnerable to extinction throughout its range" (Carlson, 2003), and the state's recently released Comprehensive Fish and Wildlife Conservation Strategy lists bison as Tier 1—those species in greatest need of conservation—and proposes large-scale bison restoration (Montana Fish, Wildlife and Parks, 2005).

Native American Tribes have made available thousands of acres of land for bison restoration and thus there is considerable potential for tribes to play an important role in the ecological recovery of bison. Tribes often take a "hands-off" approach to bison management and allow, to the extent possible, natural processes to unfold. Because many of the tribal bison herds were started or reinforced with surplus bison from national parks and refuges, some herds may be free of domestic cattle introgression and most, if not all, are brucellosis-free.

The InterTribal Bison Cooperative provides technical assistance to many tribes involved in bison restoration and has created a network where tribes can share information on management practices. The Cooperative has a membership of 55 tribes that collectively have more than 8000 bison which, depending on the tribe, are managed for various marketing, spiritual and conservation purposes. According to its web site, the Cooperative is "committed to reestablishing buffalo herds on Indian lands in a manner that promotes cultural enhancement, spiritual revitalization, ecological restoration, and economic development" (InterTribal Bison Cooperative, 2006).

5. The way forward

Although the restoration of bison in North America faces a new set of social and ecological circumstances and challenges, we need to avoid repeating mistakes evident in the history of bison conservation. Bison need to be established as a free-ranging wildlife species with the appropriate social and ecological values. We should avoid the pitfall of conducting species conservation at the expense of ecological function.

Conservation of the plains bison urgently needs to move forward simultaneously on two fronts. First, the genetically important herds, both those that are apparently free of cattle genes and those that harbor unique parts of the total bison gene pool, need to be conserved. This means developing best management practices and applying them to existing herds. A precautionary approach dictates that we create viable satellite herds of each of the existing genetically important bison herds in North America. Second, we need to restore large herds numbering in the thousands on native grasslands where the ecological role of the bison can be fully expressed. There is ample need and opportunity here for both public and private lands to contribute to this effort.

Restoration efforts are moving forward on several fronts. The US National Park Service is now developing management guidelines to maintain the genetic health of federal herds. The IUCN Bison Specialist Group is currently completing a new status assessment and conducting a review to determine if the species should be red-listed as threatened or endangered. In addition, the IUCN Bison Specialist Group, World Wildlife Fund, Turner Endangered Species Fund, and Turner Enterprises hosted a meeting in May 2005 of bison researchers and managers from across North America to kick off the preparation of North American conservation strategy for the plains bison. The Wildlife Conservation Society is conducting a comprehensive review of the range-wide status of bison in follow-up to Boyd's earlier work and is working in concert with the IUCN Bison Specialist Group. In 2005, the centennial year of the American Bison Society, the Wildlife Conservation Society also revitalized the principles of the historic American

Bison Society campaign to help bring about ecological recovery of American bison across its entire historic range.

Meanwhile, on-the-ground conservation efforts need to continue. As refuges and national parks now focus on developing a strategy for managing and expanding their important conservation herds, one significant constraint is the absence of public lands currently available for creating large, new public herds. In Canada, Grasslands National Park reintroduced bison from the Elk Island population in December 2005, and Banff National Park is investigating the feasibility of bison reintroduction in the Central Rockies ecosystem. Management plans for Waterton Lakes and Banff National Parks mention plains bison restoration, but no operational plans have been developed at this time. We know of no other formal federal or state/provincial initiatives at this time to establish new conservation herds of bison in the Canada, Mexico, or the United States.

At least three initiatives by the non-profit sector to create conservation herds of bison are underway: Nature Conservancy Canada's Old-Man-on-His-Back Preserve in Alberta with Elk Island animals; American Prairie Foundation and World Wildlife Fund in Montana with Wind Cave source stock; and The Nature Conservancy in South Dakota, also with animals from Wind Cave. Elsewhere in the private sector, Turner Enterprises has separated the apparently cattle-gene-free Castle Rock herd into three units to reduce risk and grow the herd (Joe Truett, personal communication).

Tribal initiatives are also underway. The Cheyenne River Sioux Tribe has started a 8900-hectare Tribal Wildlife Reserve with approximately 1100 bison (Cheyenne River Sioux Tribe, 2006). The Rosebud Sioux Tribe has officially endorsed "The Million Acre Project" developed by the Great Plains Restoration Council and centered on the Pine Ridge Indian Reservation in South Dakota, with plans to restore bison and a prairie ecosystem (Great Plains Restoration Council, 2006). Additionally, Native American Tribes may have the opportunity to manage or co-manage federal lands adjacent to or within reservation boundaries and create large contiguous blocks of federal and tribal land that may be suited for large-scale bison restoration. At least one tribe, the Lower Brule Sioux Tribe, has formalized the early stages of this vision in a strategic plan (Lower Brule Sioux Tribe. In review. 10-year strategic plan. Lower Brule Sioux Tribe Department of Wildlife, Fish and Recreation, Lower Brule, South Dakota).

The Great Plains is at an ecological and socioeconomic cross-roads. Change could be swift, massive, and far-reaching. The next decade—a very narrow window on the conservation time scale—will be our best chance to capitalize on a new era of land use that embraces wild bison on vast, intact grasslands, alongside sustainable agriculture and other suitable land uses, as an ecological and socioeconomic cornerstone for the region. As one of North America's most charismatic megafauna, bison hold great potential for sparking the public's imagination about, and support for, restoring the wildlife spectacle that once graced the Great Plains. Through public and private initiatives and partnerships, tens of thousands of largely wild and free-roaming bison could again populate these grassland ecosystems by the end of this century. Bringing back the wild bison is not only important for conserving the bison genome and restoring its ecological and economic roles in North America's native grasslands. It also promises the intrinsic value of having countless numbers of bison and other wildlife on a vast, horizon-to-horizon prairie vista, and the power of that vista for uplifting the human spirit.

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