American Bison

Status Survey and Conservation Guidelines 2010

Edited by C. Cormack Gates, Curtis H. Freese, Peter J.P. Gogan, and Mandy Kotzman

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American Bison
Specialist
Group

SSC
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Acronyms

ABS	American Bison Society
ABSG	American Bison Specialist Group, a division of the IUCN BSG
ADFG	Alaska Department of Fish and Game
AGFD	Arizona Game and Fish Department
ALCES®	A Landscape Cumulative Effects Simulator, FOREM Technologies
ANPP	Herbaceous above ground net primary productivity
APF	American Prairie Foundation
APFRAN	Animal Plant and Food Risk Assessment Network, Canada
APHIS	U.S. Department of Agriculture Animal and Plant Health Inspection Service
BLU	Bluetongue
BNP	Badlands National Park, South Dakota
BRCP	Bison Research and Containment Program, Northwest Territories
BSE	Bovine spongiform encephalopathy
BSG	IUCN Bison Specialist Group
BTB	Bovine tuberculosis
BVD	Bovine viral diarrhoea
CAMP	Conservation Action Management Plan process, IUCN Captive Breeding Specialist Group
CATG	Council of Athabascan Tribal Governments, Alaska
CBA	Canadian Bison Association
CBD	International Convention on Biological Diversity
CBSG	IUCN/SSC Conservation Breeding Specialist Group
CDOJ	Canadian Department of Justice
CFIA	Canadian Food Inspection Agency
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CMN	Canadian Museum of Nature
CONANP	Comision Nacional De Areas Naturales Protegidas, Mexico
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CSP	Custer State Park, South Dakota
CWS	Canadian Wildlife Service
CWCS	Comprehensive Wildlife Conservation Strategy
DNDC	The Department of National Defence, Canada
EHD	Epizootic hemorrhagic disease
EINP	Elk Island National Park, Alberta
EIS	Environmental Impact Statement
ESA	U.S. Endangered Species Act
ESU	Evolutionarily significant unit
FAD	Foreign Animal Disease
FEARP	Federal Environmental Assessment Review Panel, Canada
FMD	Foot-and-mouth disease, or heartwater
FNNWR	Fort Niobrara National Wildlife Refuge, Nebraska
GEU	Geminate evolutionary unit
GTNP	Grand Teton National Park, Wyoming
GWBE	Greater Wood Buffalo Ecosystem, Canada
GWBNP	Greater Wood Buffalo National Park, Canada
GYA	Greater Yellowstone Area
HMSP	Henry Mountains State Park, Utah
HOAA	Health of Animals Act, Canada
InVEST	Integrated Valuation of Ecosystem Services and Tradeoffs
ITBC	Intertribal Bison Cooperative
IUCN SSC	IUCN Species Survival Commission
IUCN SUSG	IUCN Sustainable Use Specialist Group
JD	Johne's disease
MBS	Mackenzie Bison Sanctuary, Northwest Territories
MCA	Montana Code Annotated
MCF	Malignant catarrhal fever
MDOL	State of Montana Department of Livestock
MFWP	State of Montana Department of Fish, Wildlife and Parks
MLVA	Multiple locus, variable number, tandem repeat analysis
MtDNA	Mitochondrial deoxyribonucleic acid
N	Population size

NBA	National Bison Association, U.S.A
NBMB	Northern Buffalo Management Board, Canada
NBR	National Bison Range, Montana
NCC	Nature Conservancy of Canada
Ne	Effective population size
NEP	Nonessential experimental population
NEPA	National Environmental Policy Act, U.S.A
NER	National Elk Refuge, Wyoming
NGO	Non-governmental organisation
NPS	U.S. National Park Service
NRCS	Natural Resource Conservation Service, U.S.A
NWT	Northwest Territories, Canada
NTENR	Northwest Territories Environment and Natural Resources
OIE	World Organization for Animal Health
PANP	Prince Albert National Park, Saskatchewan
PCA	Parks Canada Agency
PES	Pay-for-Environmental Services
PHVA	Population and Habitat Viability Assessment
PPAs	Private protected areas
PVA	Population viability analysis
RAC	Research Advisory Committee for bison disease research in WBNP
RDR	Reportable Diseases Regulations
$\hat{r}$	Observed exponential rate of population increase
r_m	Maximum exponential rate of population increase
RMEF	Rocky Mountain Elk Foundation
SAGARPA	Secretary of Agriculture, Livestock Production, Rural Development, Fishery and Food, Mexico
SCBD	Secretariat of the Convention on Biological Diversity
SDGFP	South Dakota Game, Fish and Parks
SEMARNAT	Secretaría de Medio Ambiente y Recursos Naturales, México
SENASICA	Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria, Mexico
SERI	Society for Ecological Restoration International
SERS	Society for Ecological Restoration Science
SHNGP	Sully's Hill National Game Preserve, North Dakota
SRL	Slave River Lowlands, Northwest Territories, Canada
SNMNH	Smithsonian National Museum of Natural History
SWAP	State Wildlife Action Plan (name varies by state)
TB	Tuberculosis
TGPP	Tallgrass Prairie Preserve, Oklahoma
TNC	The Nature Conservancy
TRNP	Theodore Roosevelt National Park, North Dakota
TSE	Transmissible spongiform encephalopathies
TESF	Turner Endangered Species Fund
USNARA	U.S. National Archives and Records Administration
USDA	U.S. Department of Agriculture
USDOI	U.S. Department of the Interior
USFS	U.S. Forest Service
USFWS	U.S. Fish and Wildlife Service
USGSBRD	U.S. Geological Survey Biological Resources Division
VJDHSP	Voluntary Johne's Disease Herd Status Programme (for cattle)
WBNP	Wood Buffalo National Park, Alberta and Northwest Territories
WBP	Wainwright Buffalo Park, Alberta
WCNP	Wind Cave National Park, South Dakota
WCS	Wildlife Conservation Society
WHO	World Health Organization
WMNWR	Wichita Mountains National Wildlife Refuge, Oklahoma
WWF	World Wildlife Fund
YDOE	Yukon Department of the Environment
YNP	Yellowstone National Park, Idaho, Montana and Wyoming
YT	Yukon Territory, Canada

Executive Summary

Curtis H. Freese and C. Cormack Gates

The publication of this IUCN American Bison Status Survey and Conservation Guidelines is timely owing to a recent convergence of factors: new research findings on bison genetics and ecology, assessment and awareness of the precarious status of many bison conservation herds, new initiatives by government and non-profit institutions to improve management of existing herds and to establish conservation herds, growing interest among Native Americans in restoring bison as part of their cultural heritage, and an increasing awareness by the commercial bison industry that conservation of wild-type bison is in the long-term interest of the industry. There is also a growing body of evidence that the biodiversity of ecosystems within the original range of bison can benefit from bison restoration, from the desert grasslands of northern Mexico, through the Great Plains, to the lowland meadow systems of interior Alaska. The ten chapters of this book examine these and other aspects of the biology and conservation of the species, and offer guidelines for what we anticipate will be a new era of bison conservation in North America. Under the auspices of the IUCN American Bison Specialist Group, twenty-nine chapter coordinators and contributors share their knowledge and ideas in this comprehensive review of the diverse topics that need to be considered by researchers, managers, policy makers and others interested in restoring and conserving this magnificent animal.

In the introductory chapter, C. Gates and P. Gogan explain the overall purpose of the IUCN American Bison Specialist Group and this document. The Specialist Group is composed of more than 60 registered members and numerous collaborators from the three nations comprising North America and ranging from Chihuahua State in Mexico to the State of Alaska. The Group operates under the aegis of the IUCN Species Survival Commission. The authors note that the purpose of this volume is to contribute to the development of strategies and actions that, where feasible, will conserve and ecologically restore bison as wildlife throughout their original range. Gates and Gogan acknowledge that large-scale restoration of bison is an ambitious and complex undertaking, perhaps unparalleled in species conservation efforts in North America. Their introduction briefly reviews the major issues facing bison conservation and the strong influence that bison historically exerted on ecosystems across much of the continent. Apart from the ecological importance of bison, the social and cultural significance of bison restoration is recognised when they state, “no other wildlife species has exercised such a profound influence on the human history of a continent.”

In Chapter 2, B. Potter and co-authors trace the evolutionary and recent history of bison, beginning with the earliest fossil records showing bison in Asia at least two million years ago, and continuing with their expansion, much later, into North America across the Bering Land Bridge during the middle Pleistocene. The evolution and distribution of various bison species and subspecies in North America present a complex story shaped, in large part, by bison habitat and ranges that shifted widely with advancing and retreating continental ice sheets. The result of this evolutionary history today is two species, the European bison and American bison, and two subspecies of American bison, wood bison and plains bison. Five hundred years ago, tens of millions of plains bison probably inhabited North America, from southern Canada to northern Mexico, and from nearly the west coast to the east coast, with the Great Plains as their centre of abundance. Wood bison, because of a more restricted boreal forest habitat, were much less numerous. For many native peoples of North America, thousands of years of coexistence had led to bison being central to their survival and cultures, a history that Potter *et al.* explore in some detail. European colonisation of North America brought rapid change to both bison and Native Americans. Commercial hunting, competition with livestock, killing of bison as government policy to subjugate Indian tribes, and other causes led to the precipitous decline of both plains and wood bison. By the end of the 19th Century a few hundred bison survived in various small captive and wild herds across North America. Fortunately, conservation efforts quickly emerged in both Canada and the United States (U.S.) and, once protected, bison numbers began to recover. Their iconic status now seems to be recovering also. Potter *et al.* echo what other authors of this volume have expressed when they note that no other North American species holds such great cultural and political significance.

In Chapter 3, D. Boyd and co-authors review the confusing and disputed evidence for, and diverse opinions about, bison taxonomy. Agreement seems to end with the consensus that bison belong to the family Bovidae. Much of the debate centres on whether bison belong to the genus *Bos*, the genus of cattle, guar, yak, and oxen, or to their own genus, *Bison*. Both names are currently used in the scientific literature. Differences of opinion are largely based on the importance of morphological (phenetic) versus molecular (phylogenetic) lines of evidence, and on historical precedence and usage. Within *Bison*, there are also some people who question the designation of European bison and American bison as separate species. Boyd *et al.* conclude

that "Further research and debate by taxonomists, and the bison conservation community, is required to reconcile molecular, behavioural and morphological evidence before a change in nomenclature could be supported, and thus, for this document, the American Bison Specialist Group adheres to the genus *Bison* with two species, *B. bonasus* and *B. bison*. Not surprisingly, disagreement also exists regarding the subspecies status of wood and plains bison. However, Boyd *et al.* emphasise that this debate does not negate the importance of conserving the two forms as separate entities. From a conservation perspective, the goal is to conserve "evolutionarily significant units" or "distinct population segments," among other terms used to define geographic variation among populations, a concept recognised by both the U.S. Endangered Species Act and the Committee on the Status of Endangered Wildlife in Canada. Keeping wood bison and plains bison as separate non-interbreeding units is the recommended precaution.

Genetics play a particularly complex and important role in bison conservation, as explained by D. Boyd and co-authors in **Chapter 4.** The rapidly advancing science of genetics has recently brought new information and insights into not just the evolutionary relationships among bison taxa, but also to managing for viable bison populations and conserving the wild bison genome. Boyd *et al.* review the current state of bison genetics and what needs to be done to address the major threats to genetic diversity and integrity—demographic bottlenecks, founder effects, genetic drift, and inbreeding—all of which bison have experienced. Although population bottlenecks can lead to significant loss of genetic diversity, bison appear to have largely avoided this problem during their population bottleneck in the late 1800s. Given the good diversity within the bison gene pool, and recent evidence that shows several conservation herds are genetically distinguishable, one of the most important management questions is how to manage the population genetics of these often relatively small herds. Should this be accomplished as one large metapopulation or as closed herds to maintain localised diversity? The best conservation strategy is to do both, and, where possible, to increase the size of small herds to attain a large effective population size. Hybridisation also poses challenges for bison conservation. Although the introduction of plains bison into wood bison range has resulted in some hybridisation, the two forms remain distinct and avoiding further hybridisation is a priority. Much more widespread, and of greater concern, is the introgression of cattle genes into the bison genome, a legacy of attempts to cross-breed cattle and bison that began when bison numbers were still low in the early 1900s. Genetic testing reviewed by Boyd *et al.* indicates that most conservation herds have some level of cattle-gene introgression in the nuclear and (or) mitochondrial DNA. By inference this strongly suggests that a vast majority of commercial herds have cattle-gene introgression. The effects of introgression on bison biology are largely unknown. No introgression has been detected in several conservation herds, which consequently deserve priority attention for maintaining in reproductive isolation, and as source stock for establishing new conservation herds. Finally, Boyd *et al*. note that the approximately 400,000 bison in commercial herds in North America, some 93% of the total continental population, are undergoing artificial selection for domestic traits, such as ease of handling, body conformation, carcass composition, and so on. Domestication, whether intentional or not, poses a special challenge to conserving the wild bison genome.

In Chapter 5, K. Aune and co-authors provide a comprehensive review of how diseases, particularly those that are "reportable" according to federal or state/provincial regulations, have a major influence on bison restoration and management. They describe the characteristics and implications of nine diseases for bison conservation, ranging from anthrax and bluetongue to bovine brucellosis and bovine spongiform encephalopathy. Federal and state/provincial regulations for, and management responses to, a particular disease depend on several factors, including potential effects on bison, threat to livestock and humans, and whether it is indigenous or exotic to bison and the ecosystem. The authors describe the complex and difficult management challenges that diseases present in three of North America's most important conservation herds: the plains bison herds of Yellowstone National Park (YNP) and Grand Teton National Park/National Elk Refuge that harbour brucellosis, and the wood bison herds in and around Wood Buffalo National Park that are infected with both bovine tuberculosis (BTB) and brucellosis. Diseases such as brucellosis also severely limit the translocation of bison from infected, important conservation herds, such as the Yellowstone herd, to establish new herds in new areas because of concerns about potential transmission to cattle. While the policies and legal framework for controlling disease in domestic livestock are well established, they do not work well when applied to wildlife, including bison, because they often conflict with conservation goals and our ability to manage and maintain wild populations. The recent development of national wildlife health strategies in both Canada and the U.S. could help address this problem.

Chapter 6, by P. Gogan and co-authors, addresses general biology, ecology, and demographics of bison. Bison are remarkably adaptable to a wide range of ecosystems and climatic regimes. Physiologically, bison are much better adapted to climate extremes than cattle. Behaviourally, bison exhibit a relatively simple social structure with cow-calf pairs at the core and, more loosely and somewhat seasonally, large groups of cows, calves and immature males, and separate, smaller groups of mature bulls. Bison exhibit individual and group defence against large predators such as wolves. Historically, plains bison made seasonal migrations between summer and winter ranges, in some cases north-south and in others between the prairies

and foothills. Bison have a profound influence on ecosystems and create habitat heterogeneity through various means. As primarily graminoid (grasses and sedges) eaters, variable grazing pressure by free-ranging bison and their interaction with fire create habitat patchiness on which grassland bird diversity depends. Wallowing behaviour further promotes heterogeneity by forming temporary pools and changing surface hydrology and runoff and creating local patches of disturbed soil in which some flowering plant species prosper. Bison are dispersers of seeds, and are sources and redistributors of nutrients for predators, scavengers, plants, and ecosystem processes. Gogan *et al.* describe foraging patterns and habitat use by wood and plains bison in various ecoregions, from the arid southwest to humid cold boreal regions. The authors also review bison population structure and reproduction and demonstrate that under natural conditions newly established bison populations can double every four to six years. Population numbers are affected by both density-independent events, such as severe winters and wild fires, and density-dependent factors such as disease and wolf predation. While humans were a bison predator for thousands of years, the advent of firearms greatly increased human predation, so that by the mid-1800s, an estimated 500,000 plains bison were killed annually for subsistence and 100,000 for hides. The human-firearm-commerce combination, it would seem, largely voided the density-dependent relationship between bison and human predation until it was almost too late for the American bison.

In Chapter 7, C. Gates and co-authors assess the status of conservation herds using seven criteria: numerical status, geographic status, population size and class distribution, opportunity for mate competition among mature males, presence of wolves, presence of diseases that could affect conservation status, and occurrence or likely occurrence of cattle-gene introgression. The designation "conservation herd" is assigned to herds managed by federal or state/provincial governments or non-governmental organisations (NGOs) whose mission is nature conservation. Remarkably, little progress has been made in recent decades in increasing the number of animals in conservation herds. From the few hundred that remained in the late 1800s, the number of animals in conservation herds increased in the first half of the 1900s, but then levelled off, or in the case of the wood bison, even declined, while the number of conservation herds has continued to grow to the present day. As of 2008, there were 62 plains bison conservation herds containing about 20,500 animals, and 11 conservation herds of wood bison containing nearly 11,000 animals. Meanwhile, starting in the 1980s, the commercial bison industry prospered with the total population growing to around 400,000 animals in 2007, roughly evenly divided between the U.S. and Canada. Although a few conservation herds exceed 1,000 animals, most conservation herds of both wood and plains bison have fewer than 400 animals and, in the case of the plains bison, many are fenced in areas of only a few thousands hectares and not subject to natural predation. Until recently, there was a wild bison herd inhabiting a trans-boundary area between Mexico and the U.S., the only herd meriting conservation status in Mexico. But now, it has been restricted to a private ranch on the U.S. side. The American bison nearly qualifies for listing as Vulnerable Ca2(1) under IUCN criteria and is currently listed as Near Threatened on the IUCN Red List.

As K. Aune and co-authors describe in **Chapter 8**, bison conservation must deal with a complex maze of legal and policy issues. Much of this complexity is due to a history of bison being treated like livestock. As the authors note, "During the great restoration period of wildlife management, bison were routinely classified and managed by state/provincial and federal agencies across North America as a form of livestock, while other wildlife were classed and managed as free-roaming wild animals." They subsequently provide a detailed review of the legal status of, and conservation initiatives underway for, bison in Mexico, the U.S., and Canada. The legal recognition of bison as wildlife or livestock, or both, varies across various federal, state, and provincial jurisdictions in North America. For example, only ten U.S. states, four Canadian provinces and two territories, and one Mexican state classify bison as wildlife; all other states and provinces within the bison's historic range designate them as domestic livestock. Overlaying this legal map for bison are several stakeholder groups that manage bison: public wildlife and land management agencies, Native American groups, non-profit conservation organisations, and private producers. Reportable diseases present another set of legal issues that affect international and interstate transport of bison. Aune *et al.* suggest that a paradigm shift is required whereby the public recognises bison as wildlife, and that there is much greater social tolerance, especially in the agricultural community, if major progress is to be made in re-establishing free-ranging bison on their native range. Moreover, large-scale restoration over big landscapes will typically require partnerships and co-management among multiple landowners and resource managers, and more enlightened and coordinated government regulations and policies.

In Chapter 9, J.E. Gross and co-authors provide guidelines for population, genetic, and disease management for both existing conservation herds and for the full recovery of bison over both the short and long term. As the authors explain, conservation focuses on retaining existing ecological, cultural, and genetic characteristics of bison, whereas full recovery entails a broader vision of bison inhabiting landscapes that permit the full expression of natural behaviours and ecosystem interactions that once existed. The guidelines first address bison behaviour, particularly the importance of ensuring natural mating systems that involve avoiding a skewed sex ratio and allowing

competition among bulls, as well as other factors, such as natural movements and mortality rates. Given the small size of many existing herds and newly established herds, guidelines for population and genetic management are particularly important. Herds of 1,000 or more animals are important for conserving genetic diversity, and factors such as non-random mating, skewed sex ratios, and large swings in population size need to be avoided in relatively small herds. Managing bison for restoring and maintaining biodiversity involves allowing animals to naturally move and forage across the landscape, and to interact with other natural processes such as fire, drought, and snow cover. Guidelines are provided for active management, including handling and herding and the type of infrastructure required, with the caveat that active management and handling should be minimised. Disease guidelines address prevention, surveillance and, when pathogens are detected, management. Gross *et al.* stress the importance of well-designed reintroduction programs for establishing new herds and offer suggestions ranging from stakeholder involvement to sourcing animals and ensuring proper herd structure. Given concerns about the genetic uniqueness of some herds and cattle-gene introgression, similar care needs to be given in transferring animals between herds with the goal of maintaining genetic diversity and (or) aiding in the recovery of small or threatened herds. The chapter concludes with recommendations for using modelling and computer simulations to assess bison populations and habitat.

The concluding chapter (10) on guidelines for ecological restoration by C. Gates and co-authors is directed at establishing new, large populations of bison on large landscapes. Because bison were an ecologically dominant species over much of their range, restoring historic ecological processes and biodiversity in areas they once inhabited depends on restoring large, free-roaming herds. Full ecological restoration is defined as "the re-establishment of a population of several thousand individuals of the appropriate subspecies in an area of original range in which bison interact in ecologically significant ways with the fullest possible set of other native species and biophysical elements of the landscape, with minimal necessary management interventions." Although the focus of this chapter is on restoring large herds over large areas, where processes such as migration and natural selection are most likely fulfilled, Gates *et al.* point out that small herds can also contribute to restoring many ecological processes that occur at smaller scales. The chapter provides guidelines for planning and executing large-scale re-introductions, including a feasibility analysis that addresses both biological questions and a thorough assessment of socioeconomic variables and legal requirements, sourcing and then reintroducing suitable stock, and follow-up monitoring, evaluation and adaptation as experience is gained and lessons learned. As noted as well in chapter 8, one of the biggest challenges facing large-scale restoration is that assembling a landscape of hundreds of thousands or millions of hectares will usually require partnerships and co-management of multiple landowners, both public and private, and the support of many stakeholders.

Chapter 1 Introduction: The Context

Lead authors: C. Cormack Gates and Peter J. P. Gogan

1.1 The Species Survival Commission and the American Bison Specialist Group

The International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) is a science-based network of approximately 8,000 volunteer experts from almost every country of the world, working together towards *"A world that values and conserves present levels of biodiversity."* Within the SSC, over 100 specialist groups and more than 15 independent Red List Authorities are set up to track species' status, monitor biodiversity, analyse issues, develop solutions, and implement actions (SSC Strategic Plan 2001-2010). Among them, the Bison Specialist Group is distinguished by two organisational units, one for the European bison (*Bison bonasus*), and the other, for the American bison (*Bison bison*).

The primary goals of the American Bison Specialist Group (ABSG), and the intent of this document, are to contribute to the development of comprehensive and viable strategies and management actions to promote conservation and ecological restoration of bison as wildlife where feasible throughout the original range of the species. Conservation and ecological restoration of bison, as wildlife, at the scale of its original continental range are ambitious and complex endeavours, perhaps more so than for any other North American species. Enhancing the long-term security of bison, as wildlife, will require the commitment and participation of key sectors, including public wildlife and land management agencies, non-government environmental organisations, aboriginal governments and communities, local communities, and conservation-oriented commercial producers. Toward this goal, the ABSG was established to include a broad network of people interested in bison conservation and recovery. There are more than 60 registered members and numerous other collaborators. As with other specialist groups, this network of volunteers represents the functional capacity of the IUCN to monitor the status and management of American bison in relation to global and local biodiversity. Specialist Group participants contributed the scientific and practical knowledge assembled in this report, and can offer expert advice and, in many instances, the means to make things happen on the ground by implementing actions or encouraging and facilitating others to advance the conservation and ecological restoration of bison as wildlife.

The ABSG is a group of volunteers representing a variety of disciplinary backgrounds, expertise, and professional experience. They are geographically distributed across the breadth of the original continental range of the species, from Mexico to Alaska, and from the Tallgrass Prairie in the east to the intermountain west. They work for a variety of institutions including governments, conservation organisations, and academic institutions (see Acknowledgements).

The primary goal of the American Bison Specialist Group (ABSG) is to contribute to the development of comprehensive and viable strategies and management actions to enhance conservation and achieve ecological restoration of bison as wildlife where feasible throughout the original range of the species.

1.2 Context

Prior to European settlement, the American bison had the largest original distribution of any indigenous large herbivore in North America, ranging from the desert grasslands of northern Mexico to the floodplain meadows of interior Alaska (List *et al.* 2006; Stephenson *et al.* 2001) and almost from coast to coast. The ecological scope of the species was limited only by its habitat requirements and specialised diet. An obligate grazer, grasses and sedges present in grasslands and meadows are the mainstay of the American bison's diet and habitat. Bison have been continuously present in North America for at least 300,000 years, persisting in various forms during the late Pleistocene through sequential glacial and interglacial periods, then into the Holocene and present times (MacDonald 1981; Shapiro *et al.* 2004; Wilson *et al.* 2008). They have been associated with successive cultures since humans first occupied the continent about 12,000 years ago.

Over hundreds of thousands of years, bison have contributed to the co-evolution of other biota, including grazing adaptations in plants, mutualistic, commensal and trophic interrelationships, and bison have functioned as a key component of the native biodiversity in vast areas of the continent. Key species, such as bison, have a marked influence on the patterns of occurrence, distribution, and density of other species (Meffe and Carroll 1994; Paine 1969). Where present, bison play important ecological roles by influencing the structure, composition and stability of both plant (Campbell *et al.* 1994; Knapp *et al.* 1999) and animal communities (Bogan 1997; Roe 1970; Truett *et al.* 2001).

No other wildlife species has exercised such a profound influence on the human history of a continent. As the great ice sheets receded, and grasses and sedges colonised the emerging landscape, beginning 14,000 years ago, bison, then human cultures followed. Widespread and abundant (Shaw 1995), bison were a staple resource for more than 12,000 years in the subsistence economies of successive cultures of Native North Americans. During brief recent history, over the last 500 years or so, Europeans colonised the eastern seaboard, explored westward into the Native-occupied prairies and the North, fought for resources, dominated indigenous peoples, and prospered as new settlers and industrial societies. Trading posts recruited indigenous people to harvest bison for meat and pemmican for the forts and to fuel the trade in furs (Gates *et al.* 1992). Armies clashed under the prairie skies (Greene 1996) and railways were built to connect the West to eastern markets. Millions of plains bison were killed for their meat, hides for machine belts and robes, for sport, and to subjugate the First Nations, making way for settler society and domestic European livestock (Hornaday 1889; Isenberg 2000). In less than a century, from Chihuahua State in Mexico to the State of Alaska, the most abundant indigenous large herbivore in North America was driven close to extinction. Had it not been for the interest of private citizens in rearing a few survivors in captivity (Coder 1975), and the remoteness of a lone wild population in what is now Yellowstone National Park (YNP) (Meagher 1973), plains bison would have disappeared from the continent. Similarly, by the end of the "Great Contraction" of plains bison late in the 19th Century (Flores 1996), wood bison were also reduced to a single surviving population of fewer than 300 animals in a remote area in the forested borderlands of Alberta (AB) and the Northwest Territories (NWT) (Gates *et al.* 1992; 2001).

During the 20th and into the 21st Century, federal and state/provincial agencies and conservation organisations played an important role in the conservation and recovery of bison as wildlife. Sixty-two plains bison and 11 wood bison herds have been established for conservation, representing about 7% of the continental population. In parallel, since about 1980, the number of bison raised under captive commercial propagation has increased markedly, and now represent about 93% of the continental population (Chapter 7).

1.3 Current Challenges for Conservation and Ecological Restoration of Bison as Wildlife

Conservation of any wildlife species requires ensuring both long-term persistence of a sufficient number of populations and maintaining the potential for ecological adaptation resulting from natural selection operating on individuals in viable populations in the wild (IUCN 2003; Secretariat of the Convention on Biological Diversity 1992; Soulé 1987). In wild mammal populations, limiting factors, such as predation, seasonal resource limitation, and mate competition, contribute to maintaining the wild character, genetic diversity, and heritable traits that enable a species to adapt to, and persist, in a natural setting (Knowles *et al.* 1998). The long-term conservation of American bison as wildlife is faced with several important challenges that need to be acknowledged and addressed by public agencies, non-profit organisations and producer organisations. They include the rarity of large wild populations in extensive native landscapes, conserving the wild character and genome of bison, and the presence of regulated diseases.

1.4 Large Wild Populations

Bison can best achieve their full potential as an evolving, ecologically interactive species in large populations occupying extensive native landscapes where human influence is minimal and a full suite of natural limiting factors is present. While such conditions remain available in the north of the continent, it is challenging to find extensive landscapes for restoring and sustaining large free-roaming wild bison populations in southern, agriculture-dominated regions. Ecological restoration is the intentional process of assisting recovery of an ecosystem that has been modified, degraded, damaged or destroyed relative to a reference state or trajectory through time (SERI and IUCN Commission on Ecosystem Management 2004). As described by the IUCN Commission on Ecosystem Management, ecological restoration has, as its goal, an ecosystem that is resilient and self-sustaining with respect to structure, species

Plate 1.1 *Free ranging bison in Yellowstone National Park. Photo: John Gross.*

composition and function, as well as being integrated into the larger landscape, and supporting sustainable human livelihoods. Ecological restoration involving bison as an integral component of ecosystems faces two major challenges: 1) how to undertake restoration across large areas with diverse land-use and ownership patterns; and 2) how to undertake restoration in a way that improves both biodiversity and human wellbeing. Large-scale ecological restoration involves biological and social complexity. Attitudes, economics and politics, from local to regional and international scales, will shape the future of bison conservation on occupied lands. These challenges are addressed in Chapter 10.

1.5 Conserving the Wild Character and Genome of Bison

Bison in captive herds may be managed to achieve various objectives, including the ecological services that bison provide (e.g., grazing, nutrient cycling, and terrain disturbance), education and display, commercial production, and conservation of bison as wildlife. Conserving bison as wildlife is not necessarily served by managing a population for other purposes. For example, the ecological effects of herbivory may be achieved by grazing a variety of livestock species. Although some rangelands formerly used for cattle production have been converted to bison production, the substitution of bison for cattle production does not, by itself, necessarily contribute to bison conservation, or to ecological restoration of bison as wildlife. Similarly, display herds may serve conservation education objectives without otherwise contributing to species conservation.

In the absence of intentional policies and actions to conserve the wild character and genome of bison, captivity and commercialisation can lead inadvertently or intentionally to a variety of effects that may be deleterious to bison as a wildlife species in the intermediate to long term (Chapter 4). These include effects on the genome: founder effect; reduced genetic diversity; persistence and phenotypic penetration of deleterious genes; or inadvertent selection for heritable morphology, tameness or adaptation to captivity. Small populations are particularly susceptible to such effects. The sex and age structure of captive conservation populations may be manipulated to reduce the risk of escape, remove aggressive animals, or to alter fecundity or the rate of population increase. The age composition of males in captive herds is typically substantially different from wild populations.

The common practice in captive commercial herds of eliminating males, before they become morphologically and behaviourally mature, poses a challenging question about the roles of mate competition and natural selection for fitness in such populations. In general, selection pressures on captive wildlife are substantially different from those in the wild. O'Regan and Kitchener (2005) posited that domestication may occur inadvertently in captive wild mammals through passive selection for individuals behaviourally suited to captivity, with concomitant morphological changes over several generations. Most changes are thought to result from increasing paedomorphosis, whereby juvenile characteristics are retained in the adult form of an organism (O'Regan and Kitchner 2005). Clutton-Brock (1999) described changes in large mammals under captive conditions including reduced body and brain size, altered external appearance, the gaining of a fat layer beneath the skin and a reduction of the facial region. Inadvertent selection for tameness and adaptation to a captive environment is typical in mammals (Frankham *et al.* 1986), and in addition to altering "wildness", can reduce the chances for successful reintroduction of captives into the wild. A loss of response to predators and alteration of defensive and sexual behaviours have also been reported in captive wildlife (Price 1999; 2002). Many commercial bison producers directly select for marketable traits such as early maturity, coat colour, body size and conformation. The latter "show ring traits" are promoted in bison industry advertisements, publications and at auctions.

The large size of the commercial captive population is the basis for a popular misconception that the species is "secure", leading wildlife management agencies to ignore actions necessary for conservation of wild type bison. Today, among North American jurisdictions, there is a confusing array of classifications of bison as wildlife, domestic livestock, or both (Chapter 8).

Hybridisation with cattle is another serious challenge for bison conservation. In the U.S., Canada, and Europe, agricultural interests attempted to develop an improved range animal by hybridising bison and cattle. Forced-mating of bison and cattle can be readily achieved in a controlled environment. However, they preferentially mate with their own species under open range conditions (Boyd 1908; Goodnight 1914; Jones 1907). In Europe, the European bison (*Bison bonasus*), a relative of the American bison, and the aurochs (*Bos taurus primigeneus*), progenitor of modern cattle, were sympatric, yet evolutionarily divergent, units. Typical of sympatric species occupying similar trophic niches, behavioural and ecological specialisation provides niche separation, leading to reproductive isolation and progressively to speciation (Bush 1975; Rice and Hostert 1993). Species divergence and reproductive incompatibility are evident from the low fertility of first generation (F1) bison x cattle offspring (Boyd 1908; Steklenev and Yasinetskaya 1982) and the difficulty producing viable male offspring (Boyd 1914; Goodnight 1914; Steklenev and Yasinetskaya 1982; Steklenev *et al.* 1986). Unfortunately, forced hybridisations between *B. bison* and *Bos taurus* in North America have left a legacy of cattle mitochondrial (Polziehn *et al.* 1995; Ward *et al.* 1999) and nuclear DNA (Halbert 2003; Halbert *et al.* 2005). This introgression is

widespread among contemporary bison populations, in both public and private sector herds (Chapter 4). The implications for bison conservation are just beginning to be understood and appropriate interventions considered.

1.6 Reportable Diseases

Bison host numerous parasites and pathogens (Reynolds *et al.* 2003; Tessaro 1989), some of which are important to conservation. Livestock diseases that restrict trade or pose a risk to human health and are 'reportable' under federal, provincial, and state legislation are particularly important because they may induce management actions that negatively affect bison conservation and restoration (Chapter 5). Management interventions may include depopulation, limiting dispersal and range expansion to protect adjacent bison or livestock populations, and restraining translocations. The presence or perceived risk of reportable diseases in bison devalues them as wildlife and constrains conservation and recovery potential. Large free-ranging bison populations are infected with exotic (non-native) reportable diseases in two areas of the continent, the Greater Yellowstone Area (GYA) mainly in Montana and Wyoming (bovine brucellosis), and the Greater Wood Buffalo Ecosystem in Alberta and the Northwest Territories (bovine brucellosis and tuberculosis). Balancing conservation with intensive interventions is a perpetual challenge for the agencies responsible for managing these populations.

1.7 Purpose of this Document

This document provides an authoritative summary of the biology and status of American bison, including: prehistoric to recent history and cultural context (Chapter 2); taxonomy and related issues (Chapter 3); genetic variation and effects of human interventions on the genome (Chapter 4); diseases that directly or indirectly affect bison conservation (Chapter 5); biology and ecology of the species (Chapter 6); the numeric and geographic status of American bison, emphasizing herds managed primarily for conservation (Chapter 7); legislation and policies pertaining to bison in all range states (Chapter 8). Guidelines for bison conservation are provided in the final two chapters of this document (Chapter 9 Population and Genetics Guidelines; Chapter 10 Ecological Restoration Guidelines). Throughout the document reference is made to challenges requiring actions ranging from urgent to long term.

Non-prescriptive guidance is offered on how conservation and ecological restoration of bison as wildlife may be achieved, while respecting the principles of democratic governance in the three nations forming North America, the sustainability of economic use of ecological resources, cultural heritage values, and ecological values of intact ecosystems.

Chapter 2 History of Bison in North America

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Contributors: Delaney P. Boyd, Gerald A. Oetelaar, and James H. Shaw

2.1 Palaeobiology and Phylogeny

Bison have existed in various forms for more than 2,000,000 years (Danz 1997; McDonald 1981). Early forms originated in Asia and appear in Villafranchian deposits, and in the early fossil record in India, China, and Europe (Guthrie 1990; Shapiro *et al.* 2004). Bison occupied Eurasia about 700,000 years ago then moved across the Bering Land Bridge into Alaska during the middle Pleistocene 300,000–130,000 years ago (Illinoin Glaciation; Marine Oxygen Isotope Stages (MIS) 8 to 6 (Shapiro *et al.* 2004). All Siberian and American bison shared a common maternal ancestor about 160,000 years ago (Shapiro *et al.* 2004). Fossil evidence indicates there was a single species, or at least a similar large-horned form with variable species/sub-species designations, the steppe bison, *Bison priscus*, throughout Beringia (Guthrie 1990).

Plate 2.1 *Skull of* Bison priscus, *Yukon Canada. Photo: Cormack Gates.*

Steppe bison probably reached their maximum distribution and abundance during the last glacial period (Wisconsinan, 100,000–12,000 years B.P.; MIS 2-4 and 5a-d). These are the typical bison fossils found in the Yukon and Alaska during that period. Steppe bison had relatively long hind legs, similar to the European bison (*B. bonasus*), and large horns with tips curved back, and a second hump (Guthrie 1990). Analysis of ancient mitochondrial DNA (mtDNA) (Shapiro *et al.* 2004) suggests that Late Pleistocene bison, found from the Ural Mountains to northern China, were descendants of one or more reverse dispersals from North America. The most recent common ancestor of bison specimens analysed by Shapiro *et al.* (2004) existed towards the end of the Illinoian Glacial Period (MIS6).

Villafranchian: a major division of early Pleistocene time, named for a sequence of terrestrial sediments studied in the region of Villafranca d'Asti, an Italian town near Turin. This was a time when new mammals suddenly appeared.

Holarctic: a term used by zoologists to delineate much of Eurasia and North America, which have been connected by the Bering land bridge when sea levels are low during glacial periods.

Plesitocene: Ice Age. A division of geological time; epoch of the Quaternary period following the Pliocene. During the Pleistocene, large areas of the northern hemisphere were covered with ice and there were successive glacial advances and retreats.

Beringia: a 1,000 mile wide ice-free grassland steppe, in Asia and North America linked together by the "Bering Land Bridge" when sea levels were low. Animals traveled in both directions across this vast steppe, and humans entered the Americas from what is now Siberia.

Glacial periods: There have been at least four major ice ages. The present ice age began 40 million years ago with the growth of an ice sheet in Antarctica. Since then, the world has seen cycles of glaciation with ice sheets advancing and retreating on 40,000- and 100,000-year time scales. The most recent glacial period ended about ten thousand years ago.

Marine isotopic stages (MIS): alternating warm and cool periods in the Earth's ancient climate, deduced from oxygen isotope data reflecting temperature curves derived from data from deep sea core samples.

Ural Mountains: a mountain range that runs roughly north and south through western Russia. They are sometimes considered as the natural boundary between Europe and Asia.

Phenotype: Observable physical or biochemical characteristics of an organism. Phenotype is determined by both genetic makeup and environmental influences.

Clade: A biological group (taxa) that share features inherited from a common ancestor.

Holocene: A geological period, which began approximately 11,550 calendar years B.P. (about 9600 BC) and continues to the present. It has been identified with MIS 1 and can be considered an interglacial in the current ice age.

Phylogenetics: The study of evolutionary relatedness among groups of organisms.

Glacial maximum: The time of maximum extent of the ice sheets during the last glaciation (the Würm or Wisconsin glaciation), approximately 20,000 years ago.

Taphonomic processes: The transition of the remains, parts, or products of organisms in soil, e.g. the creation of fossil assemblages through burial.

Taxonomy: The science of classification of organisms. Nomenclature is the system of naming organisms in relation to their phylogeny.

Bison moved south into the grasslands of central North America when the ice sheets retreated at the beginning of the Sangamon Interglacial (MIS 5e) 130,000-75,000 years B.P. (MacDonald 1981), evolving there into a large form, *B. latifrons*. This giant bison possessed a horn span of more than two metres and was abundant in the central continent during the Sangamon Interglacial. It underwent a gradual reduction in body size and horn span (Guthrie 1980; van Zyll de Jong 1993). During the subsequent Wisconsin Glaciation (110,000-12,000 years B.P.; MIS 2-4 and 5a-d), Beringian and southern populations became separated as the Laurentide continental ice sheet extended into western Canada from 20,000-13,000 years B.P. (Burns 1996; Wilson 1996). Geographic separation had profound biological, taxonomic, and evolutionary effects. Southern bison evolved into distinctive phenotypes (van Zyll de Jong 1993) and separate mtDNA clades. All modern American bison now belong to a single clade that is distinct from Beringean bison, with a most recent common ancestor between 22,000 and15,000 years B.P. (Shapiro *et al.* 2004). This interpretation is consistent with complete separation between northern and southern populations at the time of the last glacial maximum (20,000-18,000 years B.P.).

Data presented by Shapiro *et al.* (2004) and Wilson *et al.* (2008) support the hypothesis that modern bison are descended from populations that occurred south of the ice sheet before the Last Glacial Maximum. Southern bison underwent rapid *in situ* evolution during the early Holocene from *B. antiquus* to an intermediate form *B. occidentalis*, then to the modern form *B. bison* (Wilson *et al.* 2008). When the continental ice sheets began to melt, bison invaded the emerging ice-free corridor from the south where thawing and melting occurred first. Colonisation from Beringia was limited (Shapiro *et al.* 2004). Overlap between northern and southern bison occurred in the vicinity of the Peace River in north-eastern British Columbia where northern bison were present by 11,200-10,200 years B.P. (Shapiro *et al.* 2004), and southern forms of bison were present 10,500 years B.P. Molecular research by Shapiro *et al.* (2004) indicates that all modern bison are descended from populations living south of the ice sheet before the Last Glacial Maximum. The two modern North American subspecies (plains bison and wood bison) diverged by about 5,000 years ago (Gates *et al.* 2001; van Zyll de Jong 1986). The wood bison (*B.b. athabascae*) was the most recent variant to occur in Alaska, the Yukon and Northwest Territories and the plains bison (*B.b. bison*) is the most recent southern variant of the North American species (van Zyll de Jong 1993 Stephenson *et al.* 2001). Small-horned bison similar to wood bison also occurred in northern Eurasia during the Holocene (Flerov 1979; Lazarev *et al.* 1998; van Zyll de Jong 1986, 1993). Although the European bison (*B. bonasus*) is morphologically similar to and readily interbreeds with the American bison, they form distinctly different clades based on mtDNA sequences of the 273 bp-long fragment of cytochrome b gene (Prusak *et al.* 2004). This is consistent with geographic separation between these two species starting during the mid-Pleistocene and before reverse-dispersal occurred from North America to Siberia.

2.2 Original Range

Previous typologies divide the Holocene range of bison into “prehistoric” and “historic” periods (van Zyll de Jong 1986). The distinction between them is not based on objective or biologically meaningful criteria, and provides an artificial and confusing temporal dichotomy that persists despite well-informed arguments to the contrary (Stephenson *et al.* 2001). A preferred and more accurate alternative is to refer to the previous range of bison as “original” range, thereby avoiding the necessity to distinguish between written records and other sources including zooarchaeological evidence and orally transmitted knowledge (Gates *et al.* 2001).

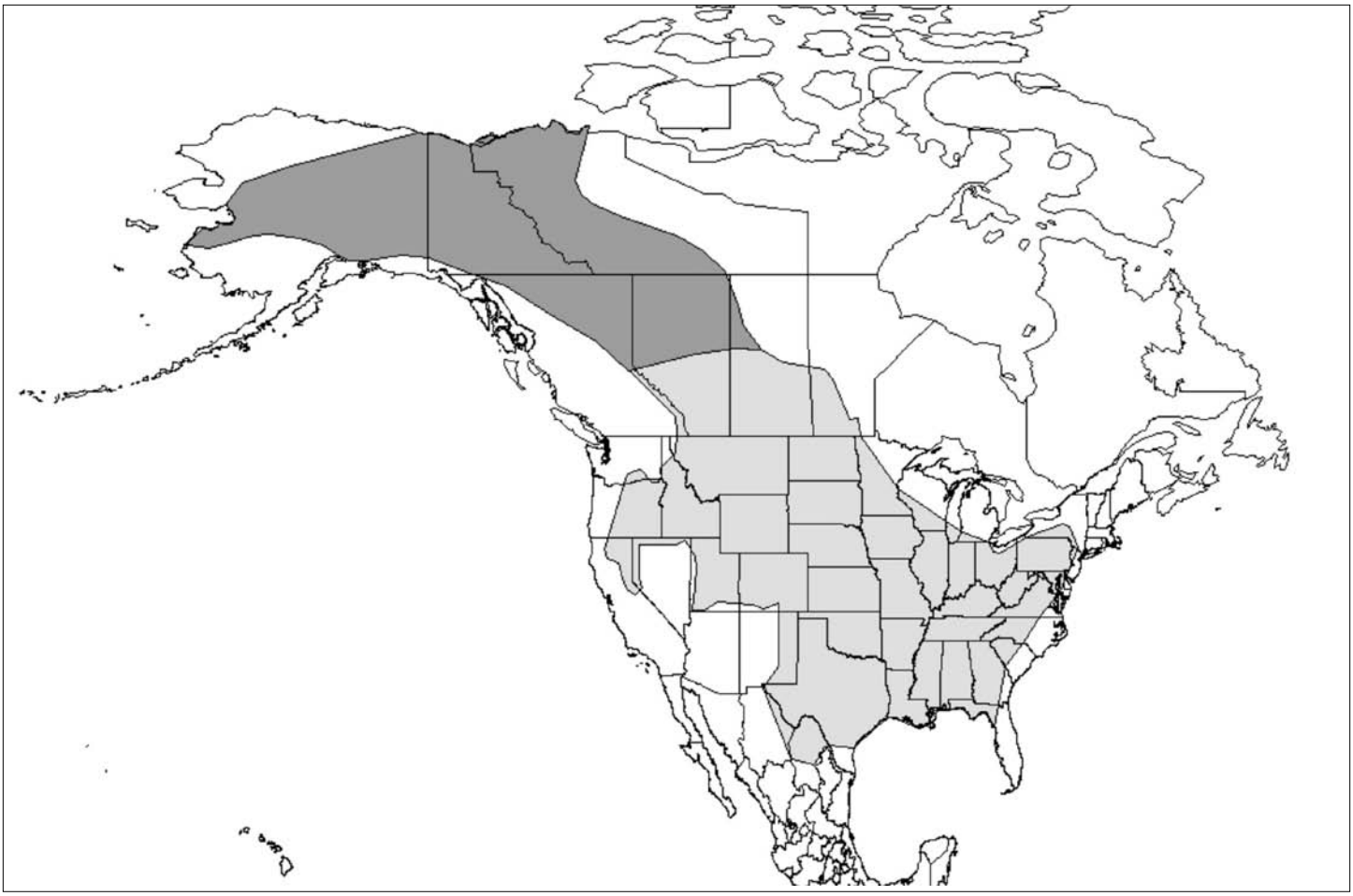

Figure 2.1 *Original ranges of plains bison and wood bison. Recreated by Boyd (2003) based on van Zyll de Jong (1986) and Stephenson et al. (2001).*

Modern bison originally ranged across most of North America (Figure 2.1). Plains bison were most abundant on the Great Plains, but also radiated eastward into the Great Lakes region, over the Allegheny Mountains toward the eastern seaboard, northward as far as northern New England, and then south into Florida; westward, they were found in Nevada and parts of the Great Basin, the Cascade and Rocky Mountains northward to mid-Alberta and Saskatchewan prairie lands, and further south along the Gulf of Mexico into Mexico (Danz 1997; Reynolds *et al.* 1982). There are records of bison occurring at surprisingly high elevations in mountainous regions, particularly along the Front Range of the Rocky Mountains (Fryxell 1928; Kay and White 2001; Meagher 1986). Evidence also indicates that bison inhabited areas of the Greater Southwest, including Arizona, New Mexico, and northern Mexico, areas not generally recognised as within the original range of plains bison (Truett 1996). Whether apparent or real, bison scarcity in the American Southwest is usually attributed to a combination of insufficient water and grass and human hunting (Truett 1996). The original range of wood bison includes northern Alberta, north-eastern British Columbia, a small area of north-western Saskatchewan, the western Northwest Territories, Yukon, and much of Alaska (Stephenson *et al.* 2001). More recent research incorporating oral narratives of aboriginal people in Alaska, Yukon, and Northwest Territories, in combination with archaeological and palaeontological records, demonstrates that wood bison were present in the Yukon and Alaska within the last two centuries, and that these areas are within the original range of the subspecies (Lotenberg 1996; Stephenson *et al.* 2001).

2.3 Abundance

Historical and archaeological records demonstrate that plains bison thrived on the grasslands of the Great Plains (Malainey and Sherriff 1996; Shaw and Lee 1997). Explorers, settlers, and Euroamerican hunters described enormous herds of plains bison, with population estimates ranging from 15 to 100 million (Dary 1989; Shaw 1995). In the 1890s, naturalist Ernest Thompson Seton posited the widely accepted estimate for American bison at 60 million (Dary 1989; McHugh 1972; Roe 1970; Shaw 1995).

Several quantitative and qualitative methods have been used to estimate pre-settlement bison abundance, including direct observation, carrying capacity calculations, and counts of bison killed for market in the late 1800s. Even when used in combination, all methods are fraught with uncertainty, untested,

even unwarranted assumptions, and arbitrary population attributions (Shaw 1995). Regardless, there is little doubt that prior to Euroamerican settlement, plains bison numbered in the millions, and probably even in the tens of millions (Shaw 1995).

Wood bison were not as numerous as plains bison owing to limited habitat, although they did inhabit a vast region of the boreal forest in north-western North America (Gates *et al.* 2001c). Soper (1941) estimated the total wood bison population in 1800 to be 168,000, an estimate that was highly speculative. The Soper estimate is based on the number and distribution of wood bison existing in Wood Buffalo National Park (WBNP) during the 1930s, with some fuzzy extrapolation from the WBNP density to the presumed area of the original wood bison range. The estimate did not account for regional variability in habitat availability. Furthermore, Stephenson *et al.* (2001) documented a considerably larger original range than Soper (1941). Therefore, wood bison may have been more numerous than estimated by Soper.

2.4 Extirpation

Continental bison numbers declined dramatically and rapidly following European settlement. Specific regional impacts on numbers, distribution, and abundance are recorded in many historical accounts and references (e.g., Dary 1974). Large-scale seasonal migrations of both the northern and southern plains bison herds may have temporarily masked their decline, although by the late 1800s it was obvious that the American bison population had been decimated and was in serious decline (Krech 1999). Commercial hunting by Euroamericans and some Native North Americans for meat and hides was a primary cause (Hornaday 1889; Isenberg 2000). The American military quietly approved illicit market hunting on federally protected tribal lands in the northern and southern plains. Other factors included indiscriminate slaughter for sport and recreation. Sport hunting was exacerbated by the westward push of colonization from the east and across the prairies with the implicit and explicit approval of politicians and military leaders anxious to resolve the food supply side of the so-called "Indian problem." (Danz 1997; Dary 1989; Hewitt 1919; Isenberg 2000; McHugh 1972).

Environmental factors, such as regional drought, introduced bovine diseases, and competition from domestic livestock (horses, cattle, sheep) and wild horses also played a role in reducing bison numbers (Flores 1991; Isenberg 2000). Furthermore, because bison provided sustenance for North American aboriginals and commodities for their barter economy, the elimination of bison was viewed by Euroamericans as the most expedient method to subjugate the Native Americans and force them onto reserves, making way for agrarian settlement and continued western development (Danz 1997; Geist 1996; Isenberg 2000; Mayer and Roth 1958). To this end, the U.S. government unofficially supported the slaughter of bison by providing ammunition and supplies to commercial buffalo hunters (Mayer and Roth 1958). Although an overt political policy to decimate bison was never formally established, the Canadian and U.S. governments capitalised on widespread hunger among aboriginal communities caused by the near extirpation of bison as a means to subjugate and control the aboriginal population (Geist 1996; Stonechild and Waiser 1997). By the late 19th Century it was estimated that there were fewer than 1,000 remaining bison in North America (Hornaday 1889; Seton 1927). Wood bison were concentrated in northern Alberta and the Northwest Territories, and plains bison were scattered in isolated groups across the Central Great Plains and, notably, in what is now Yellowstone National Park (YNP).

2.5 Early Recovery

As the great herds diminished, there was some public outcry, but few laws were enacted to protect the bison (Danz 1997). Most early plains bison conservation efforts happened through the independent actions of private citizens. Prominent figures in the conservation movement included James McKay and

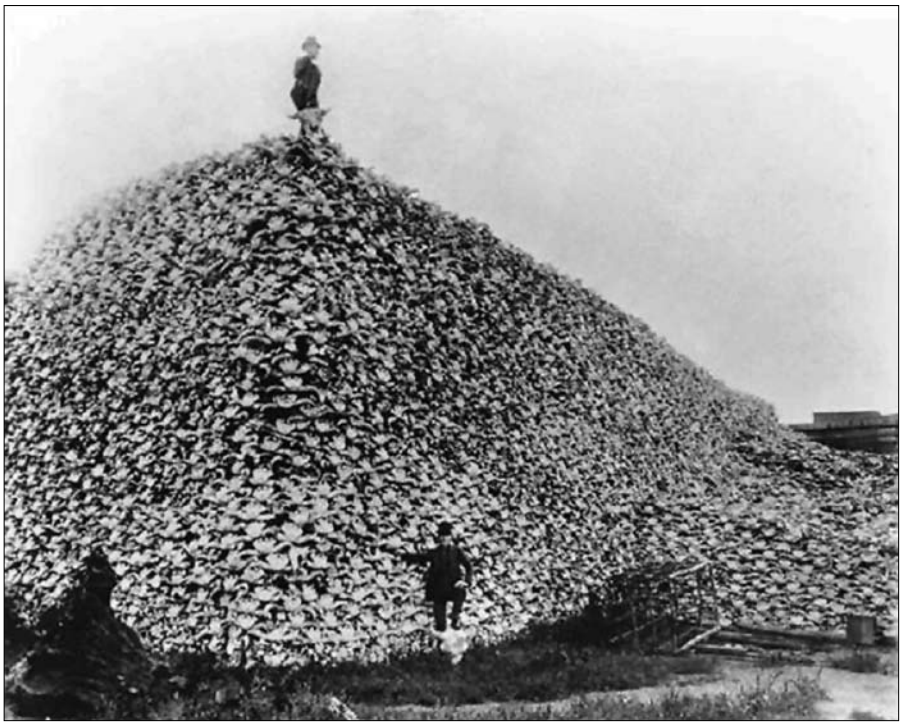

Plate 2.2 *An enormous pile of bison skulls waiting to be ground for fertilizer (c. mid-1870s). Copyright expired - Courtesy of the Burton Historical Collection, Detroit Public Library - downloaded from English Wikipedia 20 Aug 2009.*

Charles Alloway (Manitoba), Charles Goodnight (Texas), Walking Coyote (Montana), Frederick Dupree (South Dakota), Charles J. Jones (Kansas), and Michel Pablo and Charles Allard (Montana) (Coder 1975; Danz 1997; Dary 1989; Geist 1996). Their efforts to establish herds from the few remaining bison secured the foundation stock for most contemporary public and private plains bison herds. Formed in 1905, the American Bison Society (ABS) pressed Congress to establish several public bison herds at Wichita Mountains National Wildlife Refuge, the National Bison Range (NBR), Sully's Hill National Game Preserve (SHNGP), and Fort Niobrara National Wildlife Refuge (Coder 1975; Danz 1997). National parks in both the U.S. and Canada also figured prominently in bison recovery efforts (Danz 1997; Ogilvie 1979).

Once plains bison were protected from hunting (beginning in the 1870s), their numbers increased considerably, doubling between 1888 and 1902. By 1909, the subspecies was considered safe from extinction (Coder 1975). Initially sparked by nostalgia and reverence for the animal, motivations for bison recovery became increasingly driven by their commercial value (Yorks and Capels 1998). By 1970, there were 30,000 plains bison in North America, with approximately half in public herds located in national parks, wildlife refuges, and state wildlife areas, and half in private herds (Shaw and Meagher 2000). As reviewed in chapter 7, the number of plains bison currently is more than 20,500 in 62 conservation herds, while the number under commercial propagation is about 400,000.

The wood bison population fell to a low of 250 animals at the close of the 19th Century, then slowly grew to 1,500-2,000 by 1922 owing to the enforcement of Canadian laws enacted to protect the animal (Gates *et al.* 2001c; Soper 1941). In 2008, there were about 10,870 wood bison in 11 conservation herds (Chapter 7).

2.6 Cultural Significance

Few species enjoy a history as rich in archaeology, palaeontology, story and legend, oral and documentary history as the American bison. Nor is there another North American species for which the cultural and political significance of an animal is so great. For thousands of years various forms and populations of bison have coexisted with humans in North America, providing sustenance and shaping human social and economic patterns, and influencing national history and international political relationships. Although a comprehensive review of human-bison interactions from the colonisation of North America to recent times is encyclopaedic in scope, a brief summary and discussion is provided here.

Bison were important in the subsistence economies of the first Beringian colonisers of the western hemisphere, and later figured prominently, but differentially, in Palaeo-Indian, Archaic, and subsequent North American cultural horizons and traditions. Bison were economically and culturally important throughout most of North America, including interior Alaska, Yukon and Northwest Territories, but they were particularly significant for groups living in the Great Plains, from north-central Texas to southern Alberta. Various forms of bison have been identified as key subsistence resources in the Palaeolithic of north-eastern Asia, forming part of a megafaunal complex adapted to the steppe-tundra of Late Pleistocene northern Eurasia and Beringia, along with mammoths and horses (Guthrie 1990). While bison remains are commonly found in Siberian archaeological sites, standard zooarchaeological methods (Ermolova 1978) indicate they do not appear to have contributed greatly to subsistence. By comparison, reindeer, mammoths, and horses are relatively abundant in Siberian archaeological sites. Bison seem to have played a more important role in North American archaeological complexes. In Alaska, there is empirical evidence from numerous archaeological complexes spanning 12,000 to 1,000 years B.P. that links bison with cultural traditions using conservative,

Palaeo-Indian: (12,000-6,000 B.P.) A group of Late Pleistocene–Early Holocene cultures associated with the colonisation of central North America. While their subsistence economies are debated, many archaeologists consider them to be big game hunting specialists (including mammoth).

Folsom: (11,000-10,200 B.P.) A Palaeoindian culture, characterised by very high mobility and specialised bison hunting.

Archaic: (6,000-2,300 B.P.) A group of Middle Holocene cultures characterised by broad spectrum foraging (i.e., subsisting on a wide variety of big and small game, fish, shellfish, and plant foods). They do not have permanent villages or agriculture.

Plains Woodland: (2,300-1,000 B.P.) A group of Late Holocene cultures characterised by semi-permanent villages, horticulture (maize and beans) in addition to hunting and gathering.

Altithermal: also the Holocene Climate Optimum. A warm period during the interval 9,000 to 5,000 years B.P. This event is also known by other names, including: Hypsithermal, Climatic Optimum, Holocene Optimum, Holocene Thermal Maximum, and Holocene Megathermal.

Plate 2.3 *Arvo Looking Horse performing a ceremony honouring slaughtered bison after a harvest near Yellowstone National Park. Photo: Jim Peaco, National Park Service.*

efficient microblade technology (Holmes and Bacon 1982; Potter 2005; 2008). Microblades are small elongate sharp stone blades inserted into pieces of bone or wood to make composite tools (Guthrie 1983).

Bison played a key role in Palaeo-Indian, Archaic, and later economies in North America, particularly in the Great Plains. While some have questioned early Palaeo-Indian dependence on bison and other large-bodied ungulates (Grayson and Meltzer 2002), other studies show a clear pattern of specialised large mammal hunting during the Late Pleistocene and Early Holocene in North America (Hofman and Todd 2001; Waguespack and Surovell 2003). Although there are disagreements as to whether Early Palaeo-Indians should be classified as specialised big-game hunters or broad-spectrum foragers, bison evidently played an important role in their subsistence economies. A recent survey by Waguespack and Surovell (2003) reported that 52% of 35 Early Palaeo-Indian components (Clovis, 11,300-10,900 years B.P.) included bison remains. With the extinction of the mammoth and other Pleistocene megafauna, bison became a greater economic focus for late Palaeo-Indian complexes (Folsom and others present during the Early Holocene). Changes in projectile point forms have been linked to specialisations for bison hunting (Stanford 1999). In particular, Folsom complex adaptations have been linked to intensive bison hunting (Amick 1996). Communal bison hunting probably played an important role in seasonal aggregations of Palaeo-Indian populations, with human groups combining to hunt and then dispersing into smaller groups in relation to seasonal bison migrations (Kelly and Todd 1988).

On the Great Plains, the Holocene Climatic Optimum or Altithermal (about 7,500 years B.P. in mid-latitude North America) resulted in warmer and drier conditions and increased seasonality. Climate change apparently limited bison abundance and geographic distribution, and induced human adaptations to new climatic and ecological conditions (Sheehan 2002; but see Lovvorn *et al.* 2001). Human populations adjusted primarily by developing new economic strategies, termed “Archaic” by North American archaeologists. Adaptations involved new technologies such as ground stone for processing a variety of plant foods, and incorporating a more diverse array of smaller game and plants into the subsistence economy. During this period, some portions of the Great Plains appear to have been abandoned entirely by people (Meltzer 1999). However, the dearth of sites could also be explained by taphonomy (deep burial or destruction through erosion) (Artz 1996; Walker 1992). Some evidence indicates that during this period bison and people concentrated their activities in localised refugia, such as river valleys (Buchner 1982). Throughout North America, there was a general shift to mixed foraging economies based on more locally abundant resources, with bison playing a much smaller role except in specific areas of the Great Plains.

After 2,000 years B.P., archaeological records for the North American grasslands show evidence of widespread human occupation and regional specialisation in habitat use (Manning 1995; Speth 1983). The so-called Plains Woodland complexes showed local patterns of adaptation represented as widespread networks of cultural interactions that linked the eastern woodlands, and perhaps even the Greater Southwest, to the grasslands through trade and religious or ceremonial interactions (Frison 1991). Technologies shifted again to include bows and arrows, pottery and distinctive regional ceramic traditions. Much later, the use of horses formed the basis for the mounted,

nomadic "Plains Indian Culture" observed by European explorers and missionaries at first contact (Duke 1991; Wedel 1959). Native North Americans, during, and even after the Plains Woodland tradition, lived in larger more permanent villages. They depended on maize, bean, and gourd horticulture to name some of the most important domesticates, with winter dependence on deer and seasonal movements in the fall and spring to take advantage of migrating bison herds (Wilson 1987). This pattern is well represented ethnographically in the Middle Missouri Region. Groups like the Siouxan-speaking Mandan and Hidatsa, and the Caddoan-speaking Pawnee and Arikara, with the Wichita and others, were scattered along major Prairie rivers and tributaries like the Loup, Lower Loup, Canadian, and Washita, as far south as Nebraska, Kansas, and Oklahoma (Weltfish 1965). Large kill events, such as those represented at the Head-Smashed-In site in Alberta, generally did not occur until very late in the history of bison hunting on the Plains, and are represented from the Late Archaic and later periods (Byerly *et al.* 2005). The shift in hunting strategies may have been a response to increasing herd sizes, introduction of bow and arrow, and/or changes in social organisation (Driver 1990; Reeves 1990; Walde 2006).

With increased resolution and clarity afforded by ethnohistoric and ethnographic investigations, human-bison interactions among historic native peoples are better described and documented than for the late Pleistocene and Holocene. Bison continued to be the preferred game for many native North American cultures, especially on the Great Plains and Prairies, providing food, clothing, shelter, and tools (Geist 1996; Roe 1970). Sustained by bison and plant resources, many native groups likely affected densities of other large herbivore species (Kay *et al.* 2000; Martin and Szuter 1999). In addition to significant ecological relationships, the bison was a central element in oral tradition, rituals, dances, and ceremonies of native peoples of the Plains (Wissler 1927), and it remains symbolically important in the cultural traditions of many native Tribes to this day.

The arrival of Europeans in North America, after 1492, resulted in significant changes in human-bison interactions, and changed the fabric of Native American life forever. Introduced diseases such as smallpox decimated indigenous human populations (Crosby 1986), and altered subsistence, settlement, demography, and social organisation for many different groups. Bison hunting by native people was seasonal in nature. Bison were incorporated into a broad spectrum of plant and animal procurement activities (Holder 1970; Isenberg 2000). Bison provided the economic basis for stable, resilient land use regimes and social systems. However, effects of Native American warfare and raiding during the historic period disrupted and destabilised these land use and social systems. The spread of horses into Great Plains aboriginal economies by the 1750s, and increasing commoditisation of bison products caused by the emergence of a European commercial market for wildlife products by the 1820s, contributed to the near extinction of the bison (Flores 1994; Isenberg 2000:27). Native peoples traded bison hides for Euro-american commodities, with the market in bison robes reaching a peak in the 1840s. Hide hunters began to significantly participate in the market hunting of plains bison in the 1850s, and by the 1890s had decimated the herds. Even bones were cleaned for sale to the eastern fertilizer market, an activity that continued to 1906 (Dary 1974).

Numerous native North American tribes manage bison on native and tribal lands, but cultural, social and spiritual relationships with this animal are changing. For many Native Americans there is still a strong spiritual and symbolic connection, but for others it is the potential commercial value of bison that is most important. For still others, it is the pragmatic use of bison for food, and the relationship between local control over food production and land, food security, tribal sovereignty, and decreasing reliance on outside sources for food and commodities that is emerging as a topic of concern, and a theme underlying tribal decision-making.

It is not just the relationship between Native Americans and bison that is changing, but the role of bison in the overall North American food system is changing as well. The North American perspective is shifting from the view that bison are an artifact from the past to be viewed as such in parks and preserves, to one that sees bison as a dynamic component of the American diet. Along with a new vision for a healthy ecological and genetic future for the American bison, food system researchers, food system enthusiasts, and the biomedical research community envision a new role for bison in the American diet. This role elevates the animal to priority over industrially raised beef and pork, and secures for it a place as the healthy alternative to a fatty, sugar-based diet that already has significant health impacts in terms of increased rates of cardiovascular disease, colorectal and other forms of cancer, and diabetes. Free-range bison meat is higher in omega-3 fatty acids than are grain-fed animals, perhaps even as high as wild salmon and other cold water fish species, and it is also high in conjugated linoleic acid, a fat-blocker and anti-carcinogen with the potential to reduce the risk of cancer, diabetes, and obesity. The extent to which bison can be produced efficiently and in healthy ways that do not further degrade ecosystems and ecosystem services, and marketed as a healthy food at an affordable price, will perhaps be the tipping points for how important bison become in a future American food system.

Whether Native American or not, cultural values, attitudes, and perspectives are reflected in how we think about, manage, and handle animals in the wild, in commercial production systems, and after butchering and processing through marketing. Bison are perhaps unique in that we manage them both as wildlife and

as livestock, with wood bison in Alaska and Canada an example of the former, and plains bison in the Canadian and American Plains an example of the latter. The jury is probably still out on whether we will manage bison as wildlife, as livestock, or as both in the future, but it is clear that there is a bright role for this animal in an emerging North American food system and tradition. Native Americans are both recovering and restoring their long-established cultural relationship with the American bison, and Native Americans and other non-native North Americans are finding new ways to relate to this animal in ways that will enhance the conservation of the species.

Chapter 3 Taxonomy and Nomenclature

Lead Authors: Delaney P. Boyd, Gregory A. Wilson, and C. Cormack Gates

The purpose of naming organisms is to facilitate recognition and communication and to identify patterns and apply practical structure to the natural world. Taxonomy can support the conservation and sustainable use of biological diversity by contributing to identification, assessment, and monitoring programmes (Environment Australia 1998). Taxonomy is also vital for the creation and interpretation of laws, treaties, and conservation programmes because it creates legal identities for organisms (Geist 1991). While it is important to strive for accuracy in taxonomic classification, semantic issues and uncertainty can create substantial management challenges by distracting conservation decision makers from the issues threatening a taxon or biological unit worthy of conservation.

Despite the extensive history, and the economic and symbolic importance of bison to North American societies, there remains significant confusion and disagreement about bison taxonomy. The issues range from an historical discrepancy over the common name, to ongoing scientific debate over the systematics of the genus, species, and subspecies designations.

3.1 An Historical Misnomer: Bison vs. Buffalo

The bison is not a buffalo. True 'buffalo' are native only to Africa (cape buffalo, *Syncerus caffer*) and Asia (four species of water buffalo, *Bubalus spp.*). The use of the term buffalo for American bison derived perhaps from other languages used by explorers to describe the unfamiliar beast, e.g., *bisonte, buffes, buffelo, buffles*, and *buffilo* (Danz 1997; Dary 1989). These terms are similar to *bufle* and *buffe*, which were commonly used to refer to any animal that provided good hide for buff leather (Danz 1997). Despite the misnomer, the term 'buffalo' has been used interchangeably with "bison" since early explorers first discovered the North American species (Reynolds *et al.* 1982). The term has become entrenched as a colloquialism in North American culture and language. Although scientific convention dictates use of 'bison', the term 'buffalo' persists as an accepted, non-scientific convention for habitual and nostalgic reasons.

3.2 Genus: *Bos* vs. *Bison*

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

The debate over the appropriate genus arises from the conflict between the traditional practice of assigning names based on similar features distinguishable by morphology (the phenetic approach) versus using evolutionary relationships (the phylogenetic approach) (Freeman and Herron 2001; Winston 1999). Systematists develop evolutionary trees by analysing shared derived characteristics (Freeman and Herron 2001; Winston 1999). In this scheme, only monophyletic groups, or clades, which represent all descendants of a common ancestor, are named. A phenetic scheme might assign names to partial clades, or paraphyletic groups, which exclude one or more descendants (Freeman and Herron 2001). Some taxonomists and systematists suggest that the traditional naming system be replaced with a phylogenetic scheme (Freeman and Herron 2001). While not all biologists agree this is prudent, given that a strictly phylogenetic scheme could ignore functionally and ecologically important differences among species (Freeman and Herron 2001), the phylogenetic approach provides some useful insights about evolutionary relationships within the family Bovidae.

Bison reside in the family Bovidae, subfamily Bovinae, tribe Bovini, which currently contains four genera: *Bubalus* (Asian water buffalo); *Syncerus* (African buffalo); *Bos* (domestic cattle

and their wild relatives), and *Bison* (bison) (Wall *et al.* 1992; Wilson and Reeder 2005). Studies of nuclear-ribosomal DNA (Wall *et al.* 1992), mitochondrial DNA (Miyamoto *et al.* 1989; Miyamoto *et al.* 1993), and repetitive DNA sequences (Modi *et al.* 1996) within this tribe have revealed that the genus *Bos* is paraphyletic with respect to the genus *Bison*. Mitochondrial DNA studies do not support the traditional organisation of the tribe Bovini because the yak (*Bos grunniens*) is more closely related to bison than to its congener cattle (*Bos taurus*) (Miyamoto *et al.* 1989; Miyamoto *et al.* 1993). Ribosomal DNA studies have not fully clarified this relationship (Wall *et al.* 1992). However, skeletal analysis by Groves (1981) noted that bison and yak have 14 thoracic vertebrae while other members of the Tribe *Bovini* have only 13, underscoring the importance of considering heritable morphological differences that may not be revealed using molecular methods.

A comparison of various phylogenetic trees for the tribe Bovini further illustrates the naming conflict. Figure 3.1(a) depicts a conventional scheme based on morphological characteristics (Bohlken 1958), while Figures 3.1(b-d) show different interpretations based on cranial or genetic evidence. Although non-conventional schemes do not share identical branching patterns for every species, the position of *Bison* within the pattern of development for each alternative is equally incongruous. In the conventional scheme, *Bos* branched off the tree later than *Bison*; however, the arrangements based on more recent evidence suggest that a *Bos* branch was followed by *Bison*, then by *Bos*. Each alternative demonstrates that *Bos* is paraphyletic because it is lacking one of its descendant branches (denoted as *Bison*). Under a phylogenetic scheme, bison would be included in the *Bos* clade to correct this incongruity.

For four decades, there have been suggestions to combine *Bison* and *Bos* into one genus (Baccus *et al.* 1983; Gentry 1978; Groves 1981; Miyamoto *et al.* 1989; Modi *et al.* 1996; Stormont *et al.* 1961; Van Gelder 1977). Studies of DNA, blood types, and chromosomal, immunological, and protein sequences

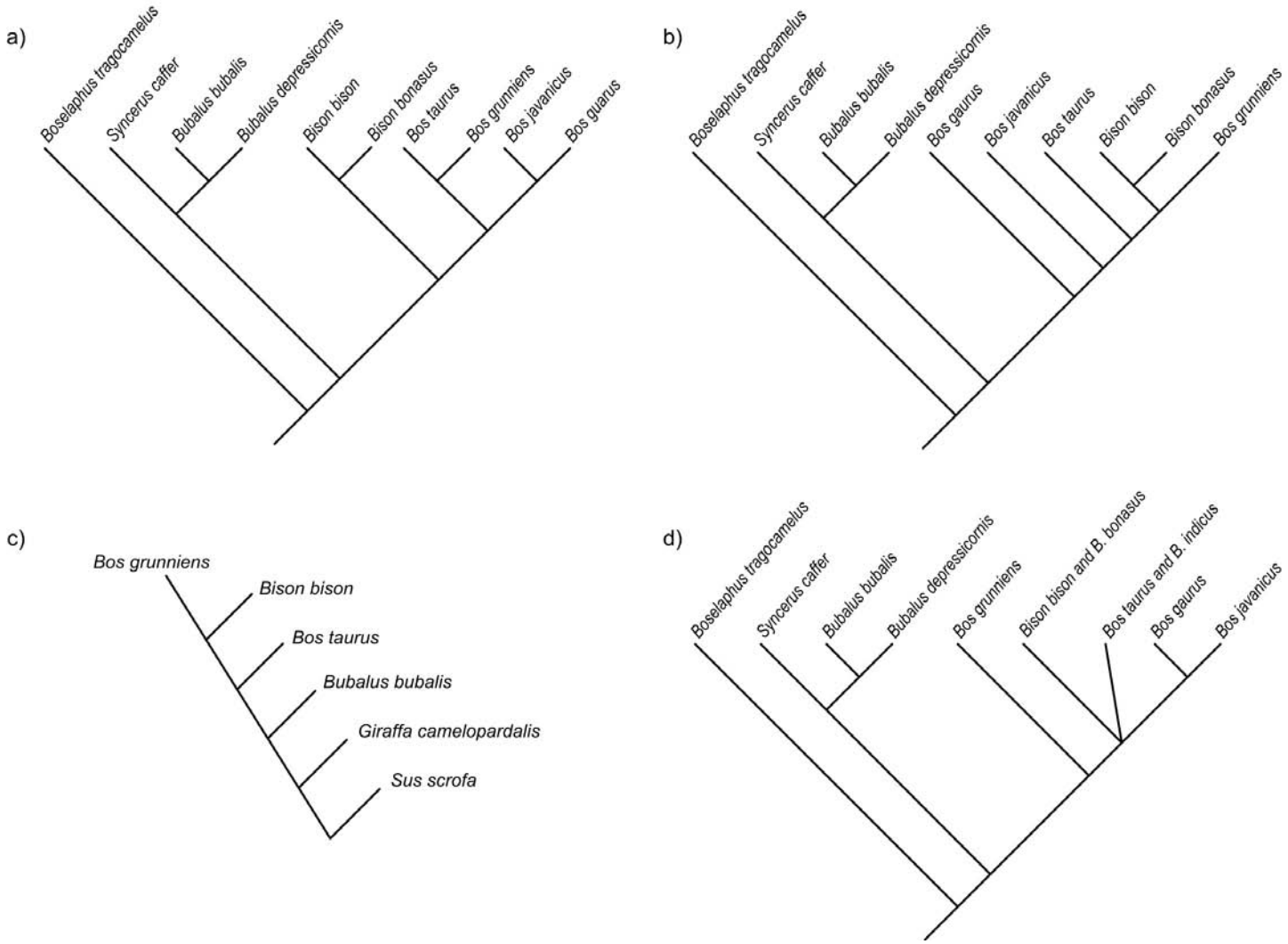

Figure 3.1 *Comparison of phylogenetic hypotheses for the tribe Bovini based on: (a) conventional morphological analysis (Bohlken 1958); (b) cladistic analysis of cranial characteristics (Groves 1981); (c) mtDNA sequences (Miyamoto et al. 1989); and (d) ribosomal DNA analysis (Wall et al. 1992).*

demonstrate that *Bison* and *Bos* were genetically similar, given molecular methods existing at the time (Beintema *et al.* 1986; Bhambhani and Kuspira 1969; Dayhoff 1972; Kleinschmidt and Sgouros 1987; Stormont *et al.* 1961; Wilson *et al.* 1985). Additionally, the percent divergences among mitochondrial DNA (MtDNA) sequences of *Bison bison*, *Bos grunniens*, and *Bos taurus* were comparable to those calculated among other sets of congeneric species assessed until 1989 (Miyamoto *et al.* 1989). Reproductive information also supports the inference of a close phylogenetic relationship between *Bos* and *Bison*; *Bison* and some members of *Bos* can hybridise under forced mating to produce partially fertile female offspring (Miyamoto *et al.* 1989; Van Gelder 1977; Wall *et al.* 1992; Ward 2000). Species divergence and reproductive incompatibility are evident with the low fertility of first generation (F1) bison x cattle offspring (Boyd 1908; Steklenev and Yasinetskaya 1982) and the difficulty producing viable male offspring (Boyd 1908; Goodnight 1914; Steklenev and Yasinetskaya 1982; Steklenev *et al.* 1986). Behavioural incompatibility is also evident. Although mating of bison and cattle can readily be achieved in a controlled environment, they preferentially associate and mate with individuals of their own species under open range conditions (Boyd 1908; 1914; Goodnight 1914; Jones 1907). Differences in digestive physiology and diet selection between cattle and American bison (reviewed by Reynolds *et al.* 2003) and European bison (Gębczyńska and Krasińska 1972) provide further evidence of the antiquity of divergence between cattle and bison. Based on palaeontological evidence, Loftus *et al.* (1994) concluded that the genera *Bos* and *Bison* shared a common ancestor 1,000,000–1,400,000 years ago.

In North America, sympatry between bison and cattle is an artefact of the recent history of colonisation by Europeans and their livestock. However, in prehistoric Europe, the wisent (*Bison bonasus*) and aurochs (*Bos taurus primigeneus*), the progenitor of modern cattle, were sympatric yet evolutionarily divergent units. The divergence in behaviour, morphology, physiology, and ecology observed between bison and cattle is consistent with the theory that ecological specialisation in sympatric species occupying similar trophic niches provides a mechanism for reducing competition in the absence of geographic isolation (Bush 1975; Rice and Hostert 1993).

The assignment of an animal to a genus in traditional naming schemes can be subjective, and changing generic names can create confusion and contravene the goal of taxonomy, which is to stabilise nomenclature (Winston 1999). However, we caution that maintaining a stable nomenclature should not occur at the expense of misrepresenting relationships. A change of *Bison* to *Bos* may reflect inferred evolutionary relationships and genetic similarities between *Bison* and *Bos* species. It could also potentially provide continuity and stability to the scientific reference for bison, which currently has two species names in use (*B. bonasus* and *B. bison*). However, and in contrast, based on divergence on a cytochrome b gene sequence analysis, Prusak *et al.* (2004) concluded that although American and European bison are closely related, they should be treated as separate species of the genus *Bison*, rather than subspecies of a bison species. There is also the potential that changing the genus from *Bison* to *Bos* would complicate management of European (three subspecies) and American bison (two subspecies) at the subspecies level and disrupt an established history of public policy and scientific community identification with the genus *Bison*.

Further research and debate by taxonomists and the bison conservation community is required to reconcile molecular, behavioural and morphological evidence before a change in nomenclature could be supported by the American Bison Specialist Group (ABSG). In consideration of the uncertainties explained above, and in keeping with the naming conventions for mammals used for the 1996 Red List and the 2008 Red List (Wilson and Reeder 1993; Wilson and Reeder 2005), the ABSG adheres to the genus *Bison* with two species, European bison (*B. bonasus*) and American bison (*B. bison*), in this document.

3.3 Subspecies

A controversial aspect of American bison taxonomy is the legitimacy of the subspecies designations for plains bison (*B. Bison bison*) and wood bison (*B. bison athabascae*). The two subspecies were first distinguished in 1897, when Rhoads formally recognised the wood bison subspecies as *B. bison athabascae* based on descriptions of the animal (Rhoads 1897). Although the two variants differ in skeletal and external morphology and pelage characteristics (Table 3.1), some scientists have argued that these differences alone do not adequately substantiate subspecies designation (Geist 1991). The issue is complicated by the human-induced hybridisation between plains bison and wood bison that was encouraged in Wood Buffalo National Park (WBNP) during the 1920s. Furthermore, the concept of what constitutes a subspecies continues to evolve.

The assignment of subspecific status varies with the organism, the taxonomist, and which of the various definitions of subspecies is applied. Mayr and Ashlock (1991:430) define a subspecies as *"an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species."* Avise and Ball (1990:59-60) adapted their definition from the Biological Species Concept, which defines species as groups of organisms that are reproductively isolated from other groups (Mayr and Ashlock 1991): *"Subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups."*

Table 3.1 *Comparison of structural and pelage characteristics for the two bison subspecies.*

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

Crucial to this definition is the argument that evidence for phylogenetic distinction must derive from multiple concordant, independent, genetically-based (heritable) traits (Avise and Ball 1990). Essentially, subspecies should demonstrate several conspicuous morphological differences, geographic allopatric population patterns, and normally possess genetic divergences at several genes (Winston 1999). Hybridisation between subspecies is possible along contact interfaces (Winston 1999).

The fossil record and observations of variability among living bison suggest that the species exhibited considerable geographic variation. This variation led to claims identifying various forms of the species, most notably a northern and a southern plains bison, which differed in pelage and conformation (van Zyll de Jong 1993). Analysis of cranial, horn, and limb measurements for plains bison suggests clinal variation along a north-south axis (McDonald 1981; van Zyll de Jong 1993). It is possible that external characteristics, such as pelage colouration, also varied along this axis (van Zyll de Jong *et al.* 1995). Therefore, the continuous gradation of intermediate bison forms prevents definitive recognition of northern and southern forms of plains bison at the trinomial level.

Unlike the clinal variation reported for plains bison, a phenotypic discontinuity exists between plains bison and wood bison (van Zyll de Jong 1993), reflected in size and in morphological differences independent of size (van Zyll de Jong 1986; Gates *et al.* 2001). Discontinuous variation occurs when a barrier impedes gene flow between populations of a species, causing genetic differences to accumulate on either side of the barrier (van Zyll de Jong 1992). Reproductive isolation caused by differing habitat preferences and seasonal movements, and the natural barrier formed by the boreal forest, contributed to maintaining the phenotypic differences between plains bison and wood bison (van Zyll de Jong 1986; van Zyll de Jong 1993; Gates *et al.* 2001). The Society for Ecological Restoration International (SERI) and IUCN Commission on Ecosystem Management (2004) explicitly recognise the continuous nature of biological processes, such as speciation, in its guidelines for restoration of ecosystems that have been *"… degraded, damaged, or destroyed relative to a reference state or a trajectory through time"* (Chapter 9). Analysis of ancient mtDNA indicates that modern American bison are derived from a most recent common ancestor existing 22,000 to 15,000 years B.P. (Shapiro *et al.* 2004; Chapter 2).

The allopatric distribution and quantified phenotypic differences between the bison subspecies are consistent with the subspecies concept. Nevertheless, there has been a suggestion that the two subspecies are actually ecotypes, that is, forms exhibiting morphological differences that are simply a reflection of local environmental influences rather than heritable traits (Geist 1991). This hypothesis is not supported by observations of transplanted plains and wood bison. Wood bison transplanted

from their original habitat near the Nyarling River in WBNP to very different environments in the Mackenzie Bison Sanctuary (MBS) (in 1963) and Elk Island National Park (EINP) (in 1965) do not differ from each other, or from later specimens taken from the original habitat (van Zyll de Jong 1986; van Zyll de Jong *et al.* 1995). Furthermore, despite the passing of over 40 years, the EINP wood bison, which live under the same conditions as plains bison residing separately within the park, show no evidence of morphological convergence with the plains bison form (van Zyll de Jong 1986; van Zyll de Jong *et al.* 1995). Similarly, plains bison introduced to Delta Junction, Alaska (in 1928) from the National Bison Range (NBR) have clearly maintained the phenotypic traits of plains bison (van Zyll de Jong 1992; van Zyll de Jong *et al.* 1995). Such empirical evidence suggests that the morphological characteristics that distinguish plains and wood bison are genetically controlled (van Zyll de Jong *et al.* 1995).

Hybridisation between the subspecies in WBNP after an introduction of plains bison during the 1920s has complicated the consideration of subspecies designations. The controversial decision to move plains bison from Wainwright Buffalo Park (WBP) in southern Alberta to WBNP (from 1925 to 1928) resulted in the introduction of domestic bovine diseases to wood bison (Chapter 5), and threatened the distinctiveness and genetic purity of the subspecies. In 1957, Canadian Wildlife Service researchers discovered a presumably isolated population of 200 wood bison near Nyarling River and Buffalo Lake. The researchers believed that this herd had remained isolated from the hybrid herds, and therefore, represented the last reservoir of original wood bison (Banfield and Novakowski 1960; Ogilvie 1979; Van Camp 1989). In an effort to salvage the wood bison subspecies, bison from the Nyarling herd were relocated to establish the MBS and EINP wood bison herds in the 1960s. Later analysis has indicated that the Nyarling herd, and bison elsewhere in WBNP and adjacent areas, did have contact with the introduced plains bison (van Zyll de Jong 1986; Aniskowicz 1990), but it was minimal enough that the animals continued to exhibit predominately wood bison traits (van Zyll de Jong *et al.* 1995). Studies on the impact of the plains bison introduction have determined that the hybridisation did not result in a phenotypically homogeneous population, as was feared (van Zyll de Jong *et al.* 1995). Sub-populations within WBNP demonstrate varying degrees of plains bison traits depending on their proximity to, or ease of access from, the original plains bison introduction site (van Zyll de Jong *et al.* 1995).

Although descriptive morphology and quantitative morphometry provide substantial evidence supporting the subspecific designations (van Zyll de Jong *et al.* 1995), early analysis of blood characteristics and chromosomal homology did not detect a difference (Peden and Kraay 1979; Stormont *et al.* 1961; Ying and Peden 1977). Preliminary analysis of growth regulating genes within the two subspecies suggests that the bison subspecies have reached a stage of evolutionary divergence due to geographic isolation (Bork *et al.* 1991); however, under the Biological Species Concept, subspecies may be defined at the next stage of speciation, that is when hybrid offspring exhibit reduced fitness, which does not appear to be the case in WBNP (Bork *et al.* 1991). Furthermore, analysis of mtDNA from Nyarling River wood bison and plains bison did not produce monophyletic groups (Strobeck 1991; 1992). This, however, does not mean that there is no difference. In isolated populations, mtDNA diverges at a rate of 1 to 2% per million years (Wilson *et al.* 1985). It is estimated that the two bison subspecies diverged approximately 5,000 years ago (van Zyll de Jong 1993; Wilson 1969), and human-induced subspecies hybridisation further complicated the phylogeny. Therefore, current genetic analysis techniques may not be able to detect existing differences in the mitochondrial genome. In addition, because mtDNA is maternally inherited, mtDNA within the Nyarling River herd, as well as other herds in WBNP, reflects the contributions from maternal populations, which had a biased representation of plains bison cows (Gates *et al.* 2001). Therefore, the inability to detect a difference with a molecular test comparing limited sequences of genomic material does not necessarily mean there is no genetic difference; it may just be beyond the current resolution of technology.

Recent studies of DNA microsatellites indicate that the genetic distances between plains bison and wood bison are greater than those within either of the two subspecies (Wilson 2001; Wilson and Strobeck 1999). The wood bison populations studied formed a distinctive group on a Nei's minimum unrooted tree; a strong grouping despite the pervasive hybridisation with plains bison (Wilson 2001; Wilson and Strobeck 1999). Wilson and Strobeck (1999) and Wilson (2001) concluded such a strong clustering indicates wood bison and plains bison are functioning as distinct genetic entities, and should continue to be managed separately. Based on the available evidence, Canada's National Wood Bison Recovery Team concluded: (1) historically, multiple morphological and genetic characteristics distinguished wood bison from the plains bison; (2) wood bison and plains bison continue to be morphologically and genetically distinct, despite hybridisation; and (3) wood bison constitute a subspecies of bison, and therefore, should be managed separately from plains bison (Gates *et al.* 2001).

The issue of subspecies designations is relevant to conservation in that a decision to combine forms at the species level would invite hybridisation and effectively eliminate any evolutionary divergence that had occurred. Establishing definitive recognition of bison subspecies is complicated by ongoing change of genus, species and subspecies concepts (Winston 1999). However, other classifications and concepts, such as the evolutionarily significant unit (ESU; Ryder 1986), and genetic and ecological

exchangeability, move beyond traditional trinomial taxonomy to incorporate evolutionary considerations. Conservation biologists are reconsidering definitions of conservation units that incorporate both the history of populations reflected in molecular analysis, and adaptive differences revealed by life history and other ecological information (Crandall *et al.* 2000; DeWeerdt 2002). For example, the geminate evolutionary unit identifies conservation units that are genetically similar but ecologically or behaviourally distinct (Bowen 1998). Crandall *et al.* (2000) argue for a broad categorisation of population distinctiveness based on non-exchangeability of ecological and genetic traits. Each of these concepts presents challenges, as does any concept that attempts to divide the biological continuum for the convenience of human interests. Essentially, differentiation on any level within a species warrants a formal decision and recognition. Of note, The U.S. Endangered Species Act recognises this conservation issue and provides for protection of "distinct population segments". Similarly, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), which is responsible for assessing the status of wildlife, includes any indigenous species, subspecies, variety or geographically defined population of wild fauna or flora as a "species".

While there appear to be sufficient grounds for formal recognition of American bison subspecies, the debate may continue. This, however, should not preclude conservation of the two forms as separate entities (van Zyll de Jong *et al.* 1995; Wilson and Strobeck 1999). Regardless of current genetic, biochemical or other evidence about the subspecies question, there are notable phenotypic differences, and potentially other types of variation that may not be detectable with technologies available at this time. Geneticists predict that genetic analysis in the future will be able to better identify groupings within species (Wilson 2001).

Although genetic and morphological evidence often correspond, this is not always the case (Winston 1999). This can lead to debate over recognising variation that cannot be measured using alternative morphological or molecular methods. Nevertheless, all forms of geographic and ecological variation within a species contribute to biodiversity (Secretariat of the Convention on Biological Diversity 2000). All variants of a species may carry evolutionarily important ecological adaptations (Chapter 4), and possess the potential to develop genetic isolating mechanisms leading in evolutionary time to new species (O'Brien and Mayr 1991). Prediction of which variants will evolve to become species is not possible; this is an outcome of natural selection and chance. Therefore, to maintain biodiversity and evolutionary potential, it is important to not dismiss any form of differentiation within a species, and to maintain the opportunity for evolutionary processes to function (Crandall *et al.* 2000). Debating whether a name is warranted within a relatively arbitrary taxonomic system does not absolve humans of the responsibility to recognise and maintain intraspecific diversity as the raw material of evolution. The risk of losing evolutionary potential suggests it would not be prudent to prematurely dismiss existing groupings such as the plains and wood bison.

Chapter 4 Genetics

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As a science, population genetics is concerned with the origin, nature, amount, distribution and fate of genetic variation present in populations through time and space. Genetic variation constitutes the fundamental basis of evolutionary change and provides the foundation for species to adapt and survive in response to changing intrinsic and extrinsic stressors. Therefore, loss of genetic diversity is generally considered detrimental to long-term species survival. In the short-term, populations with low levels of genetic diversity may suffer from inbreeding depression, which can increase their probability of extirpation and reduce fitness. Plains and wood bison experienced severe and well-documented population declines in the 19th Century that reduced the census size of this species by over 99.99%. The spectacular recovery to around 430,000 animals today (Chapter 7) is a testament to their genetic constitution, and represents one of the most significant accomplishments in modern conservation biology. American bison have, however, undergone artificial hybridisation with domestic cattle, been subjected to domestication and artificial selection, and been separated into many relatively small isolated populations occupying tiny fractions of their original range. As well, all wood bison populations contain some level of plains bison genetic material due to artificial hybridisation between the subspecies. All of these factors have had an effect on the current levels of genetic diversity and on the integrity of the bison genome. As a result, preservation of bison genetic diversity is a key long-term conservation consideration. The following sections discuss some of the major issues that are important for the genetic management of this species into the future.

4.1 Reduction of Genetic Diversity

Within species, genetic diversity provides the mechanism for evolutionary change and adaptation (Allendorf and Leary 1986; Chambers 1998; Meffe and Carroll 1994; Mitton and Grant 1984). Reduction in genetic diversity can result in reduced fitness, diminished growth, increased mortality of individuals, and reduced evolutionary flexibility (Allendorf and Leary 1986; Ballou and Ralls 1982; Franklin 1980; Frankham *et al.* 1999; Mitton and Grant 1984;). There are four interrelated mechanisms that can reduce genetic diversity (heterozygosity and number of alleles): demographic bottlenecks, founder effects, genetic drift, and inbreeding (Meffe and Carroll 1994). Unfortunately, over the last two centuries, bison in North America have, to some degree, experienced all of these mechanisms.

As American bison approached extinction in the late 1800s, they experienced a severe demographic bottleneck, leading to a concern that extant bison populations may have lower genetic diversity than pre-decline populations. The consequences of a genetic bottleneck depend on the pre-bottleneck genetic diversity within a species, the severity of the decline, and how quickly the population rebounds after the bottleneck (Meffe and Carroll 1994; Nei *et al.* 1975). The decline of bison was severe, with a reduction from millions to fewer than 1,000 individuals. Recovery efforts, however, enabled bison populations to grow quickly, more than doubling between 1888 and 1902 (Coder 1975). Although the effects of the bottleneck on the genetic diversity of the species are not clear (Wilson 2001), there are several possible repercussions. First, after a severe reduction in population size, average heterozygosity is expected to decline (Allendorf 1986; Nei *et al.* 1975). Heterozygosity is a measure of genetic variation that is a direct reflection of the past breeding history of a population. Heterozygosity values are expressed as the frequency of heterozygotes (i.e., genes with dissimilar alleles) expected at a given locus (Griffiths *et al.* 1993). A reduction in the level of heterozygosity can result in inbreeding effects. At the same time, a loss of alleles may limit a population's ability to respond to natural selection forces and reduce the adaptive potential of a population (Allendorf 1986; Meffe and Carroll 1994; Nei *et al.* 1975; Robertson 1960).

After the demographic crash, several small bison herds remained in North America, many of which were derived from very few animals. Overall levels of genetic variation in current populations can, in theory, vary directly with the number of original founders (Meffe and Carroll 1994; Wilson and Strobeck 1999). Remnant populations may not have been representative of the original gene pool and, consequently, suffered reduced genetic variability. Through time, the detrimental effects of genetic drift may have compounded the effects of the earlier bottleneck. Genetic drift involves the random change in gene frequencies and leads to the loss of alleles over time. The rate of this loss, or fixation of alleles, is roughly inversely proportional to the population size (Allendorf 1986; Meffe and Carroll 1994). However, the actual count of breeding individuals in a population is not appropriate for determining the rate of genetic drift because factors such as unequal sex ratios, differential reproductive success, overlapping generations, and non-random mating result in the "effective" population size always being less than the census size. For bison, the ratio of effective population size (N_e) to the census population size (N) has most commonly

been estimated to be between 0.16 and 0.42 (Berger and Cunningham 1994; Shull and Tipton, 1987; Wilson and Zittlau, 2004), although Shull and Tipton (1987) suggested that the ratio could be as low as 0.09 in some managed populations.

It is possible that American bison experienced reductions in overall genetic diversity due to the population bottleneck of the late 1800s; however, this effect may not have been as great as once expected. McClenaghan, Jr. *et al.* (1990) found that plains bison have greater genetic variability than several other mammals that experienced severe demographic bottlenecks. Furthermore, Wilson and Strobeck (1999), Halbert (2003) and Halbert and Derr (2008) found levels of DNA microsatellite variability in bison populations to be similar to other North American ungulates. Some authors speculate that prior to the bottleneck, the American bison, with the possible exception of the wood bison, expressed surprising homogeneity despite its extensive range (Roe 1970; Seton 1910). Plains bison ranged over large areas. This suggests that extensive animal movements, and thereby gene flow, may have existed among populations (Berger and Cunningham 1994; Wilson and Strobeck 1999). Similar to other large mammals, bison are expected to be less genetically diverse than small mammals (Sage and Wolff 1986). Despite founder effects and low gene flow, which increase genetic distance values, recent studies demonstrate that the genetic distances between existing bison herds are lower than expected, indicating that existing isolated populations are likely derived from one large gene pool (Wilson and Strobeck 1999). Furthermore, foundation herds for contemporary bison originated from across the species' range, suggesting that much of the pre-existing diversity was likely retained (Halbert 2003). Analysis of ancient DNA may provide an opportunity for assessing pre-bottleneck genetic diversity for comparative purposes (Amos 1999; Cannon 2001; Chambers 1998). Unfortunately, it is not possible to recover the genetic material lost as a result of the bottleneck underscoring the importance of maintaining existing genetic diversity while minimising any future genetic erosion.

Inbreeding, or the mating of related individuals, can lead to the expression of deleterious alleles, decreased heterozygosity, lower fecundity, and developmental defects (Allendorf and Leary 1986; Berger and Cunningham 1994; Lande 1999; Meffe and Carroll 1994). Inbreeding is difficult to assess and does not always have measurable deleterious consequences (Berger and Cunningham 1994; Meffe and Carroll 1994); however, it remains a potential cause of reduced diversity in bison. To decrease the effects of inbreeding, some bison herds were founded or augmented with animals from different regions (Wilson 2001). Over time, the translocation of animals among herds may have reduced the impacts of inbreeding and founder effects, which are most severe in isolated, small populations with low levels of genetic diversity. While few bison herds have truly exhibited signs thought to be the result of inbreeding depression, such as high rates of physical abnormalities, reduced growth rates, and reduced fertility, inbreeding depression has been linked to low levels of calf recruitment and high levels of calf mortality in a plains bison herd (Halbert *et al.* 2004; 2005), and has been suggested to affect male reproductive success in another population (Berger and Cunningham 1994).

Although existing bison populations may be derived from a largely homogeneous gene pool, recent studies using DNA microsatellites reveal that several plains bison herds are genetically distinguishable (Halbert and Derr 2008; Wilson and Strobeck 1999). This raises the issue of whether conservation herds should be managed as a large metapopulation, with translocation of bison among herds to maintain local diversity, or as closed herds to preserve emerging localized differentiation. Some populations may be adapting to non-native habitats or changing conditions in the natural environment, and would, therefore, benefit from localized differentiation. Other populations may be adapting to, or inadvertently selected for, unnatural conditions, and would benefit from periodic augmentation (Wilson *et al.* 2002b). A precautionary approach may be to diversify conservation efforts by transferring randomly selected animals among some herds, to maximise intra-population genetic diversity, while maintaining other herds as closed populations with the possibility of the establishment of satellite populations to increase overall effective population sizes (Halbert and Derr 2008). Managers should carefully consider the implementation of metapopulation management plans as a tool to preserve genetic diversity due to historical differences in morphology, behaviour, physiology, and disease status (Lande 1999; Ryder and Fleischer 1996; Wilson *et al.* 2002b) and to limit the spread of domestic cattle genes between bison populations (Halbert *et al.* 2005a; 2006).

Genetic analysis could be used to monitor genetic diversity by building an inventory of diversity held within conservation herds. There are several measures of genetic diversity including heterozygosity, alleles per locus, and proportion of polymorphic loci (Amos 1999; Templeton 1994; Wilson *et al.* 2002b). While early work on bison genetics involved blood groups (Stormont 1982; Stormont *et al.* 1961), some authors suggest that such studies are inappropriate for assessing genetic diversity because selection for blood group type may be high, violating the assumption of selective neutrality (Berger and Cunningham 1994; Knudsen and Allendorf 1987; Yamazaki and Maruyama 1974). More recent studies have used allozymes (Knudsen and Allendorf 1987; McClenaghan *et al.* 1990), mitochondrial DNA (MtDNA) (Polziehn *et al.* 1996), nuclear DNA restriction fragment length polymorphisms (Bork *et al.* 1991), and DNA microsatellites (Wilson and Strobeck 1999) to assess diversity. Investigation of individual genomic regions can reflect overall diversity, allowing for data from various techniques to be combined to provide an accurate representation of genetic diversity (Chambers 1998).

Selection for diversity in one system, such as blood group proteins, or biased selection for maintaining specific rare genetic characteristics could lead to reduced diversity in other parts of the genome (Chambers 1998; Hedrick *et al.* 1986). Biased selection for maintaining rare alleles is especially questionable if it is not known what the rare allele does, or if it is detrimental (i.e., it may be rare because it is being expunged from the bison genome through natural selection). Variation throughout the genome, rather than the maintenance of one specific rare allele, conveys evolutionary flexibility to a species (Chambers 1998; Vrijenhoek and Leberg 1991). Therefore, it is crucial for a genetic management plan to consider all available measures for managing genetic diversity in the policies and procedures for breeding and culling decisions.

An assessment of overall genetic diversity should examine at least 25-30 loci distributed across the nuclear genome (Chambers 1998; Nei 1987). While genetic diversity for some herds has been assessed (Baccus *et al.* 1983; Berger and Cunningham 1994; Knudsen and Allendorf 1987; Wilson and Strobeck 1999), these studies did not include a sufficient number of loci and comparisons between studies are not possible due to differences in marker systems (allozymes vs. microsatellites). Other studies have included larger numbers of loci and populations; however, several conservation herds have not been fully examined (e.g., some U.S., Canadian and Mexican state, federal and private bison herds; Halbert 2003; Halbert and Derr 2008). Clearly it is important to create a more complete assessment of bison genetic diversity to allow for more informed management decisions.

In general, maintaining genetic diversity of American bison requires an understanding of herd population dynamics to assess the probability of long-term persistence of that diversity. Most bison populations are composed of fewer than 1,000 individuals, and it is possible for a relatively small number of dominant males to be responsible for a high percent of the mating in a given year (Berger and Cunningham 1994; Wilson *et al.* 2002; Wilson *et al.* 2005; Halbert *et al.* 2004). This, in turn, can reduce genetic diversity over time, especially in the absence of natural migration and exchange of genetic diversity among populations (Berger and Cunningham 1994). The potential for disproportionate reproductive contributions emphasises the importance of maintaining large herds with large effective population sizes, that given proper management, will prevent loss of genetic diversity (Frankham 1995; Franklin 1980). Assessment of genetic uncertainty, based on Ne, founder effects, genetic drift, and inbreeding, is a required component of a population viability analysis (PVA) (Gilpin and Soulé 1986; Shaffer 1987).

4.2 Hybridisation

Hybridisation involves the interbreeding of individuals from genetically distinct groups, which can represent different species, subspecies, or geographic variants (Rhymer and Simberloff 1996). Some authors argue that hybridisation is a potentially creative evolutionary force, which generates novel combinations of genes that can help species adapt to habitat change, although such hybrids often experience reduced fitness (Anderson and Stebbins 1954; Lewontin and Birch 1966; Hewitt 1989). Hybridisation through artificial manipulation or relocation of animals, however, can compromise genetic integrity through genetic swamping of one genome over another and disruption of locally adapted gene complexes (Avise 1994). It can also produce offspring that are devalued by the conservation and legal communities (O'Brien and Mayr 1991; Chapter 7). The genetic legacy of introducing plains bison into a wood bison population in northern Canada, and crossbreeding bison and cattle, have made hybridisation a controversial topic in bison conservation.

4.2.1 Plains bison x wood bison

Based on their geographic distribution and morphology, plains bison and wood bison were historically distinct entities (Chapter 3). It can be argued that the introduction of plains bison into range occupied by wood bison was a "negligible tragedy" (Geist 1996), because some consider the two groups to be ecotypes (Geist 1991). Others maintain that the interbreeding of these two types should have been avoided to preserve geographic and environmental variation (van Zyll de Jong *et al.* 1995). The introduction of either subspecies into the original range of the other could, in theory, erode the genetic basis of adaptation to local environmental conditions (Lande 1999). Therefore, hybridisation between plains and wood bison should be considered detrimental to maintaining the genetic integrity and distinctiveness of these two geographic and morphologically distinct forms.

While historically there may have been natural hybridisation events between the subspecies in areas of range overlap, the current hybridisation issue is the consequence of an ill-advised and irreversible decision made nearly 85 years ago. In 1925, the Canadian government implemented a plan to move more than 6,000 plains bison from the overcrowded Wainwright National Park to Wood Buffalo National Park (WBNP). Biological societies from U.S. and Canada strenuously challenged this action, as interbreeding would eliminate the wood bison form, resulting hybrids might not be as fit for the environment, and diseases such as bovine tuberculosis (BTB) would spread to formerly healthy animals (Howell 1925; Harper 1925; Lothian 1981; Saunders 1925). Proponents of the plan countered the criticism by questioning the subspecies designations, arguing

Plate 4.1 *Hereford x bison hybrid; cattle gene introgression is morphologically evident. Photo: Bob Heinonen.*

that the introduction site was isolated from, and unused by, the wood bison population, and suggesting that the introduced animals were too young to carry BTB (Fuller 2002; Graham 1924). These arguments did not consider the future habitat needs of the growing wood or plains bison populations, nor the likelihood that the two subspecies would not remain isolated. As well, a recommendation that only yearlings that passed a tuberculin test be shipped to WBNP was rejected (Fuller 2002).

It was not until 1957 that the discovery of a seemingly isolated herd of 200 animals near the Nyarling River and Buffalo Lake alleviated fears that wood bison was lost to hybridisation (van Camp 1989). Canadian Wildlife Service researchers determined that these animals were morphologically representative of wood bison (Banfield and Novakowski 1960). To salvage the wood bison subspecies, bison from the Nyarling herd were captured and relocated to establish two new herds. Sixteen animals were moved to the MBS north of Great Slave Lake in 1963 (Fuller 2002; Gates *et al.* 2001c), and 22 animals were successfully transferred to Elk Island National Park (EINP) east of Edmonton, Alberta in 1965 (Blyth and Hudson 1987). Two additional calves were transferred to EINP between 1966 and 1968 (Blyth and Hudson 1987; Gates *et al.* 2001c). Of those bison transferred, 11 neonates formed the founding herd.

Subsequent studies revealed that there was contact between the Nyarling herd and the introduced plains bison (van Zyll de Jong 1986). Although hybridisation within WBNP did not result in a phenotypically homogenous population (van Zyll de Jong *et al.* 1995), genetic distances among subpopulations in the park are small, indicating that there is gene flow and influence of the plains bison genome throughout all regions of the park (Wilson 2001; Wilson and Strobeck 1999). Despite hybridization, genetic distances between plains and wood bison are generally greater than those observed within subspecies. Moreover, wood bison form a genetic grouping on a Nei's minimum unrooted tree, suggesting genetic uniqueness (Wilson 2001; Wilson and Strobeck 1999).

Morphological and genetic evidence suggest that care should now be taken to maintain separation between these historically differentiated subspecies. Efforts are in place to ensure representative wood bison and plains bison herds are isolated from each other to prevent future hybridisation between these important conservation herds (Harper *et al.* 2000).

4.2.2 Domestic cattle x bison

The concept of crossing bison with domestic cattle dates back to Spanish colonisers of the 16th Century (Dary 1989). There are many accounts of historical attempts to hybridise bison and cattle (Coder 1975; Dary 1989; Ogilvie 1979; McHugh 1972; Ward 2000). Private ranchers involved with salvaging bison had aspirations to combine, through hybridisation, the hardiness and winter foraging ability of bison with the meat production traits of cattle (Dary 1989; Ogilvie 1979; Ward 2000). The Canadian government actively pursued the experimental production of crossbred animals from 1916-1964 (Ogilvie 1979; Polziehn *et al.* 1995).

Historical crossbreeding attempts have created a legacy of genetic issues related to the introgression of cattle DNA into bison herds. Introgression refers to gene flow between populations caused by hybridisation followed by breeding of the hybrid offspring to at least one of their respective parental populations (Rhymer and Simberloff 1996). The introgressed DNA replaces sections of the original genome, thereby affecting the genetic integrity of a species, and hampering the maintenance of natural genetic diversity. Many contemporary bison herds are founded on, and supplemented with, animals from herds with a history of hybridisation (Halbert 2003; Halbert *et al.* 2005a; 2006; Ward *et al.* 1999; 2000). This extensive history of hybridisation between these two species raises questions about the integrity of the bison genome and the biological effects of cattle DNA introgression.

Fertility problems thwarted many of the original crossbreeding attempts because crosses result in high mortality for offspring and mother (Ward 2000). Experimentation has revealed that crosses of bison females with domestic cattle males produce less mortality in the offspring than the more deadly reverse

cross, however, the latter is more common because it is very difficult to compel domestic cattle bulls to mate with bison females. All F1 generation hybrids experience reduced fertility and viability relative to either parent: F1 males are typically sterile, but the fertility of F1 females makes introgressive hybridisation possible (Ward 2000). Genetic studies have found no evidence of cattle Y-chromosome introgression in bison, which is supported by the sterility of F1 hybrid males from the cross of cattle males with bison females, and by the behavioural constraint preventing domestic bulls from mating with female bison (Ward 2000).

However, a number of studies using modern molecular genetic technologies have reported both mtDNA and nuclear DNA introgression in plains bison from domestic cattle. The first of these studies (Polziehn *et al.*1995) found cattle mtDNA among Custer State Park plains bison. Subsequently, more comprehensive examinations of public bison herds revealed cattle mtDNA in seven of 21 bison conservation herds (Ward 2000; Ward *et al.* 1999), suggesting that hybridisation issues between these two species were widespread and a significant concern to long-term bison conservation efforts. Further investigations based on high-resolution nuclear DNA microsatellites detected domestic cattle nuclear DNA markers in 14 of these 21 U.S. federal conservation herds (Ward 2000).

All major public bison populations in the U.S. and Canada have now been examined using mtDNA, microsatellite markers, or a combination of these 2 technologies. Combining evidence from both mtDNA and nuclear microsatellite markers with information regarding population histories provides a more complete view of hybridisation between the two species. To date, no genetic evidence of domestic cattle introgression has been reported in 9 of these conservation populations (plains bison unless otherwise noted; n = sample size examined): EINP (wood bison, n = 25); MBS (wood bison, n = 36); WBNP (wood bison, n = 23); EINP plains bison (n = 25); GTNP (n = 39); HMSP (n = 21); SHNGP (n = 31); Wind Cave National Park (WCNP)(n = 352); and YNP (n = 520) (Halbert *et al.* 2005a; 2006; Ward *et al.* 1999).

However, the ability to detect nuclear microsatellite DNA introgression is highly dependent on the number of bison in each population, the number of bison sampled from each population and the actual amount of domestic cattle genetic material present in the population (Halbert *et al.* 2005a). Considering statistical confidence (greater than 95%) allowed by detection limits of the technology (Halbert *et al.* 2006), adequate numbers of bison have been evaluated from only two of these herds that displayed no evidence of hybridisation (WCNP and YNP). These two herds represent less than 1.0% of the 420,000 plains bison in North America today (Freese *et al.* 2007; Chapter 7) and both of these herds are currently providing animals for the establishment of new satellite herds for conservations efforts (Chapter 7). Further evaluation is urgently needed to more accurately assess levels of domestic cattle genetics in other public bison herds.

Hybridisation issues with domestic cattle must be considered along with other genetic and non-genetic factors in determining which populations are designated as 'conservation herds'. For example, although some public herds are known to have low levels of domestic cattle genetics, these herds may also represent distinct lineages that reflect historical and geographic differences in genetic diversity (Halbert 2003; Halbert and Derr 2006; Halbert and Derr submitted). Caution is needed in long-term conservation planning to ensure that genetic diversity that represents historical bison geographic differences is identified and conserved for all important populations and not just those thought to be free of domestic cattle introgression. Nevertheless, defining genetic histories that include hybridisation is a first step in developing a species-wide conservation management plan. Given that there are several substantial bison herds that appear to be free of cattle gene introgression, it is of paramount importance to maintain these herds in reproductive isolation from herds containing hybrids.

Plate 4.2 *Custer State Park plains bison bull; a high level of cattle gene introgression is not morphologically evident. Photo: Cormack Gates.*

4.3 Domestication

The number of bison in commercial herds has grown rapidly over the past five decades as many ranchers enter the bison industry to capitalise on the economic opportunities offered by this species (Dey 1997). The increase in commercial bison production may reflect the recognition of the advantages afforded by the adaptations and ecological efficiency of bison as an indigenous range animal. Bison possess several traits that make them preferable to cattle as a range animal, including a greater ability to digest low quality forage (Hawley *et al.* 1981; Plumb and Dodd 1993), the ability to defend against predators (Carbyn *et al.* 1993), the ability to survive harsh winter conditions, and a low incidence of calving difficulties (Haigh *et al.* 2001). According to federal government surveys, the commercial bison population in North America is about 400,000, divided almost equally between the U.S. and Canada (Chapter 7). Despite the current plateau in beef and bison meat prices, both the Canadian Bison Association and the U.S.-based National Bison Association predict very favourable long-term growth of the bison industry. The number of bison in conservation herds is currently estimated at only 20,504 plains bison and 10,871 wood bison. Therefore, approximately 93% of American bison are under commercial production and experiencing some degree of domestication.

Domestication is a process involving the genotypic adaptation of animals to the captive environment (Price 1984; Price and King 1968). Purposeful selection over several generations for traits favourable for human needs, results in detectable differences in morphology, physiology, and behaviour between domestic species and their wild progenitors (Darwin 1859; Clutton-Brock 1981; Price 1984). Humans have practiced domestication of livestock species for at least 9,000 years (Clutton-Brock 1981). As agriculture precipitated the settlement of nomadic human cultures, the domestication of several wild mammal species made livestock farming possible (Clutton-Brock 1981). Intensive management practices and competition between domesticated animals and their wild ancestors often pushed wild varieties and potential predators to the periphery of their ranges or to extinction (Baerselman and Vera 1995; Hartnett *et al.* 1997; Price 1984). Examples of extinct ancestors of domesticated animals include the tarpan (*Equus przewalski gmelini*), the wild dromedary (*Camelus dromedarius*), and the aurochs (*Bos primigenius*) (Baerselman and Vera 1995).

The domestication of cattle provides a relevant history from which to consider the issues of bison domestication. Before cattle (*Bos taurus*) were introduced to North America they had experienced thousands of years of coevolution with human cultures in Europe (Clutton-Brock 1981; Hartnett *et al.* 1997). During the domestication process cattle were selected for docility and valued morphological and physiological traits, but not without adverse consequences. Genetic selection has produced an animal that is dependent on humans, is unable to defend itself against predators, and has anatomical anomalies, such as a smaller pelvic girdle, which cause calving and walking difficulties (Kampf 1998; Knowles *et al.* 1998; Pauls 1995). Domestication has altered the wild character of cattle, producing animals maladapted to the natural environment. Furthermore, because the aurochs, the wild ancestor of European domestic cattle, became extinct in 1627 (Silverberg 1967), domestic cattle have no wild counterpart to provide a source of genetic diversity for genetic enhancement and maintenance.

While it has been suggested that domesticated animals can be reintroduced into the wild and revert to a feral state (Kampf 1998; Lott 1998; Turnbull 2001), such attempts do not restore the original genetic diversity of a species (Price 1984; van Zyll de Jong *et al.* 1995). Experience has shown that recovery of original genetic diversity is difficult or impossible once domestic breeds are highly selected for specific traits and wild stocks are extinct (Price 1984; Turnbull 2001; van Zyll de Jong *et al.* 1995). For example, in the 1920s, two German brothers, Heinz and Lutz Heck, set out to “re-create” the aurochs by back-breeding domestic cattle with other cattle demonstrating aurochs-like qualities (Fox 2001; Silverberg 1967; Turnbull 2001). They produced one successful line, the Hellabrunn breed, also known as Heck cattle. This is an animal that looks very much like an aurochs, but is devoid of the wild traits and hardiness of the original wild form (Fox 2001; Silverberg 1967). This illustrates that the original wild genotype is no longer available to the cattle industry for improving domestic breeds. The history of the aurochs offers a lesson for bison: domestication can lead to altered genetically based behaviour, morphology, physiology, and function, and the loss of the wild type and the genetic diversity it contains.

The primary goal of many commercial bison ranchers is to increase profits by maximising calf production, feed-to-meat conversion efficiency, and meat quality (Schneider 1998). This requires non-random selection for traits that serve this purpose, including conformation, docility, reduced agility, growth performance, and carcass composition. Selection for these traits reduces genetic variation and changes the character of the animal over time (Schneider 1998). Although a growing number of consumers prefer naturally produced meat products without hormones, antibiotics, or intensive management (Morris 2001), the demand for bison cannot currently compete with the much larger scale of the beef industry. Therefore, many bison producers apply cattle husbandry practices and standards to bison. Artificial selection based on husbandry and economics may make good business sense in the short term, but it will not conserve native bison germplasm.

The long term objectives and goals that drive commercial bison production generally differ from the major issues associated with

the conservation of the wild species. Furthermore, commercial bison operations could pose a threat to conservation populations through a form of genetic pollution if genetically selected commercial animals are mixed into conservation herds or escape and join wild herds. The most prudent action is to identify and maintain existing conservation herds, and avoid mixing commercially propagated stock into those herds. Bison producers and the bison industry could benefit in the long term by supporting efforts to restore and maintain conservation herds, particularly those subject to a full range of natural selection pressures (Chapter 7). Conservation herds secure the bison genome for the future use of producers—an option not available for most other domestic animals.

Chapter 5 Reportable or Notifiable Diseases

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Throughout their range, bison host numerous pathogens and parasites, many of which also occur in domestic cattle (see reviews: Berezowski 2002; Tessaro 1989; Reynolds *et al.* 2003). In this review, we consider only infective organisms that may negatively affect bison populations, or their conservation, either through direct pathobiological effects, or indirectly as a consequence of management interventions. Livestock diseases that restrict trade or pose a risk to human health may be "reportable" or "notifiable" under federal and provincial/state legislation.

In Canada, reportable and immediately notifiable diseases are listed nationally under the authority of the Health of Animals Act and Regulations (http://laws.justice.gc.ca/en/H-3.3/, accessed 15 April 2009) and under provincial statutes and legislation. The Canadian Health of Animals Act requires owners and anyone caring for animals, or having control over animals, to immediately notify the Canadian Food Inspection Agency (CFIA) when they suspect or confirm the presence of a disease prescribed in the Reportable Diseases Regulations. The CFIA reacts by either controlling or eradicating the disease based upon a programme agreed to by stakeholders (CFIA 2001).

In the U.S., the U.S. Department of Agriculture Animal and Plant Health Inspection Service (APHIS) conducts federal eradication programmes for several reportable livestock diseases and is involved in a negotiated multi-jurisdictional brucellosis management programme for bison in Yellowstone National Park (YNP) (APHIS, USDA 2007; NPS-USDOI 2000). In both countries, Federal legislation supersedes state and provincial disease control legislation. In the U.S. and Canada there are specific state and provincial regulations that require testing for, and reporting of, various diseases. These regulations may be more extensive than federal requirements, but typically include those diseases regulated by the federal animal health authorities.

Much like the U.S and Canada, Mexico has federal animal disease regulations that are administered by the Secretary of Agriculture, Livestock Production, Rural Development, Fishery and Food (SAGARPA). Disease surveillance programmes and zoosanitary requirements, including disease reporting, are established by federal law to protect trade in Mexico and are administered by a decentralised branch of SAGARPA titled the National Service of Health, Safety, and Agricultural Food Quality (SENASICA, see http://www.senasica.gob.mx). SAGARPA also negotiates bi-lateral disease management agreements for important livestock diseases along the U.S. border, including bovine tuberculosis, brucellosis, and screwworm.

In addition to federal, state and provincial regulatory agencies there is an international organisation that influences animal disease reporting in North America. The World Organization for Animal Health (OIE) is an intergovernmental organisation created by international agreement in 1924. In 2008 the OIE had 172 member countries. Every member country is committed to declaring the animal diseases it may detect in its territory. The OIE disseminates this information to help member countries to protect themselves from the spread of disease across international boundaries. The OIE produces sanitary codes with rules that must be observed by member countries to prevent the spread of significant diseases around the world. OIE has established Sanitary Codes for Terrestrial Animals, and the Manual for Diagnostic and Vaccine Tests for Terrestrial Animals, which may influence the international movement of bison (http://www.oie.int/eng/normes/mcode/en_sommaire.htm). All three countries in North America are members of OIE.

Depending on the nature of the disease, management of reportable diseases in captive or commercial herds in North America may involve development and application of uniform protocols to reduce disease prevalence, zoning of management areas by disease status, or imposition of procedures for disease eradication, including test and slaughter, or depopulation. Where reportable diseases are detected, federal, state or provincial legislation affects management of wild bison populations. Interventions may include limiting the geographic distribution of an infected wild population, (e.g., removals at park boundaries to reduce the risk of the disease spreading to adjacent livestock population), quarantine, treatment, or eradication of infected captive conservation breeding herds, or limiting inter-population or inter-jurisdictional transport of bison. Public perception of bison as specific, or non-specific, carriers of diseases is a potential barrier to re-establishing conservation herds, particularly in regions where conventional livestock grazing occurs. National and state/provincial governments may restrict the import/export of bison for conservation projects based on real or perceived risks of infection and transmission of reportable diseases.

5.1 Diseases of Conservation Concern

The American Bison Specialist Group (ABSG) recognises nine federally listed diseases of concern for bison conservation in North America. Regulations applicable to each disease may vary among jurisdictions and in their impact on bison conservation and restoration efforts. The OIE lists seven of these diseases as "notifiable" under international standards.

5.1.1 Anaplasmosis

The etiologic agent of anaplasmosis is *Anaplasma marginale*, a rickettsia that parasitises the red blood cells of host animals. The organism is transmitted by blood sucking insects, such as ticks, which serve as a vector between hosts (Radostits *et al.* 2000). The interplay of susceptible wild ruminants and arthropod vectors is critical to the epizootiology of the disease. Anaplasmosis is a disease of international regulatory concern and, therefore, significantly impacts livestock trade between Canada and the north-central and north-western U.S. Anaplasmosis is a disease of major economic importance to the cattle industry in infected regions. Bison are known hosts of *A. marginale* (Zaug 1986) and wild bison have demonstrated serologic titres for the disease (Taylor *et al.* 1997). They have also been experimentally infected (Kocan *et al.* 2004; Zaugg 1986; Zaugg and Kuttler 1985). Serodiagnosis in wild ungulates has proven largely unreliable, but modern molecular diagnostic procedures have provided an excellent alternative (Davidson and Goff 2001). Naturally occurring infections have been reported in the National Bison Range (NBR), Montana, where 15.7% of bison tested positive for anaplasmosis (Zaugg and Kuttler 1985). Recent studies demonstrated *A. marginale* infection in two widely separated bison herds in the U.S., one in Oklahoma (Nature Conservancy Tallgrass Prairie Preserve) and one in Saskatchewan (De La Fuente et al. 2003). In the Canadian herd, serology and polymerase chain reactions indicated that 10 individuals were infected with *A. marginale* whereas 42 of 50 bison culled from the Tallgrass Prairie Preserve (TGPP) tested positive serologically as carriers of *A. marginale*. The U.S. bison isolate of *A. marginale* was found to be infective when inoculated into susceptible splenectomised calves. Clinical symptoms in bison are similar to those described for cattle. They include anaemia, jaundice, emaciation, and debility (Radostits *et al.* 2000). Experimentally infected bison calves demonstrated mild clinical signs suggesting that bison may be more resistant than cattle (Zaugg and Kuttler 1985). The disease occurs commonly in Africa, the Middle East, Asia, Australia, the U.S., Central and South America, and southern Europe. If anaplasmosis is diagnosed in Canadian cattle or bison, Canada's current foreign animal disease strategy calls for its eradication through the testing of infected and exposed herds and the removal of infected individuals. Every bison imported into Canada from the U.S. must be quarantined from the time of its importation into Canada until it proves negative to tests for anaplasmosis performed at least 60 days after it was imported into Canada (CFIA 2007). Programmes for managing this disease in domestic animals include vector control, vaccination and antibiotic therapy (Davidson and Goff 2001). Anaplasmosis is not infectious to humans.

5.1.2 Anthrax

Anthrax is an infectious bacterial disease caused by the endospore-forming bacterium *Bacillus anthracis* (Dragon and Rennie 1995). After inhalation or ingestion by a susceptible host, *B. anthracis* endospores germinate and the vegetative form of the bacterium replicates in the bloodstream, releasing toxins that cause septicaemia and death (Dragon and Rennie 1995; Gates *et al.* 2001b). Upon release from a carcass, highly resistant endospores can remain viable in the soil for decades before infecting a new host (Dragon and Rennie 1995). Humans have played an important role in the evolution of anthrax by increasing the proliferation and dispersal of this global pathogen. Observations of the role of climatic factors, such as season of year, ambient temperature, and drought in promoting anthrax epizootics have been made for several decades (APHIS, USDA 2006). The commonality of summer months, high ambient temperatures, drought, and anthrax epizootics are non-contentious. The roles of environmental factors such as soil types and soil disturbances via excavation are poorly defined despite attempts to evaluate these potential factors.

Bacillus anthracis is divided into three genotype branches with distinct geographic sub-lineage compositions that vary regionally around the globe (Van Ert 2007). Van Ert (2007) analysed 273 isolates of *B. anthracis* in North America, reporting a cosmopolitan assortment of 44 multiple locus, variable number, tandem repeat analysis genotypes. One hypothesis holds that *B. anthracis* was introduced from the Old World to the New World in spore-infected animal products (wool, skins, bone meal, shaving brushes) transported to the south-eastern seaboard during the European colonial-era (Hanson 1959; Van Ness 1971). Consistent with this hypothesis, Van Ert (2007) found a single dominant sub-group in North American (A.Br. WNA; 70% of genotypes) that is closely related to the dominant European sub-group A.Br.008/009. The diversity of sub-lineages represented varies geographically in North America. A.Br.WNA predominates in the north, while the industrialised south-eastern region of the continent contains a cosmopolitan assortment of less common *B. anthracis* genotypes in addition to the dominant form A.Br.WNA.

The geographic pattern of sub-lineage occurrence in North America is consistent with the hypothesis of an early initial introduction of a limited number of sub-lineages (perhaps

one) followed by its widespread dispersal and ecological establishment. Wild bison were abundant and widely distributed at the time of European colonisation. Once infected with anthrax they may have played an important early role in the ecological establishment and widespread dispersal of A.Br.WNA. The broad diversity of anthrax lineages represented in the industrialised south-eastern region of the continent (Van Ert *et al.* 2007) is suggestive of the accumulation of additional sub-group types over time. A likely mechanism is importation of contaminated animal products into mills and tanneries on the eastern seaboard and New England which process imported hair, wool, and hides. The World Health Organisation (WHO 2008) commented on the role of tanneries as a point source of anthrax outbreaks. Contaminated products come from animals that died of anthrax. Wastewater effluent from plants can contaminate downstream sediments and pastures with anthrax spores, providing a source of local outbreaks in livestock and further proliferation of novel introduced variants of the pathogen. Marketing of inadequately sterilised bone meals and fertilisers, rendered from contaminated materials, can result in long distance redistribution and introducing "industrial" strains to livestock remote from the original source (Hugh-Jones and Hussaini 1975).

Under certain environmental conditions, concentrations of endospores have caused periodic outbreaks among wood bison in the Slave River Lowlands (SRL), Mackenzie Bison Sanctuary (MBS), and Wood Buffalo National Park (WBNP) (Dragon and Elkin 2001; Gates *et al.* 2001b; Pybus 2000). Between 1962 and 1971, anthrax and the associated depopulation and vaccination programmes employed to control the disease, accounted for over 2,800 wood bison deaths (Dragon and Elkin 2001). Further outbreaks occurred in the MBS in 1993, in the SRL in 1978, 2000 and 2006, and in WBNP in 1978, 1991, 2000, and 2001 (Gates *et al.* 1995; Nishi *et al.* 2002c). Four factors that are associated rather consistently with these epizootics are high ambient temperatures, intense mating activity, high densities of insects, and high densities of bison as they congregate and compete for diminishing water and food supplies (APHIS, USDA 2006). Based on these four factors, two hypotheses have been proposed to explain outbreaks of anthrax in bison in northern Canada: (1) "the modified host resistance hypothesis" (Gainer and Saunders 1989) and (2) "the wallow concentrator hypothesis" (Dragon *et al.*, 1999). These two hypotheses are not mutually exclusive.

A recent outbreak was reported in a commercial herd in south-western Montana that killed over 300 bison pasturing on a large foothills landscape beneath the Gallatin Mountain Range (Ronnow 2008). Despite mass deaths of bison during anthrax outbreaks, the sporadic nature of outbreaks and predominance of male deaths suggest that the disease plays a minor role in long-term population dynamics unless operating in conjunction with other limiting factors (Joly and Messier 2001b; Shaw and Meagher 2000). Anthrax is not treatable in free-ranging wildlife, but captive bison can be vaccinated or treated with antibiotics (Gates *et al.* 1995; Gates *et al.* 2001b). Carcass scavenging facilitates environmental contamination with anthrax spores (Dragon *et al.* 2005); therefore timely carcass treatment and disposal during an active outbreak in free-ranging bison is considered an important preventative strategy for reducing the potential for future outbreaks (Hugh-Jones and de Vos 2002; Nishi *et al.* 2002a). Anthrax is a public health concern and humans are susceptible, however, exposure from naturally occurring outbreaks requires close contact with animal carcasses or hides. In addition, humans have rarely been exposed to anthrax through the purchase of curios purchased by tourists (Whitford 1979).

5.1.3 Bluetongue

Bluetongue (BLU) is an insect-borne viral hemorrhagic disease affecting many ungulates in the lower latitudes of North America. The BLU virus is a member of the genus *Oribivirus* of the family Reoviridae. Worldwide there are 24 known BLU serotypes, but only six are active in domestic and wild ruminants from North America (Pearson *et al.* 1992). Bluetongue viruses are closely related to the viruses in the epizootic hemorrhagic disease and BLU is known to infect a wide variety of wild and domestic ruminants (Howerth *et al.* 2001). Bison are susceptible to BLU, and the virus has been isolated under field, captive, and experimental conditions (Dulac *et al.* 1988). The arthropod vectors of the bluetongue virus are various species of Culicoides midges (Gibbs and Greiner 1989; Howerth *et al.* 2001). Clinical symptoms include fever, stomatitis, oral ulcerations, lameness, and occasionally, reproductive failure (Howerth *et al.* 2001). There are subacute, acute, and even chronic expressions of the disease in many wild ungulates and domestic livestock. BLU typically occurs in the late summer and early fall depending upon the seasonal patterns of vector activity (Howerth *et al.* 2001). Factors influencing the frequency and intensity of disease outbreaks are innate herd immunity, virulence factors associated with viruses, and vector competency and activity. BLU occurs in livestock over much of the U.S. and its distribution parallels that of domestic livestock. Its distribution is more limited in Canada where it once was a regulated disease until rules were relaxed in July 2006 (CFIA website). There is considerable difference in the epidemiology of the disease between northern and southern portions of North America depending on the consistency of vector activity. In the southern areas, vector activity is more common and animal populations exhibit a higher prevalence of seroreactivity and antibody protection. BLU has not been widely reported in bison herds in North America. Serologic surveys of several Department of Interior bison herds in the U.S. have not found seroreactors for bluetongue virus (T. Roffe personal communication; Taylor *et al.* 1997). The U.S. Fish and Wildlife Service (USFWS) has opportunistically examined bison

near a recent outbreak of BLU in deer and found no evidence of exposure (T. Roffe personal communication). As with many vector-born diseases, climate change is a potential factor affecting the distribution of vectors and therefore the occurrence of BLU (Gibb 1992). There is no effective treatment and, under natural conditions, the disease is not considered a significant threat to human health. There has been one human infection documented in a laboratory worker (WHO website).

5.1.4 Bovine spongiform encephalopathy

Bovine spongiform encephalopathy (BSE), or "mad cow disease" as it is commonly known, is one of a suite of distinct transmissible spongiform encephalopathies (TSE) identified during the past 50 years. TSEs are apparently caused by rogue, misfolded protein agents called prions (PrPSC) that are devoid of nucleic acids (Prusiner 1982). No other TSE in man or animal has received more worldwide attention than BSE (Hadlow 1999). It was first identified in 1986 in England and has since had far reaching economic, political, and public health implications. BSE is a neurologic disease characterised by spongiform change in gray matter neurophil, neuronal degeneration, astrocytosis, and accumulation of misfolded PrPSC (Williams *et al.* 2001). Clinically the disease is progressive, displaying gradual neurologic impairment over months or years and is usually fatal. The disease causes progressive weight loss, low-level tremors, behavioural changes, ataxia, and postural abnormalities. Substantial evidence exists for genetic variation in susceptibility among and within species (Williams *et al.* 2001). Cases of BSE were identified in 10 species of Bovidae and Felidae at a zoological collection in the British Isles (Kirkwood and Cunningham 1994). At least one of these cases included bison. Worldwide, other species susceptible to BSE include cheetah, macaques and lemurs (Williams *et al.* 2001). The recent BSE epidemic in Europe was linked to oral ingestion of contaminated feed (containing ruminant derived protein), however, there is some evidence for low-level lateral transmission. There are no known treatments or preventions for BSE. The human form called new variant Creutzfeldt-Jakob disease has been linked to consumption of BSE contaminated foods. Due to the risk of human exposure to BSE, this disease is highly regulated worldwide. Recent cases of BSE have been reported in Canada and the U.S. but are extremely rare in the livestock industry. Canada reported a case in 1993 that was imported from England and the first domestic case was detected in 2003. The U.S. reported its first case of BSE in 2003. Since then, protein by-products were banned in livestock feed, national surveillance was implemented in both countries, and several regulations were promulgated to restrict imports and exports across the U.S.-Canada boundary. Although bison are considered to be susceptible, there has not been a case of BSE reported in American bison.

5.1.5 Bovine brucellosis

Bovine brucellosis, also known as Bang's disease, is caused by infection with the bacterium *Brucella abortus* (Tessaro 1989; Tessaro 1992). The primary hosts for bovine brucellosis are cattle, bison, and other bovid species (Tessaro 1992), however, other wild ungulates such as elk (*Cervus elaphus*) are also susceptible and seem to play a role in interspecies transmission in the Greater Yellowstone Area (GYA) (Davis 1990; Rhyan *et al.* 1997; Thorne *et al.* 1978). Evidence suggests that brucellosis was introduced to North America from Europe during the 1500s (Meagher and Mayer 1994; Aguirre and Starkey 1994). The disease is primarily transmitted through oral contact with aborted foetuses, contaminated placentas, and uterine discharges (Reynolds *et al.* 1982; Tessaro 1989). The impacts of brucellosis on female bison include abortion, inflammation of the uterus, and retained placenta (Tessaro 1989). Greater than 90% of infected female bison abort during the first pregnancy; however, naturally acquired immunity reduces this abortion rate to 20% after the second pregnancy, and to nearly zero after the third pregnancy (Davis *et al.* 1990; Davis *et al.* 1991). Male bison experience inflammation of the seminal vessels, testicles, and epididymis, and, in advanced cases, sterility (Tessaro 1992). Both sexes are susceptible to bursitis and arthritis caused by concentrations of the bacterial organism in the joints, resulting in lameness, and possibly increased vulnerability to predation (Tessaro 1989; Tessaro 1992).

Serology is used to detect exposure to *B. abortus* by identifying the presence of antibodies in the blood. Sero-prevalence is the percentage of animals in a herd that carry antibodies (Cheville *et al.* 1998). A sero-positive result, indicating the presence of antibodies, does not imply current infection, and may overestimate the true level of brucellosis infection (Cheville *et al.* 1998; Dobson and Meagher 1996) because the organism must be cultured from tissue samples to diagnose an animal as infected. However, a disparity between serology results and level of infection could also be attributed to false negative culture results related to the difficulties in isolating bacteria from chronically infected animals (Cheville *et al.* 1998).

There is currently no highly effective vaccine for preventing bovine brucellosis (Cheville *et al.* 1998; Davis 1993). Strain 19 (S19) was a commonly used vaccine administered to cattle from the 1930s until 1996 (Cheville *et al.* 1998). It was only 67% effective in preventing infection and abortion in cattle (Cheville *et al.* 1998). S19 was found to induce a high frequency of abortions in pregnant bison (Davis *et al.* 1991). Other studies failed to demonstrate efficacy of S19 as a bison calfhood vaccine (Templeton *et al.* 1998). A newer vaccine, strain RB51, is now preferred over S19 because it does not induce antibodies that can interfere with brucellosis serology tests for disease exposure (Cheville *et al.* 1998; Roffe *et al.* 1999a). RB51 protects

cattle at similar levels to S19 (Cheville *et al.* 1993). Doses of RB51 considered to be safe in cattle were found to induce endometritis, placentitis, and abortion in adult bison (Palmer *et al.* 1996). However, Roffe *et al.* (1999a) found RB51 had no significant adverse effects on bison calves. The safety and efficacy of RB51 in bison remains unclear but, nonetheless, it was provisionally approved for use in bison in the U.S. The vaccine is not recognised in Canada and vaccinated cattle are not allowed into the country (CFIA 2007). Every bison imported into Canada from the U.S. must be quarantined from the time of its importation into Canada until it proves negative to tests for brucellosis performed not less than 60 days after it was imported into Canada (CFIA 2007).

Quarantine protocols have been developed for bison to progressively eliminate all animals exposed to brucellosis from a population (APHIS, USDA 2003; Nishi *et al.* 2002b). These protocols have been successful for eliminating brucellosis in wood bison through the Hook Lake project and are currently being attempted in the GYA (Aune and Linfield 2005; Nishi *et al.* 2002b). Results from these two studies, and other case studies (HMSP, WCNP and EINP), have shown that brucellosis can be effectively eliminated from exposed populations with a high degree of certainty using test and slaughter protocols.

5.1.6 Bovine tuberculosis

Bovine tuberculosis (BTB) is a chronic infectious disease caused by the bacterium *Mycobacterium bovis* (Tessaro *et al.* 1990). The primary hosts for BTB are cattle and other bovid species, such as bison, water buffalo (*Bubalus bubalis*), African buffalo (*Syncerus caffer*), and yak (*Bos grunniens*). Primary hosts are those species that are susceptible to infection and will maintain and propagate a disease indefinitely under natural conditions (Tessaro 1992). Other animals may contract a disease, but not perpetuate it under natural conditions; these species are secondary hosts. The bison is the only native species of wildlife in North America that can act as a true primary host for *M. bovis* (Tessaro 1992). Historical evidence indicates that BTB did not occur in bison prior to contact with infected domestic cattle (Tessaro 1992). Currently, the disease is only endemic in bison populations in and near WBNP, where it was introduced with translocated plains bison during the 1920s. BTB is primarily transmitted by inhalation and ingestion (Tessaro *et al.* 1990); the bacterium may also pass from mother to offspring via the placental connection, or through contaminated milk (FEARO 1990; Tessaro 1992). The disease can affect the respiratory, digestive, urinary, nervous, skeletal, and reproductive systems (FEARO 1990; Tessaro *et al.* 1990). Once in the blood or lymph systems the bacterium may spread to any part of the host and establish chronic granulomatous lesions, which may become caseous, calcified, or necrotic (Radostits *et al.* 1994; Tessaro 1992). This chronic disease is progressively debilitating to the host, and may cause reduced fertility and weakness; advanced cases are fatal (FEARO 1990). The disease manifests similarly in cattle and bison (Tessaro 1989; Tessaro *et al.* 1990). Both the U.S. and Canada perform nationwide surveillance of abattoir facilities to monitor BTB infection in cattle and domestic bison. There is no suitable vaccine available for BTB (FEARO 1990; CFIA 2000; APHIS USDA 2007). Every bison imported into Canada from the U.S. must be quarantined from the time of its importation into Canada until it proves negative to tests for BTB performed at least 60 days after it was imported into Canada (CFIA 2007). A quarantine protocol has been developed and an experimental project was attempted to salvage bison from a BTB exposed population (Nishi *et al.* 2002b). Although at first it appeared to be a successful tool for salvaging bison from an exposed herd, after 10 years, several of the salvaged animals expressed BTB, and in 2006 all salvaged animals were slaughtered (Nishi personal communication). There is some evidence that BTB can be treated in individual animals using long term dosing with antibiotics, but the duration of treatment, costs of therapy, and the need for containment make this option impractical for wildlife. The only definitive method for completely removing BTB from a herd is depopulation (CFIA 2000; APHIS USDA 2005). The only alternative to depopulation is controlling the spatial distribution and prevalence of disease through a cooperative risk management approach involving all stakeholders. The basic prerequisites for effectively addressing risk management associated with BBTB in bison are teamwork, collaboration across professional disciplines, and respect for scientific and traditional ecological knowledge among technical and non technical stakeholders (Nishi *et al.* 2006). BTB can infect humans, but it is treatable with antimicrobial drugs. Human TB due to *M. bovis* has become very rare in countries with pasteurised milk and BTB eradication programmes.

5.1.7 Bovine viral diarrhoea

Bovine viral diarrhoea (BVD) is a pestivirus that infects a wide variety of ungulates (Loken 1995; Nettleston 1990). Serologic surveys in free-ranging and captive populations demonstrate prior exposure in more than 40 mammal species in North America (Nettleston 1990; Taylor *et al.* 1997). The suspected source of BVD in wild animals is direct contact with domestic livestock. Infections in wild ruminants, like cattle, are dependent upon the virulence of the isolate, immune status of the animal host, and the route of transmission. Infections in cattle are usually subclinical, but some infections may cause death or abortions in pregnant animals. Factors influencing the persistence of BVD include population size and density, herd behaviour, timing of reproduction, and survivorship of young (Campen *et al.* 2001).

Positive serologic evidence was reported for blood samples from bison in the GYA (Taylor *et al.* 1997; Williams *et al.* 1993),

Alaska (Zarnke 1993) and from bison at Elk Island National Park (EINP) in Alberta (Cool 1999; Gates *et al.* 2001b). In YNP, positive antibody titres were detected in 31% of tested animals (Taylor *et al.* 1997). There are unpublished data regarding sero-reactivity from bison transported to Montana from WCNP in South Dakota (K. Kunkel, personal communication). The Jackson bison herd, with a known history of commingling with cattle, has demonstrated low-level titres, but no evidence of BVD antigen or clinical disease has been found (T. Roffe, personal communication). Clinical BVD was reported in the EINP plains bison herd in 1996, prompting a serological survey of plains bison and wood bison herds (Cool 1999; Gates *et al.* 2001b). Forty-seven percent of 561 plains bison from EINP tested sero-positive for BVD; one tested positive for the virus antigen. At least six plains bison deaths in EINP were attributed to the BVD virus (Cool 1999). Tissues from the suspected cases of BVD infected plains bison were submitted to the Animal Disease Research Institute, Lethbridge, Alberta, Canada, and type 1 BVD virus was isolated (Tessaro and Deregt 1999). None of 352 wood bison in the Park tested sero-positive for BVD at the time. Both plains and wood bison populations at EINP are vaccinated for BVD during annual roundups. However, calves used in translocations are not vaccinated to allow future screening of recipient populations for BVD. In Poland, Sosnowski (1977) reported BVD in a captive European bison. BVD is common in cattle in North America and poses no known risk to humans.

5.1.8 Johne's disease

Johne's disease (JD) is caused by the etiologic agent *Mycobacterium avium* subsp*. paratuberculosis*, a hardy bacterium related to the agents of leprosy and tuberculosis. It occurs worldwide affecting a variety of domestic and wild ruminants including bison, cattle, and sheep (Buergelt *et al.* 2000; Williams 2001). Infections often lead to chronic granulomatous enteritis with clinical signs of diarrhoea, weight loss, decreased milk production, and mortality. JD is common in cattle. Recent studies have shown that more than 20% of dairy herds in the U.S. have JD (Chi *et al.* 2002; Ott *et al.* 1999) causing an estimated economic loss of more than US$200 million annually. JD typically enters a herd when infected, asymptomatic animals are introduced. Unpasteurised raw milk or colostrum may be a source of infection for artificially raised calves. Animals are most susceptible to infection during their first year of life. Neonates most often become infected by swallowing small amounts of contaminated manure from the ground or from their mother's udder. Animals exposed to a very small dose of bacteria at a young age, and older animals, are not likely to develop clinical disease until they are much older. After several years, infected animals may become patent and shed mycobacteria in their faeces. Typically, pre-patent animals do not show symptoms of disease; consequently, most infections go unnoticed and undiagnosed. There is no treatment for animals infected with JD and prevention is the best control measure. Humans are not considered susceptible, but *M. a. paratuberculosis* has been isolated in patients with chronic enteritis (Crohn's disease) (Chiodini 1989). JD is not considered to be a disease problem when bison are on open rangelands and managed at low density. However, restrictions may apply to inter-jurisdictional movement of animals from known infected herds. Hence, maintaining low risk status for bison herds used as a source for conservation projects is an important consideration.

In 1998, the U.S. Animal Health Association approved the Voluntary Johne's Disease Herd Status Program for cattle (VJDHSP). The VJDHSP provides testing guidelines for States to use to identify livestock herds as low risk for JD infection. With numerous tests over several years, herds progress to higher status levels. The higher the status level, the more likely it is that a herd is not infected with JD. In April 2002, USDA-APHIS-Veterinary Service incorporated portions of this programme into national programme standards: Uniform Program Standards for the Voluntary Bovine Johne's Disease Control Program (VBJDCP). VBJDCP-test-negative herds serve as a source of low JD risk stock. Testing for JD in conservation herds has been sporadic and opportunistic. Diagnostic tools are being developed and improved. There are no reports of JD in conservation bison herds in the literature, however, some commercial operations have discovered JD, and in many cases are managing to prevent its spread and reduce its impact on the industry.

5.1.9 Malignant catarrhal fever (sheep associated)

Malignant catarrhal fever (MCF) is a serious, often fatal disease affecting many species of the Order Artiodactyla. It is caused by viruses of the genus *Rhadinovirus*. At least 10 MCF viruses have been recognised worldwide and five viruses have been linked to disease. The viruses most significant to livestock are those carried by sheep, goats or wildebeest (*Connochaetes* spp.). Although ovine herpes virus type 2 (sheep associated MCF) does not cause disease in its natural host, domestic sheep, it does cause MCF in bison. Serological testing indicated that it is common in domestic goats (61%) and sheep (53%) in the U.S. (Li *et al.* 1996). MCF is an important disease in the commercial bison industry as it is one of the most infectious diseases of bison, especially at high densities (Heuschele and Reid 2001). It causes highly lethal infections in bison, with the reported incidence of mortality in a herd of up to 100% (Schultheiss *et al.* 2001). Infections proceed rapidly to clinical disease. MCF is expressed in two forms, acute and chronic, but regardless, death ensues in most cases. In the acute form, bison usually die within 7–10 days of infection or within 48 hr of becoming symptomatic. Alternatively, death may ensue as

long as 156 days post-infection. Some animals recover and remain persistently infected (Schultheiss *et al.* 1998). Clinical signs in bison include hemorrhagic cystitis, colitis, conjunctivitis, ocular discharge, nasal discharge, excess salivation, anorexia, diarrhoea, melaena, haematuria, multifocal ulceration of the oral mucosa, fever, circling, ataxia, behaviours suggestive of blindness, lameness, and difficult urination (Liggitt *et al.* 1980; Ruth *et al.* 1977; Schultheiss *et al.* 1998). Lymphadenomegaly and corneal opacity occur in fewer than half the cases (Schultheiss *et al.* 2001). Direct contact between bison and domestic sheep is considered the most likely source of infection. Hence, bison should not be grazed in the same pastures or adjacent to pastures with sheep. Although most infections occur when bison are in close association with domestic sheep, MCF was reported in bison herds that were five kilometres (three miles) from a lamb feedlot (Schultheiss *et al.* 2001). Dr. T. Roffe has conducted serologic surveys of two U.S. Department of the Interior bison herds not associated with domestic sheep and has found no sero-reactors for MCF (T. Roffe, personal communication). There is no vaccine or effective treatment for MCF and the best way to control this disease is to minimise contact with reservoir hosts. There is no evidence that isolates of MCF are infectious to humans (Heuschele and Seal 1992).

5.2 Episodes of Reportable Diseases in Plains Bison

Based on this survey, two plains bison conservation herds in North America have significant chronic disease issues: YNP herd and the Jackson herd in GTNP/NER. These herds, which account for 4,700 bison (as of winter 2008), or 24% of the entire North American plains bison conservation population, harbour brucellosis.

5.2.1 Yellowstone National Park

Brucellosis was first detected in the YNP bison population in 1917 (Mohler 1917). The origin of brucellosis in the park is unclear, but was probably the result of transmission from cattle (Meagher and Mayer 1994). Opportunistic and systematic serological surveys in the area revealed sero-prevalence varying between 20% and 70%, while bacterial cultures indicated an infection prevalence of approximately 10% (Dobson and Meagher 1996; Meagher and Mayer 1994). Although the true prevalence of the disease is unknown, the YNP bison population is considered to be chronically infected with brucellosis (Cheville *et al.* 1998). More recent research on the epidemiology of brucellosis in Yellowstone bison found that 46% of the sero-reactor animals were culture positive (Roffe *et al.* 1999b). Recent demographic analysis indicates that brucellosis has a significant reproductive effect, that the growth rate of the population could increase by 29% in the absence of brucellosis (Fuller *et al.* 2007), and that brucellosis is not a threat to the long-term viability of the YNP bison (Mayer and Meagher 1995; USDOI and USDA 2000). Fuller *et al.* (2007) conducted a detailed analysis of the demographics of the Yellowstone population from 1900-2000 and found evidence of density dependent changes in population growth as numbers approached 3,000 animals. This population appears robust and has grown at times to exceed 4,000, although it was reduced to fewer than 3,000 several times during the past decade under the current herd management regime (R. Wallen, personal communication).

Herd management is affected by the presence of brucellosis primarily because of the potential risk the disease poses to the livestock industry (Keiter 1997). Bison leaving the park could potentially transmit the disease to domestic cattle grazing on adjacent National Forest and private lands in Montana, Wyoming or Idaho (USDOI and USDA 2000). Bison leave the park in the winter on the north and west boundaries within Montana; movement to the east and south is rare because of topographical barriers (R. Wallen, personal communication). Transmission of brucellosis from bison to cattle has been demonstrated in captive studies; however, there are no confirmed cases of transmission in the wild (Bienen 2002; Cheville *et al.* 1998; Shaw and Meagher 2000). Nevertheless, the potential exists, and this has created a contentious bison management issue in the area.

Relying on the Animal Industry Act of 1884, the U.S Department of Agriculture began preventing and controlling the spread of contagious livestock diseases in the U.S. In 1947, federal and state officials began working closely with the livestock industry to eradicate brucellosis (Keiter 1997; NPS USDOI 2000). Each state represented in the GYA is a co-operator in the National Brucellosis Program and has authority to implement control programmes for brucellosis infected or exposed animals within their respective boundaries. Due to the transmission of brucellosis to cattle, presumably by elk, Montana, Wyoming, and Idaho have each periodically lost their brucellosis-free status as certified by APHIS. Transmission of brucellosis to cattle in Montana, Wyoming or Idaho indirectly affects all producers in these states. If their APHIS status is downgraded, other states may refuse to accept cattle from producers in the GYA (Cheville *et al.* 1998).

Resolution of this issue requires the involvement of, and cooperation among, agencies in several jurisdictions: The National Park Service (NPS), the U.S. Forest Service (USFS), APHIS, and the State of Montana Department of Livestock (MDOL) and Montana Department of Fish, Wildlife, and Parks (MFWP). After many years of media and legal controversy over bison management, the agencies acknowledged the need to cooperatively develop a long-term bison management plan (Plumb and Aune 2002). In 1990, they commenced the process

for an interagency environmental impact statement to develop alternatives for the plan (USDOI and USDA 2000). A series of interagency interim plans followed, which progressively incorporated greater tolerance for bison outside the park in certain areas, and enabled NPS and MFWP personnel to lethally remove bison moving from YNP into Montana.

Legal and policy disagreements between the federal agencies and the State of Montana inhibited the development of a long-term interagency management plan until 2000 when court-ordered mediation resulted in a final decision for a long-term management approach. The long-term plan employs an adaptive management approach with three phased steps for each of the north and west boundary areas (USDOI and USDA 2000). The plan incorporates several risk management strategies including spatial and temporal separation of bison and cattle, capture, test, and slaughter of sero-positive bison, hazing of bison back into the park, vaccination, and radio-telemetry monitoring of pregnant bison to locate possible sources of infection if a cow gives birth or aborts outside the park (USDOI and USDA 2000). The ultimate purpose of the plan is to maintain a wild, free-ranging population of bison while, at the same time, protecting the economic viability of the livestock industry in Montana by addressing the risk of brucellosis transmission; it is not a brucellosis eradication plan (Plumb and Aune 2002). Although eradication of brucellosis from bison in the park is a possible future goal, such an effort is complicated by retransmission potential from elk in the GYA, which also harbour the disease (Cheville *et al.* 1998). Development of more effective vaccines and vaccination methods for bison and elk are required before considering eradication alternatives (Cheville *et al.* 1998). Recent research on genes that control natural resistance to brucellosis may also provide future methods for eradicating brucellosis (Templeton *et al.* 1998).

Recent transmission of brucellosis from elk to cattle and the subsequent loss of Montana's brucellosis status have complicated management. Current initiatives are aimed at managing the problem of brucellosis in elk and bison. Changes in the distribution of bison, elk, and cattle will generate further public debate and perhaps legal action. The GYA situation illustrates the tremendous difficulty in managing wild free ranging ungulates affected by a significant disease on a large landscape where human livelihoods are at risk.

5.2.2 Grand Teton National Park/National Elk Refuge (Jackson herd)

The Jackson herd of approximately 1,100 animals resides in the southern end of the GYA (USFWS and NPS 2007), migrating between Grand Teton National Park (GTNP) in the summer and the adjacent National Elk Refuge (NER) in the winter (Cheville *et al.* 1998). As with the YNP herd, the Jackson herd is chronically infected with brucellosis. Williams *et al.* (1993) reported sero-prevalence of 77% and infection prevalence of 36% for the herd. Serology tests over the past five years indicate a sero-prevalence of 80% (S. Cain, personal communication). A reduction of 8% in fecundity has been estimated, however, the population has been increasing since the 1970s despite the disease (S. Cain, personal communication, Chapter 6; USFWS-NPS 2007).

The Jackson herd was founded in 1948 with the reintroduction of 20 bison from YNP to a 1,500-acre display pen. These bison were confined until 1963 when brucellosis was discovered in the herd (Cheville *et al.* 1998). All but four vaccinated yearlings and five vaccinated calves were destroyed. In 1964, Theodore Roosevelt National Park (TRNP) provided 12 brucellosis-free bison to augment the Jackson herd (Cheville *et al.* 1998). In 1968, the herd escaped from the progressively deteriorating enclosure facility (Cheville *et al.* 1998; Williams *et al.* 1993). From that point the park allowed the herd to roam freely. The bison herd discovered the feed ground at the NER in 1980. Although the herd was apparently healthy when released, it is suspected that infected elk on the NER introduced brucellosis to the Jackson bison (Cheville *et al.* 1998).

Similar to the YNP herd, the free-ranging nature of the Jackson herd allows for the possibility of transmitting brucellosis to domestic livestock in the area, although since the NER excludes cattle, there is limited contact between Jackson bison and cattle during the winter feeding period (Cheville *et al.* 1998). There is potential for contact, however, when bison move among private, USFS, GTNP and NER jurisdictions, especially in summer, when cattle are maintained on grazing allotments in GTNP, private ranchlands, and adjacent USFS lands (Cheville *et al.* 1998; Keiter 1997).

A new bison and elk management plan for the NER and GTNP was approved in April 2007. An earlier bison management plan approved in 1996, after undergoing a National Environmental Policy Act (NEPA) process, was subject to litigation by an animal rights group that questioned the inclusion of a sport hunt to manage population levels and the exclusion of an analysis of elk management on the federal lands in the decision process (Cain, personal communication; USFWS-NPS 2001). The court ruled that destruction of bison for population control could not be conducted until the involved agencies analysed the effects of winter feeding on bison and elk through an additional NEPA process (USFWS-NPS 2001). The feeding grounds attract 90% of the Jackson bison and 6,000-8,000 elk to one small area, creating zones of high animal density, where transmission may be enhanced among and between elk and bison (Bienen 2002; USFWS-NPS 2007). GTNP and the NER determined that a combined elk and bison management plan is needed to address the interconnected issues of the two species, including winter feeding and disease management. The Jackson bison

and elk herds migrate across several jurisdictions including the NER, GTNP, YNP, Bridger-Teton National Forest, Bureau of Land Management, State of Wyoming, and private lands. The NPS and FWS coordinated the extensive involvement of the associated agencies, organisations, and private interests affected by this new management plan and Environmental Impact Statement (EIS). The U.S. Department of Interior (USDOI) published a record of decision in April 2007, selecting a management alternative that emphasises adaptive management of elk and bison populations while reducing their dependence upon feed grounds. The plan also calls for a brucellosis vaccination programme for elk and bison conducted by the State of Wyoming. Recent hunting programmes, modification of feeding programmes and disease management have reduced the number of bison to 700 animals and the long-term management of this herd is now prescribed in a long-term plan. Several legal challenges were mounted and the implementation of the plan remains controversial.

5.3 An Occurrence of Reportable Diseases in Wood Bison

Wood bison herds in and around WBNP, including SRL, are infected with BTB and brucellosis (Gates *et al.* 1992; Gates *et al.* 2001c). These diseased herds account for about 50% of the total wood bison conservation population. Joly and Messier (2001a) reported the sero-prevalence of the diseases to be 31% for brucellosis and 49% for tuberculosis. With the exception of free-ranging bison in the WBNP and GYA, aggressive eradication programmes in both the U.S. and Canada have reduced the probability of brucellosis and BTB in domestic cattle and bison herds to extremely low levels. The wild diseased wood bison herds in and near WBNP are the only known reservoirs of BTB among all bison conservation herds (Gates *et al.* 2001c; Reynolds *et al.* 2003; Shaw and Meagher 2000).

BTB and brucellosis were likely introduced to wood bison populations with the transfer of plains bison from Wainwright Buffalo Park in the 1920s (Fuller 2002). In 1925, the Canadian government implemented a plan to move 6,673 plains bison from the overcrowded Wainwright Buffalo Park to WBNP. The transfer proceeded despite opposition from mammalogical and biological societies in the U.S. and Canada, who warned of transmission of BTB to the resident wood bison population (Anonymous 1925; Ogilvie 1979). BTB was first reported in WBNP in 1937 (Fuller 2002; Gates *et al.* 1992; Geist 1996). Although it is not known whether BTB was endemic among wood bison prior to the transfer (Reynolds *et al.* 1982), evidence indicates that the disease was introduced to wood bison with the transfer of plains bison (Fuller 1962). Brucellosis was also present in the plains bison herd and was reported in WBNP in 1956 (Gates *et al.* 1992).

The presence of BTB and brucellosis threatens the recovery of wood bison in several ways. First, the infected animals are subject to increased mortality, reduced fecundity, and increased vulnerability to predation (Gates *et al.* 1992; Joly and Messier 2001a). In 1934, the bison population in WBNP was estimated at 12,000 animals (Soper 1941). The population decreased from approximately 11,000 in 1970 to 2,151 in 1999 (Joly 2001). This decrease has been attributed to the interactive effects of diseases and predation (Carbyn *et al.* 1998; Fuller 1991; Joly and Messier 2001a). Recently, the WBNP population increased to 4,050, although the reasons for this increase are unclear (Bradley 2002, personal communication).

Second, the potential exists for the infected herds to transmit the diseases to healthy herds, most notably the Mackenzie, Nahanni, and Hay-Zama herds (Animal Plant and Food Risk Assessment Network (APFRAN 1999). Since 1987, the Government of the Northwest Territories has managed a 39,000 km^2 Bison Control Area south of the Mackenzie River to prevent movement of diseased bison into the MBS (Nishi 2002). Recent analysis and modelling of bison movements on the landscape have demonstrated considerable risk potential for transmission of diseases to healthy wood bison herds and bison ranches in the vicinity of the diseased herds (Gates *et al.* 2001a; Mitchell 2002). The Government of Alberta announced a new hunting season for the Hay Zama herd in 2008. The purpose of the hunt is to maintain the wood bison population at approximately 400 and limit distribution of these animals until the diseased bison issue, in and around WBNP, is successfully resolved. In particular the hunt will be used to control expansion of the Hay-Zama herd eastward, preventing contact with bison emigrating from WBNP that may be infected with brucellosis or BTB. Although preliminary, results of serological tests and post mortem examination of about 100 bison harvested from the Hay-Zama population in the winter of 2008 were negative for the two bovine diseases (D. Moyles, Alberta Sustainable Resource Development, personal communication).

Much research and debate has been focused on trying to resolve the diseased bison issue in northern Canada. In 1990, the Federal Environmental Assessment Panel released its report on its analysis of the disease issues (FEARO 1990). The panel concluded that eradication of the diseased wood bison populations is the only method for eliminating the risk of transmission of brucellosis and BTB from bison to domestic cattle, non-diseased wood bison, and humans. The panel further recommended that healthy wood bison be reintroduced to the area following depopulation of the diseased herds. Sources of healthy bison for reintroduction could include the EINP wood bison herd and other captive herds supplemented by disease-free animals salvaged from the Northern Bison herds (FEARO 1990). One such salvage operation, the Hook Lake Wood Bison Recovery Project in Fort Resolution, Northwest Territories, was

attempted (Nishi *et al.* 2002b), but failed. In 2006, after 10 years of isolation and rigorous disease testing, BTB-infected bison were detected in the herd.

Several constituencies rejected the FEARO (1990) panel's recommendation to depopulate WBNP herds. The Northern Buffalo Management Board (NBMB) was formed to develop a feasible eradication plan (Chisholm *et al.* 1998; Gates *et al.* 1992). The NBMB recommended further research into bison and disease ecology before planning management actions for the region (RAC 2001). In 1995, the Minister of Canadian Heritage formed the Bison Research and Containment Program (BRCP) to focus on disease containment and ecological and traditional knowledge research (RAC 2001). The Minister then created the Research Advisory Committee (RAC) to coordinate research activities under the BRCP (Chisholm *et al.* 1998). The RAC comprised a senior scientist appointed by Parks Canada, representatives from the Alberta and Northwest Territories governments, Canadian Parks and Wilderness Society, and four aboriginal communities (Chisholm *et al.* 1998). During the mandated five year period (1996-2001), the BRCP funded projects to assess the prevalence and effects of the diseases on northern bison (Joly and Messier 2001a), and to investigate bison movements and the risk of disease transfer (Gates *et al.* 2001a). The RAC produced a future research agenda and budget for minimum research still required under the BRCP mandate (RAC 2001), but the programme was discontinued in 2001. Many of the research needs identified by the RAC align with the recommendations outlined in the National Recovery Plan for Wood Bison prepared by the Wood Bison Recovery Team (Gates *et al.* 2001c). There remains considerable disagreement between federal and provincial governments and aboriginal interests concerning a long-term solution to the WBNP disease issue. Provincial governments support disease eradication, including aggressive intervention to achieve disease eradication within the national park. Parks Canada is concerned about the conservation and biological impacts associated with aggressive intervention. A technical workshop was convened in 2005 to explore the feasibility of removing diseased bison from the Greater Wood Buffalo National Park region followed by a reintroduction of healthy bison (Shury *et al.* 2006), and there was unanimous agreement amongst participants that this option was technically feasible. The only subsequent management action undertaken at the time of writing was the implementation of a hunting season for the Hay-Zama herd in 2008-2009, intended, in part, to test disease status and to reduce the risk of infection with BTB and brucellosis by reducing population size and limiting range expansion towards infected populations (George Hamilton, Alberta Sustainable Resource Development, personal communication).

5.4 Disease Management in Perspective

A primary consideration regarding disease management in wild populations is determining when a disease is a conservation problem and whether intervention is warranted (Gilmour and Munro 1991). It can be argued that parasitism by disease organisms is a crucial ecological and evolutionary force in natural systems (Aguirre *et al.* 1995; Wobeser 2002). Classification of a pathogen as indigenous or exotic to a host species or ecosystem can influence whether a disease should be managed (Aguirre and Starkey 1994; Aguirre *et al.* 1995; National Park Service 2000). BTB and brucellosis are believed to have been transmitted to bison from domestic cattle. Therefore, management of these diseases in bison is warranted based on their exotic origins, as well as the threat they pose to domestic animals. However, many other pathogens have coevolved with bison and do not warrant veterinary intervention and should be managed in accordance with a natural system.

The most significant diseases involving bison as wildlife affect a trinity of players (wildlife, humans, and domestic animals), and involve a tangle of transmission routes (Fischer 2008). Management of wildlife diseases has often been undertaken to minimise risks to humans and domestic animals (Nishi *et al.* 2002c; Wobeser 2002). Reportable disease management for agricultural purposes is typically based on the objective of eradicating the disease from a livestock population (Nishi *et al.* 2002c). The policy and legislative framework for eradicating reportable diseases in domestic animals is well developed, however, when applied to wildlife, the protocols used by agricultural agencies are usually not compatible with conservation goals (e.g., maintaining genetic diversity, minimal management intervention) (Nishi *et al.* 2002c). Increasingly, the broader conservation community is examining wildlife disease issues in the context of their impact on the viability of wild populations, conservation translocation programmes, and global biodiversity (Daszak and Cunningham 2000; Deem *et al.* 2001; Wobeser 2002). Creative disease-ecology research is needed, and an adaptive management framework is required for coping with diseases within a conservation context (Woodruff 1999). An evaluation of the disease management methods presently applied to bison populations is needed and could assist with development of novel conservation-appropriate policies and protocols for managing the health of free-ranging bison populations (Nishi *et al.* 2002c).

Two emerging policy concepts being discussed to manage and control the transmission or distribution of disease at the domestic/wild animal interface include regionalisation and compartmentalisation (CFIA 2002; OIE 2008). Regionalisation offers one means of spatially identifying where disease control measures will occur on the land while compartmentalisation separates the control programmes of wild and domestic animals.

These concepts are being developed and put into practice by state/provincial, federal, and international health agencies to address the complications of managing intractable disease problems in wild animals ranging on large landscapes that also sustain domestic livestock industries and associated local economies (Bengis *et al.* 2002).

National wildlife health strategies have recently been developed in Canada and the U.S. in response to the many difficult disease issues surrounding free-ranging wildlife. The development of national wildlife health programmes paralleled the increasing profile of wildlife health issues in social and political arenas. These national strategies need to provide clear guidance for coordinated conservation action and a countrywide legislative and policy framework that will influence bison restoration and conservation efforts in North America. It is hopeful that mounting tension between the agriculture, human, and wildlife health communities can be mitigated by developing a comprehensive national wildlife health policy, supportive scientific research programmes, broad stakeholder engagement in decision processes, a conservation-sensitive regulatory framework, and open social discussion about the disease risks from wildlife.

Chapter 6 General Biology, Ecology and Demographics

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6.1 General Biology

An understanding of the ecology and biology of bison is fundamental to their successful management, conservation, and restoration. Bison have the broadest original range of any indigenous ungulate species in North America, reflecting physiological, morphological, and behavioural adaptations that permit them to thrive in diverse ecosystems that provide their diet of grasses and sedges. Successful population management, conservation of genetic diversity and natural selection, modelling and predicting population level responses to human activities, and managing population structure all depend on understanding the biological characteristics and ecological roles of bison. The purpose of this chapter is to summarise what is currently known about the biology of bison; for an earlier comprehensive review, see Reynolds *et al.* (2003).

6.1.1 Physiology

6.1.1.1 Metabolism

Bison exhibit seasonal variation in energy metabolism. Christopherson *et al.* (1979) and Rutley and Hudson (2000) observed that metabolisable energy intake and requirements of yearling male bison were markedly lower in winter than summer. This was attributed to a reduction in activity and acclimation. Bison are better adapted to temperature extremes than most breeds of cattle. They expend less energy under extreme cold than do cattle because of the greater insulating capacity of their pelage (Peters and Slen 1964). Cold tolerance of hybrids between bison and cattle is intermediate between the two species (Smoliak and Peters 1955). Tolerance of bison to heat has not been studied, but the original continental range of the species included the dry, hot desert grasslands of northern Mexico, where a small population of plains bison still exists today (List *et al.* 2007).

6.1.1.2 Growth

Birth weights of intensively managed plains bison have been reported as 25 kg for females and 30 kg for males (Agabriel *et al.* 1998; Agabriel and Petit 1996; Rutley *et al.* 1997). Birth weights (near-term foetuses) of free-ranging plains bison range from 14 to 32 kg (McHugh 1958; Meagher 1986; Park 1969). Gogan *et al.* (2005) estimated that the birth weight of free-ranging bison calves is on average 10% less than that of captive bison. Growth from calfhood to adulthood followed a similar pattern to that of adults, with weight gain during the summer and loss during the winter (P.J. Gogan, unpublished data). Weight gain among calf and yearling plains bison was affected by the influence of the timing and magnitude of summer precipitation on graminoid physical structure (Craine *et al.* 2009).

Differences in weights of plains bison in geographically separate herds have been attributed to differences in climate, nutritional plane, and genetic lineages (Berger and Peacock 1988; Lott and Galland 1987). At Elk Island National Park (EINP), female plains and wood bison achieved asymptotic body weight by six years and maximum body weight at 10 years (Olson 2002; Reynolds *et al.* 2003). Female plains bison at Wind Cave National Park (WCNP) reached an asymptotic body and maximum body weight at five years (Figure 6.1). Male plains and wood bison at EINP reached an asymptotic body weight at eight to nine years and maximum body weight by 13 years (Reynolds *et al.* 2003). Male plains bison at WCNP continued to gain weight through the

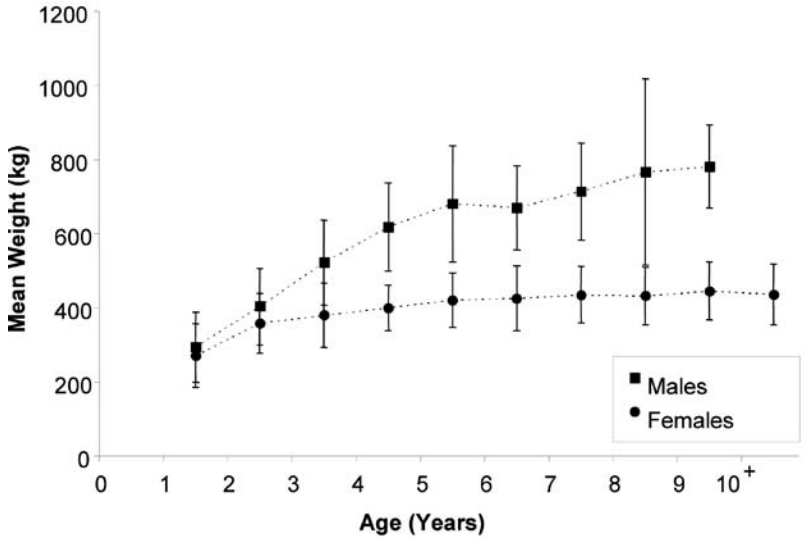


Figure 6.1 *Age-specific live-weights of male and female plains bison at Wind Cave National Park, South Dakota, obtained at fall roundups 1986–1989 and 1991–1999. Data courtesy D. Roddy and B. Meunchau, Wind Cave National Park.*

Plate 6.1 *Plains bison bull tending a cow, Jackson Valley, Wyoming. Photo: Cormack Gates.*

first eight years (Figure 6.1). While differences among populations in body size and weight may be apparent to an observer, comparisons must take in to account the annual cycle of weight gain and loss.

6.1.2 Behaviour

6.1.2.1 Social structure

There are many historical observations of huge plains bison herds roaming the Great Plains (Dary 1989; Hornaday 1889; Isenberg 2000; Roe 1970). Observers of both plains and wood bison consistently report a definable herd structure where cows, calves, and immature males form unstable mixed-sex and age groups, and large bulls form separate, smaller groups throughout much of the year (Allen 1876; Berger and Cunningham 1994; Komers *et al.* 1993; Meagher 1973; Melton *et al.* 1989; Schuler *et al.* 2006). Seasonal variations in group sizes are associated with abundance or dispersion of forage (Jarman 1974; Schuler 2006), landscape features (Berger and Cunningham 1994), breeding behaviour (Berger and Cunningham 1994; Meagher 1973; Melton *et al.* 1989; Komers *et al.* 1993) and population size (Schuler *et al.* 2006). The largest aggregations occur during the breeding season when mature bulls join the mixed-sex and age groups. Mean group sizes during the August rut at Badlands National Park range from a mean of 157 in flat terrain to 79 in broken terrain (Berger and Cunningham 1994). Mean maximum group sizes at Yellowstone National Park (YNP) increased from 140 in May to more than 250 in September (Hess 2002). Groups of more than 1,000 bison have been observed during the rut in contemporary Oklahoma (Schuler *et al.* 2006). Group size rapidly diminishes during autumn in plains bison (Hornaday 1889) to fewer than 30 (Berger and Cunningham 1994; Schuler *et al.* 2006). Similarly, in wood bison, typical group size is greatest during the pre-rut and rut, then declines during the fall (Komers *et al.* 1992). Mean maximum group sizes at YNP declined throughout winter from more than 250 in December to 16 in April as the area occupied by bison increased from 1,000 to more than 1,200 km^2 (Hess 2002).

Male bison form temporary, unstable groups, and exhibit a linear dominance hierarchy, with older, heavier animals dominant over younger smaller males (Komers *et al.* 1994; Roden *et al.* 2005). Dominance is also related to age in female bison (Rutberg 1983). Groups of adult or subadult males rarely exceed 10 individuals (Berger and Cunningham 1994).

Plains and wood bison population substructure occurs at a broad geographical scale due to traditional use of particular parts of a range by segments of a population (Joly and Messier 2001; Olexa and Gogan 2007). Plains bison within the Greater Yellowstone Area show strong fidelity to subpopulations (Christianson *et al.* 2005; Gogan *et al.* 2005; Olexa and Gogan 2007) as do wood bison in the Greater Wood Buffalo Ecosystem (GWBE) (Carbyn *et al.* 1998; 2004; Chen and Morley 2005; Joly and Messier 2004). Bison within subpopulations show stronger cohesion and coordinated movements during summer than in winter (Chen and Morley 2005; Olexa and Gogan 2007).

6.1.2.2 Reproductive behaviour

Sexually mature male plains bison join mixed-sex and age aggregations during the rut. Dominant bulls form so-called "tending bonds" with individual cows just prior to, or during, oestrus (Fuller 1960; McHugh 1958; Meagher 1973). The bull will typically attempt to keep other bulls away and to keep the cow near the edge of a mixed-sex and age group until she accepts copulation (Berger and Cunningham 1994; Lott 2002; McHugh 1958). Mature males move away from mixed-sex and age groups at the end of the rut (Berger and Cunningham 1994; Lott 2002).

Wood bison also aggregate during the summer (Joly and Messier 2001; Komers *et al.* 1992). Male wood bison become more solitary with increasing age, are more frequently aggressive, and test females for oestrus more frequently than do younger bulls (Komers *et al.* 1992). During the rut, mature males join mixed sex and groups to compete for mating opportunities and temporarily leave these groups to recover from high cost breeding activities (Komers *et al.* 1992). In the experimental absence of mature males during the rut, subadult males fed less and interacted more aggressively than when mature males were present (Komers *et al.* 1994).

6.1.2.3 Cow-calf behaviour

Female plains bison close to parturition have been described as restless and excitable (McHugh 1958). A pregnant cow may

leave the herd prior to calving or give birth within the herd (McHugh 1958). Similarly, for wood bison in the Mackenzie Bison Sanctuary (MBS), females have been observed calving in the midst of herds or in extreme isolation in the forest away from any other animals (N.C. Larter, personal observation). Birthing normally occurs while the female is lying down. The mother typically consumes portions of the afterbirth as she frees the calf from the membranes (Lott 2002; McHugh 1958). The female licks amniotic fluid from the calf's fur (Lott 2002). Suckling begins shortly after birth and may last as long as 10 minutes (McHugh 1958); although there was a report of a wood bison mother attacking the newborn calf during suckling (Carbyn and Trottier 1987). The close contact between a cow and calf begins to decline after the calf's first week of life (Green 1992). A calf is typically weaned by seven to eight months of age, although nursing may extend beyond 12 months (Green *et al.* 1993). The longest associations among bison are between cows and their female offspring; while male offspring may remain with the cow through a second summer, female offspring may remain with the cow through a third summer (Green *et al.* 1989; Shaw and Carter 1988).

The cow may use quick charges or steady advances to defend a calf against threats (Garretson 1938; Hornaday 1889; McHugh 1958). An isolated plains bison cow vigorously defended her calf from a grizzly bear (*Ursus arctos*), even though the bear was ultimately successful in killing the calf (Varley and Gunther 2002). Similarly, an isolated cow vigorously defended the calf from wolves (*Canis lupus*) (C. Freese, personal communication).

Cows and other members of mixed-sex and age groups may cooperatively protect calves from predators. In response to the approach of a grizzly bear, a mixed-sex and age group of adult plains bison responded by facing the bear in a compact group, with the calves running behind the adults (Gunther 1991). Wolves preferentially attempt to prey upon wood bison mixed-sex and age groups that include calves (Carbyn and Trottier 1987). During wolf attacks, calves moved close to the cow, or to other bison, or to the centre of the bison group (Carbyn and Trottier 1987; 1988), although this defensive response may break down when bison groups move through forested areas that may impede the movements of the calves (Carbyn and Trottier 1988).

6.1.2.4 Horning and wallowing

All age and sex classes of bison engage in behaviours referred to as horning and wallowing (McHugh 1958). Horning involves an animal rubbing an object, typically a shrub or small tree, with its head, horns, neck, or shoulders (Coppedge and Shaw 1997). Wallowing involves a bison rolling in dry loose ground (or less frequently in wet ground) and tearing at the earth with its horns and hooves as it rolls. Bison prefer to horn aromatic shrubs and saplings (Coppedge and Shaw 1997; Edwards 1978; McHugh 1958; Meagher 1973), which may have insect deterrent properties. Bison have even been observed rubbing on treated telephone posts (Coppedge and Shaw 1997). Soper (1941) observed that horning and rubbing were often associated with harassment by insects. Like wallowing, horning may also constitute aggressive display behaviour.

Bison of both sexes and all age classes engage in wallowing behaviour throughout the year (Reynolds *et al.* 2003), although sexually mature males wallow more frequently during the rut, urinating in the wallow before pawing and rolling (Lott 2002; McHugh 1958). Wallowing by mature males may stimulate oestrus in females (Bowyer *et al.* 1998), and advertise a male's physical condition to other males (Lott 2002). Plains bison may also wallow to cool themselves during the hot summer months, or to achieve relief from biting insects (McMillan *et al.* 2000; Mooring and Samuel 1998). Catlin (in Hornaday 1889) described bison creating wallows in areas with a high water table and rolling in the wallow as it filled with water. The result was pelage matted with mud and clay (Catlin in Hornaday 1889). Coat shedding, rut, and insect harassment occur simultaneously during the summer; therefore in the absence of controlled experimentation, it is not possible to determine the relative influence of these factors on the frequency of horning and wallowing (Coppedge and Shaw 1997).

6.1.2.5 Movements

Plains bison frequently travel in single file along well-established trails when moving between foraging patches (Garretson 1938; Hornaday 1889). Historically, plains bison undertook

Plate 6.2 *Wallowing modifies the landscape. Photos: Dwight Lutesy (inset) and John Gross.*

extensive seasonal north-south movements from summer to winter ranges (Seton 1929) on both sides of the Mississippi River (Garretson 1938; Roe 1970) and from the prairies into the Parkland (Campbell *et al.* 1994). Large herds also remained on the northern prairies throughout winter (Malainey and Sherriff 1996). River valleys were crucial to the survival of bison over-wintering on the grasslands (West 1995). Plains bison also undertook seasonal east-west movements from the prairies to the foothills of the Rocky Mountains in winter (Garretson 1938). Inferences from historical reports of seasonal movement patterns are confounded by the timing of the account relative to the impacts of market hunting, establishment of pioneer trails, and construction of the railroads (Roe 1970). In summer, bison on the Great Plains moved to water on an almost daily basis, and on occasion moved from 80 to 160 kilometres over several days to access water (Dary 1989).

Plains bison currently occupying the YNP spend summer at higher elevations and move to winter ranges at lower elevations (Aune *et al.* 1988; Gates *et al.* 2005; Meagher 1973; Olexa and Gogan 2007). These movements are made over a network of trails, geothermal features, and along the banks of rivers and streams, or along groomed roadways aligned with natural travel routes (Bjornlie and Garrott 2001). Adult males are often the first to pioneer previously unoccupied areas, a behaviour that has been observed in both wood bison and plains bison (Gates *et al.* 2005). Yellowstone bison have expanded their range in response to increased population densities (Taper *et al.* 2000) exacerbated by particularly severe winters (Meagher 1989).

Wood bison at Wood Buffalo National Park (WBNP) annually travel up to 50 kilometres maximum from a centre of activity (Chen and Morley 2005), and individual wood bison at the MBS range over areas of 179 to 1,442 km^2 (Larter and Gates 1990). Wood bison have slowly been expanding their range in the northern boreal forest. Range expansion is generally initiated by large males who then seasonally return from the peripheries of the range to join females and juveniles during the rut (Gates and Larter 1990; N. Larter and J. Nishi unpublished data). Subsequently, mixed-sex and groups move into the expanded peripheral range. Range expansion typically follows periodic high local population densities (Gates and Larter 1990) and is density-driven (Gates *et al.* 2005).

6.2 Ecology

6.2.1 Plains bison

6.2.1.1 Ecological role

Millions of plains bison historically ranged over North America's grasslands and functioned as a keystone species (Knapp *et al.* 1999). They shared this landscape with a variety of other large mammals including pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), deer (*Odocoileus* spp.), wolves, and grizzly bears. At the landscape level, bison served as ecosystem engineers, both responding to, and creating, heterogeneity. An estimated 100 million bison wallows had a major effect on surface hydrology and runoff (Butler 2006). Ephemeral pools of standing water that persisted in wallows for many days following spring snow melt or rainstorms (Knapp *et al.* 1999) supported a variety of wetland plant species (Collins and Uno 1983; Polley and Wallace 1986). Similarly, bison wallows provided important breeding habitat for the Great Plains toad (*Bufo cognatus*; Bragg 1940) and the plains spadefoot toad (*Spea bombifrons*; Corn and Peterson 1996). Bison directly affect vegetation communities through their grazing, physical disturbance, and by stimulating nutrient recycling and seed dispersal (McHugh 1958). Such activities help to maintain meadows and grasslands on which they, and many other animal and plant species, depend.

In tallgrass prairie, bison grazing of grasses increased soil temperature, light availability, and soil moisture availability to forb species (Fahnestock and Knapp 1993). The net result was beneficial to forbs not eaten by bison (Damhoureyeh and Hartnett 1997; Fahnestock and Knapp 1993), and may thereby have been beneficial for other herbivores such as pronghorn. Bison grazing of short and mixed-grass prairie vegetation increased the rates of nutrient cycling (Day and Detling 1990), modified plant species composition (Coppock and Detling 1986) and increased the nutritive value of grasses (Coppock *et al.* 1983a; 1983b; Krueger 1986). Locally, bison consumed forage resources (England and DeVos 1969; Hornaday 1889) and reduced forage height to levels that facilitate colonisation by prairie dogs (*Cynomys* spp.; Virchow and Hygnstrom 2002). In turn, prairie dog activities enhanced the ratio of plant live: dead material, crude protein content, and digestibility (Coppock *et al.*1983a; 1983b) and thereby encouraged further grazing by bison over more than 20% of the natural short and mixed grass prairie (Whicker and Detling 1988). While bison grazing was independent of pocket gopher (Geomyidae) activities, it influenced gopher distribution by modifying the distribution and abundance of patches of forbs used by gophers (Steuter *et al.* 1995).

Bison grazing, frequently in conjunction with fire and wallowing, enhanced the grassland heterogeneity necessary to provide suitable nesting sites for a variety of obligate grassland nesting bird species (Knapp *et al.* 1999). Bison grazing, particularly on recently burned areas, enhances the abundance of breeding bird species, such as upland sandpipers (*Bartramia longicauda*) and grasshopper sparrows (*Ammodramus savannarum*), in tallgrass prairie (Fuhlendorf *et al.* 2009; Powell 2006). Similarly, a number of bird species endemic to the short and mixed grass prairies of North America, such as the mountain plover (*Charadrius montanus*) and McCown's Longspur (*Calcarius mccownii*), were

historically dependent on a combination of bison wallows and prairie dog colonies for nesting sites. These areas were also utilised by ferruginous hawks (*Buteo regalis*) and long-billed curlew (*Numenius americanus*) (Knopf 1996). Brown-headed cowbirds (*Molothrus ater*), also called buffalo birds, occurred in association with bison throughout central North American grasslands prior to the introduction of livestock (Friedman 1929). Cowbirds feed on insects moving in response to foraging bison (Goguen and Mathews 1999; Webster 2005). Grasshopper species richness, composition, and abundance are strongly influenced by interactions between bison grazing and fire frequency (Joern 2005; Jonas and Joern 2007).

Bison facilitated dispersal of the seeds of many plant taxa as a result of the seeds becoming temporarily attached to the bison's hair (Berthoud 1892; Rosas *et al.* 2008) or via passage through the digestive tract (Gokbulak 2002). Peak passage rate for seeds was 2 days following ingestion (Gokbulak 2002).

Horning damage to trees along grassland borders is effective in slowing invasion of trees into shrub and grassland plant communities or in extending the existing grassland into the forest margin. Bison within YNP rubbed and horned lodgepole pine (*Pinus contorta*) trees around the periphery of open grasslands to the extent that some were completely girdled (Meagher 1973). Similarly horning by wood bison in the MBS has resulted in completely girdled white spruce stands on the periphery of mesic sedge meadows and willow savannas (N.C. Larter, personal observation). Several authors (Campbell *et al.* 1994; Coppedge and Shaw 1997; Edwards 1978) have suggested that bison, in combination with other factors such as fire and drought, significantly limited the historic distribution of woody vegetation on the Great Plains.

A decomposing bison carcass initially kills the underlying plants, but subsequently provides a pulse of nutrients, creating a disturbed area of limited competition with abundant resources that enhances plant community heterogeneity (Towne 2000). Carrion from dead bison is an important food resource for both grizzly and black bears (*Ursus americana*) as well as scavenging birds such as bald eagles (*Haliaeetus leucocephalus*), ravens (*Corvus corax*), and black-billed magpies (*Pica pica*).

6.2.1.2 Contemporary habitat use, nutrition, and foraging

The bison is a ruminant with a four-chambered stomach and associations of symbiotic microorganisms that assist digestion of fibrous forage. On lower quality forage, such as grasses and sedges, bison achieve greater digestive efficiencies than domestic cattle, but on high quality forages such as alfalfa, the digestive efficiency of bison and cattle converge (Reynolds *et al.* 2003). Contemporary studies of plains bison habitat selection in North American grasslands are limited to confined herds artificially maintained at varying densities (Table 6.1)—some of which may differ markedly from pristine conditions (Fahnestock and Detling 2002).

Herbivores, including bison, respond to gradients in forage quality and quantity. Hornaday (1889) described a highly nomadic foraging strategy, where plains bison seemed to wander somewhat aimlessly until they located a patch with favourable grazing. A bison herd would then remain and graze until the need for water motivated further movement. This account contrasts with more recent studies of bison foraging, which have found that plains bison actively select more nutritious forages, and forage in a highly efficient manner that satisfies their nutritional needs and compliments diet selection by sympatric herbivores (Coppock *et al.* 1983a; 1983b; Hudson and Frank 1987; Singer and Norland 1994; Wallace *et al.* 1995). Spatial variation in forage quality and quantity results from natural gradients in soil moisture, soil nutrients, fire, and other disturbance, as well as from the impacts of foraging by bison. Bison exploit variations in forage quality and quantity at all scales; from selecting small patches of highly nutritious forages on prairie dog towns, to undertaking long-distance migration in response to seasonal snowfall or drought.

The following review of bison habitat interactions is based upon North American ecoregions identified by Ricketts *et al.* (1999) and aggregated by Sanderson *et al.* (2008).

Plate 6.3 *Plains bison bull cratering in snow to forage. Photo: Yellowstone National Park.*

Table 6.1 *Diets of plains bison at select locations within North American ecoregions.*

Ecoregion	Location	Season	Plant Type					Reference
			Grasses (%)	Sedges (%)	Forbs (%)	Woody Plants (%)	Others (%)	
Northern Mixed Grasslands	Wind Cave NP, SD	Spring	81	7	9	3		Marlow *et al.* 1984
		Summer	79	9	10	2		Westfall *et al.* 1993
		Autumn	77	12	6	5		
		Winter	79	12	2	7		
		Winter	59	37	4			Wydevan and Dahlgren 1985
Central Shortgrass Prairie	Pawnee Site, CO Lightly grazed	Spring	98		2			Peden *et al.* 1974
		Summer	94		5			
		Autumn	99					
		Winter	94		4			
	Heavily grazed	Spring	95		4			Peden *et al.* 1974
		Summer	96		4			
		Autumn	87		2	12		
		Winter	81		6	11		
Tall Grasslands Prairie and Southern Shortgrass Prairie	Wichita Mountains NWR, OK	Spring & Summer	99					Buechner 1950
	Tallgrass Prairie Preserve, OK	Spring	60	39	1			Coppedge *et al.* 1998
		Summer	88	11	1			
		Autumn	84	16	1			
		Winter	79	21	1			
Northern Fescue Grasslands	National Bison Range, MT	Annual	90	1	2	1		McCullough 1980
Rocky Mountain Forests	Yellowstone Northern Range,WY	Winter	53	44[1]	1	1		Singer and Norland 1994
	Yellowstone Central Range, WY	Summer	55	37		<0.1		Olenicki and Irby 2004
Northern Forests	Elk Island NP, AB	Spring	29	65	6			Telfer and Cairns 1979
		Winter	18	82				
	Prince Albert NP, SK	Spring	35	65				Fortin *et al.* 2002
		Summer	26	73			1	
		Autumn	17	63			20	
		Winter	34	59			7	

[1] Includes rushes (Juncaceae)

6.2.1.2.1 Northern mixed grasslands

In the absence of fire, bison have been observed making extensive use of prairie dog colonies in the northern mixed grasslands ecoregion, where colonies may have covered 2-15% of the short grasslands (Knowles *et al.* 2002; Virchow and Hygnstrom 2002). Bison utilise the forb-dominated centres of prairie dog colonies for resting and wallowing, but feed at the graminoid-dominated periphery of colonies rather than at the colony centre (Coppock and Detling 1986; Krueger 1986). Bison use of prairie dog towns peaks during the summer and declines in the autumn (Krueger 1986) when the available forage biomass is low or the vegetation is senescent (Coppock *et al.* 1983a; 1983b). Bison use of colony sites also declines when recently burned grasslands are available (Coppock and Detling 1986).

Grasses and sedges were almost 90% of the year-round bison diet, and sedges formed 7 to 37% of the seasonal diet in the northern mixed grassland ecoregion (Table 6.1). Bison selected foraging sites containing more than 75% warm season (C4) grasses during the summer growing season (Steuter *et al.* 1995). C4 grasses were approximately 33% of the diet in June, and a maximum of 40% of the bison diet in late summer, but C4 grasses were less in the bison diet in autumn, winter, and spring (Plumb and Dodd 1993). Conversely, cool season grasses formed approximately 50% of the summer diet, but increased to 80% of the diet in September (Plumb and Dodd 1993).

6.2.1.2.2 Central shortgrass prairie

In a lightly grazed site, bison almost exclusively consumed grasses, but consumed more than 10% woody plants in the autumn and winter at a heavily grazed central shortgrass prairie site shared with cattle and sheep (Table 6.1). Three C4 grasses accounted for 65 to 75% of the bison diet (Peden *et al.* 1974; Schwartz and Nagy 1976).

6.2.1.2.3 Tall grasslands prairie and southern shortgrass prairie

Bison in the tall grasslands prairie and southern shortgrass prairie ecoregions utilised only recently burned areas in spring, but selected areas burned annually throughout the year (Shaw and Carter 1990; Vinton *et al.* 1993). Bison grazing and regrazing can maintain areas with a low vegetative cover and standing crop (Coppedge and Shaw 1998; Vinton *et al.* 1993). Areas grazed by bison were characterised by a lower abundance of C4 grasses, a higher abundance of C3 grasses, and greater overall plant species diversity (Hartnett *et al.* 1996). These characteristics were more pronounced in areas burned annually (Hartnett *et al.* 1996), which is consistent with greater bison use of annually burned sites (Shaw and Carter 1990; Vinton *et al.* 1993). Bison grazed little bluestem (*Schizachyrium scoparium*) more frequently post-burning, probably in response to removal of standing dead tillers by fire (Pfieffer and Hartnett 1995). The greater overall plant species diversity in burned areas was linked to increased nitrogen cycling and availability (Bakker *et al.* 2003; Johnson and Matchett 2001).

C3 grasses were the most common dietary item in winter (Coppedge *et al.* 1998). Dietary quality, as measured by faecal nitrogen, peaked in May and June, coincident with a peak in C3 grasses productivity (Post *et al.* 2001). Up to 39% of the spring diet was sedges (Coppedge *et al.* 1998).

6.2.1.2.4 Northern fescue grasslands

Understanding contemporary trophic ecology of bison in this ecoregion is confounded somewhat by a management-imposed rotational grazing, by which bison are moved throughout the National Bison Range (NBR) National Wildlife Refuge, Montana (McCullough 1980). When occupying lower elevation areas of the NBR, bison utilised level to undulating open grasslands. Once herded to higher elevation portions of the range, bison continued to utilise the more level open areas available (McCullough 1980). The year-round distribution of bison was away from higher elevation steep-slope areas. Bison showed no selection for aspect, as they tended to use the more level areas available throughout the year. Bison fed almost exclusively on grasses (Table 6.1; McCullough 1980).

6.2.1.2.5 Rocky Mountain forest

In the high topographical relief of the Rocky Mountains the heterogeneity of herbaceous productivity and standing crop is caused by the spatial distribution of moisture on the landscape. Herbaceous above ground net primary productivity (ANPP) is influenced by site-specific topographic position relative to moisture distribution and aspect (Burroughs *et al.* 2001). Herbaceous ANPP is lower at low elevations with less precipitation and at the highest elevations due to a shorter growing season attributable to lower temperatures than at mid-elevations (Coughenour 2005). In general, herbaceous ANPP occurs as a pulse of nitrogen rich vegetation that sequentially follows an elevational gradient from the lower elevation winter ranges to the higher elevation summer ranges. This pattern of ANPP makes young nutritious and concentrated forage available to bison for up to six months of each year (Frank and McNaughton 1992). Summer movements of bison to higher elevation areas reduces vegetation utilisation at lower elevations and thereby enhances the availability of vegetation at lower elevations during the non-growing season (Frank and McNaughton 1992).

Bison on Yellowstone's northern range forage on sedges within more mesic sites in winter (Meagher 1973) to the extent that the winter diet is more than 95% grasses, sedges, and rushes (Table 6.1; Singer and Norland 1994). Similarly, bison utilising the Yellowstone central range during winter primarily feed on sedges along the edges of thermally influenced drainages and

at other thermal features (Meagher 1973). Upland sagebrush-bunchgrass sites are utilised to a lesser extent in winter (Meagher 1973). The summer diet of Yellowstone bison utilising the Hayden Valley was more than 90% graminoids, with one-half of these being mesic grasses, sedges, and rushes (Olenicki and Irby 2004).

6.2.1.2.6 Northern forests

Bison at EINP are highly selective for upland grasslands year-round, and to a lesser extent, select sedge meadows in winter, and shrubland and aspen forest in spring and summer (Cairns and Telfer 1980; Telfer and Cairns 1979). The bison's year-round diet was virtually exclusively herbaceous vegetation with approximately 80% of the winter diet and 65% of the summer diet sedges (*Carex* spp.; Table 6.1; Telfer and Cairns 1979).

Plains bison foraging at Prince Albert National Park (PANP) selected the sedge *Carex atherodes*, and consumed more sedges than grasses year-round (Table 6.1; Fortin *et al.* 2002). The foraging strategy favoured short-term energy gain over long-term gain for most of the year (Fortin *et al.* 2002). However, bison also selected *Carex* in spring, when a diet of more digestible grasses would have enhanced short-term energy gain (Fortin *et al.* 2002). Bison may avoid shifts in diet to facilitate maintaining a consistent microbial rumen flora (Fortin *et al.* 2002).

6.2.1.2.7 Arctic lowland taiga

Introduced plains bison at Delta Junction, Alaska, feed on sedges and fescue grasses in winter (Campbell and Hinkes 1983). In contrast, plains bison introduced to the vicinity of Farewell, Alaska, feed on willows (*Salix* spp.) almost exclusively in summer, and a mixture of willow and shrubs in the autumn (Waggoner and Hinkes 1986). Some potential exists for competition with moose (*Alces alces*) for willow in riparian, alluvial areas, although the two species select shrubs of different sizes (Waggoner and Hinkes 1986). The drastic differences between the diet of plains bison at Delta Junction and those at Farewell are directly related to forage availability. The Farewell area is almost exclusively riparian willow growth with little in the way of graminoids due to a dominant very rocky braided river substrate. In contrast, the Delta Junction area is characterised by extensive stands of grasses and sedges and domesticated grains. These differences underscore the importance of forage availability in influencing bison diets.

6.2.1.3 Habitat and dietary overlap

Originally, plains bison associated with pronghorn (Allen 1967; Yoakum 2004), elk (Miller 2002) and mule deer (*Odocoileus hemionus*) throughout much of their range, and with moose (Boer 1997) along the northern and high elevation range limits. Of the sympatric species, the seasonal distributions of pronghorn and plains bison were most similar, but their diets were most divergent (Schwartz and Nagy 1976; McCullough 1980; Marlow *et al.* 1984; Wydevan and Dahlgren 1985; Singer and Norland 1994). Although these two species tend to have little dietary overlap, some competition for total biomass may occur (Lovaas and Bromley 1972). Similarly, sympatric plains bison and mule deer may overlap in habitat selection in winter (Cairns and Telfer 1980), but their diets differ (McCullough 1980; Wydeven and Dahlgren 1985; Singer and Norland 1994).

Plains bison and elk exhibit extensive range overlap in winter (Cairns and Telfer 1980; Barmore 2003), but less in spring and summer (Cairns and Telfer 1980). The diets of both species are predominantly graminoids from autumn through spring, with bison favouring sedges and elk favouring grasses (Barmore 2003; Singer and Norland 1994). Dietary overlap with grasses continues into the summer (McCullough 1980; Telfer and Cairns 1979), although the bison's diet contains more grass and less forbs and woody plants than that of elk (Marlow *et al.* 1984; Wydeven and Dahlgren 1985).

Plains bison and domestic cattle diets were most similar for grass consumption during the autumn and winter at a lightly grazed short grassland site, and during the spring at a nearby heavily grazed site (Peden *et al.* 1974). Bison and cattle summer and autumn diets in a shrub-steppe region were almost exclusively grasses (Van Vuren 1984; Van Vuren and Bray 1983). The diets of bison and domestic sheep were most similar during autumn at a lightly grazed short grassland site (Peden *et al.* 1974).

6.2.2 Wood bison

6.2.2.1 Original distribution and ecoregions occupied

Zooarchaeological evidence, combined with documentary records and oral narratives of aboriginal peoples in Alaska, Yukon, and Northwest Territories, indicate that the original range of wood bison included northern Alberta, north-eastern British Columbia east of the Cordillera, the Northwest Territories south and west of Great Slave Lake, the Mackenzie River Valley, and large areas of interior Alaska (Gates *et al.* 1992; Lotenberg 1996; Stephenson *et al.* 2001; van Zyll de Jong 1986). The original distribution of wood bison in northern Alberta and southern Northwest Territories centred on the Interior Plains Physiographic Region, where they ranged over the interconnected and overlapping glacial lake basins and major river valleys, where soil conditions are conducive to development of sedge-grass meadow plant communities (Gates *et al.* 1992). The total range of wood bison was more restricted than that of plains bison. Contemporary wood bison herds in the boreal regions exist in comparatively natural systems. They remain part of a fairly diverse, large ungulate fauna, which represents the prey base for several predators. Wood bison distribution overlaps with that of moose, elk, boreal and northern mountain ecotypes of

woodland caribou (*Rangifer tarandus caribou*), white-tailed deer (*Odocoileus virginianus*), mule deer and possibly stone sheep (*Ovis dalli*). Similarly, wood bison are exposed to the full suite of predators including wolf, grizzly, black bear, wolverine (*Gulo gulo*), cougar (*Felis concolor*), lynx (*Felis lynx*), and coyote (*Canis latrans*). Wolf predation is an especially important mortality factor for northern bison (Carbyn *et al.* 1993; Larter *et al.* 1994; Van Camp 1987). Furthermore, wood bison movements are generally not impeded by fences or other land uses.

6.2.2.2 Contemporary habitat relationships, nutrition, and foraging

Wood bison of the Nahanni population in the south-west Northwest Territories must cross the Liard River as it bisects the bison range for its entirety. Animals of both sexes and all age classes frequently make river crossings (Larter *et al.* 2003) making them susceptible to group mortality during spring ice breakup and rapid snowmelt. Bison use of sedges associated with wet meadows and lakes in winter also makes them susceptible to mass mortality when groups fall through weak ice. A total of 177 animals drowned in the MBS after breaking through the spring ice of Falaise Lake (Gates *et al.* 1991). Abnormally high January 2009 temperatures (+12° C) affected ice conditions which likely caused the drowning of up to 13 animals of the Nahanni wood bison population (N.C. Larter, unpublished data). Spring flooding, notably at WBNP, has caused thousands of bison deaths (Fuller 1962).

Fire, especially in the northern boreal region may improve foraging habitat for bison and, in some areas of the Northwest Territories, prescribed burning has been used as a management tool for habitat enhancement (Chowns *et al.* 1997). However, fire may play less of a role in maintaining lowland meadows than sporadic flooding (Quinlan *et al.* 2003).

6.2.2.2.1 Northern forests

Bison at WBNP and Slave River Lowlands (SRL) utilised mixed woodlands and aspen and poplar stands interspersed with meadows in summer, and upland meadows, lowland floodplains, and delta marshes in winter (Soper 1941). They feed primarily on graminoids (Table 6.2) with two genera, slough sedge (*Carex atherodes*) and reedgrass (*Calamagrostis* spp.), making up most of the annual diet (Reynolds *et al.* 1978). Willows were 8% of the summer diet (Reynolds *et al.* 1978). Bison selectively graze stands of slough sedge characterised by a biomass level that would probably minimise daily foraging time (Bergman *et al.* 2001).

6.2.2.2.2 Subarctic boreal forests

Bison exhibit sex-specific differences in habitat selection with females found in mesic sedge meadows 55% of the time in winter (compared to males, 38%) and willow savannas 77% of the time in summer (compared to males, 48%), even though these two plant communities combined constitute only about 5% of the area (Larter and Gates 1991; Matthews 1991). Both sexes utilised the most abundant coniferous forest in proportion to its availability during autumn (Larter and Gates 1991). Bison frequent areas where frozen lakes, ponds, oxbow lakes, and disturbed sites provide winter access to forage. The bison diet varied seasonally from a more diverse combination of graminoids and woody plants or forbs in summer to approximately one-third lichens and one-third grasses in autumn, to almost exclusively graminoids in winter (Table 6.2). Such feeding patterns were consistent with selection for plants with relatively high available nitrogen (Larter and Gates 1991) and to enhance short-term energy consumption (Fortin *et al.* 2002). This feeding pattern may also be attributed to dedicating time to avoid insect harassment, scanning for predators, maintaining thermal balance, or social interactions (Bergman *et al.* 2001).

In the Nahanni population of south-west Northwest Territories, bison utilise horsetails (*Equisetum*) in summer (Larter and Allaire 2007), a forage that is high in nitrogen, but also high in silica. The high silica causes rapid tooth wear, resulting in teeth wearing out 10 years earlier than in other areas.

6.2.2.3 Habitat and dietary overlap

There is little dietary overlap between wood bison and the various ungulate species that share its range. Competition with moose may occur in the Northwest Territories, where the bison's diet has a high browse component. Bison and boreal caribou in Northwest Territories/Yukon Territory both eat lichens, although during different seasons. Caribou use lichen as a diet staple in winter, whereas bison use of lichen is in autumn, when they disperse into the more forested habitats (Larter and Gates 1991). Fischer and Gates (2005) concluded that food competition between caribou and bison was low in winter.

6.3 Demographics

The abundance of the free-ranging populations of plains and wood bison, so iconic for North America, likely fluctuated considerably by location and through time. These fluctuations were probably driven by a sequence of density-dependent population regulatory factors (Eberhardt 1977; 2002; Fowler 1981; 1987; Gaillard *et al.* 1998); reduced survival of subadults, delayed age of first reproduction, decline in the reproductive rate, and increased adult mortality. This sequence was undoubtedly set back by density independent events such as episodic droughts and severe winters. Droughts and dry seasons in general were characterised by wildfires, which, on occasion, killed bison (Dary 1989; Isenberg 2000). Winters with deep snow and warming periods, resulting in ice crusting on top of

Table 6.2 *Diets of wood bison at select locations within North American ecoregions.*

Ecoregion	Location	Season	Plant Type					Reference
			Grasses (%)	Sedges[1] (%)	Forbs (%)	Woody Plants (%)	Others (%)	
Northern Forests	Wood Buffalo NP and Slave Lake, NWT and AB	Spring	16	81	1	2		Reynolds et al. 1978, Reynolds. 1976 *in* Reynolds and Peden 1987
		Summer	24	59	8	8		
		Autumn	21	71	4	2		
		Winter	36	63		1		
Subarctic Boreal Forests	MacKenzie Bison Sanctuary, NWT	Spring	6	68	1	26		Larter and Gates 1991
		Summer	11	53	2	28	6[2]	
		Autumn	32	15	4	12	37[2]	
		Winter	2	96		2		
	Nahanni Population, NWT	Summer	6	37	29	14	1[3]	Larter and Allaire 2007; Larter, N.C. unpublished data
		Autumn	19	58	7	12	4[3]	
		Early Winter[4]	16	37	10	4	33[3]	
		Mid-Winter[4]	2	89	4	3	2[3]	

[1]Includes rushes (Juncaceae); [2]Lichens; [3]*Equisetum* spp.; [4]November/December is early winter, January/February is mid-winter

the snow, led to major die-offs of bison (Dary 1989). Thousands of bison were drowned in floods that resulted from the spring melting of large snow packs (Dary 1989).

Predation by wolves may have been a significant force, taking the most susceptible age and sex classes at different times of year. Wolves may have preyed heavily on bison calves (Flores 1991) and killed older solitary males (Dary 1989). However, predation may have had little effect on large nomadic or migratory herds of bison (Terborgh 2005). Wolves maintain group territories and bear altricial young, traits that would have made it impossible for wolf packs to sustain sufficient pressure on a wide-ranging, mobile prey (Terborgh 2005). Grizzly bears killed some bison, occasionally from ambush (Dary 1989).

Prior to the availability of firearms, the small number of resident humans, and their relatively ineffective hunting, limited the human toll on bison. Pedestrian harvesting was mostly non-selective and involved surrounding or driving of bison groups over bison jumps (Flores 1991). However, by the late 17th century, firearms-equipped tribes from the Great Lakes region began moving out on to the Great Plains. At the beginning of the 19th century, tribes with horses were beginning to exert pressure on plains bison and select for breeding age females (Flores 1991). At the same time inter-tribal warfare led to buffer zones that served as refugia for bison (Flores 1991; Martin and Szuter 1999). By mid-1800s, an estimated 500,000 plains bison were killed for subsistence, and an additional 100,000 were killed for their hides annually (Isenberg 2000). Bison populations began to decline as increasing numbers of cattle and horses began to compete with bison for forage and water (Flores 1991; Isenberg 2000).

6.3.1 Population structure

Both plains and wood bison can be classified into sex and age classes based on body size and horn morphology. Free-ranging calves are readily distinguishable from all other age classes based upon pelage colour for the first three months of life, but their sexes cannot be distinguished. Yearlings may be distinguished from adults until about one and a half years old, based upon body size and conformation, when examined at close range. Sex can be determined in animals more than two years old on the basis of horn morphology and head shape (Bradley and Wilmshurst 2005; Komers *et al.* 1993), or noting the presence or absence of a penile sheath, but again this requires viewing from close range (Carbyn *et al.* 1998). Komers *et al.* (1993) described criteria for distinguishing between subadult (two to four years old), mature, and old bulls based on body size and horn morphology. The results of composition counts are frequently standardised as a ratio of selected age and sex classes per 100 adult females (Caughley 1977). Typically, within polygynous species such as bison, adult females are the most abundant class in a population and directly determine the size of the youngest age class (McCullough 1994). The presence of new calves in a population is sensitive to the timing of the count relative to the calving

season: Wolfe and Kimball (1989) reported an increase in the percentage of calves from 10.2% in late May to 12.2% in late July (i.e., count too early and you may miss some).

Similarly, segregation of age and sex classes may influence estimates of population composition. Meagher (1973) reported that calves formed 20% of mixed age and mixed sex bison herds, but 11% of the total Yellowstone bison population. Other biases are also possible. Carbyn *et al.* (1998) reported an unweighted average of 36 calves per 100 adult females for bison in Delta Area of WBNP for 1989-1996 (Table 6.3), while others reported between 20 and 30 calves per 100 adult females for the same area and during the same time period (Bradley and Wilmshurst 2005). Similarly, Carbyn *et al.* (1998) reported an average of 20 yearlings per 100 adult females for this time period, while others reported more than 10 yearlings per 100 adult females for only one of those years (Bradley and Wilmshurst 2005). Thus, composition estimates need to be interpreted with considerable caution and would benefit by inclusions of confidence intervals.

Few data sets permit evaluation of reproductive success and survival of young in relation to population densities (Table 6.4). The higher ratios of calves and yearlings per 100 adult females in the Mink Lake area of WBNP compared to MBS (Table 6.4) reflect differences between increasing and declining populations (Larter *et al.* 2000). Lower calf and yearling to adult female ratios were linked to a period of population decline at WBNP (Bradley and Wilmshurst 2005). Reynolds *et al.* (2003) reported density dependent fecundity in bison at EINP.

Information on the age structure of free-ranging bison populations not subjected to regular culling is limited. Wood bison at the MBS were assigned to age and sex classes in July 1993: calves and yearlings were not assigned to sex classes, all females two or more years old were assigned to a single category, and males more than two years old were assigned to one of four age categories following Komers *et al.* (1992). Here, the population age structure is presented with an assumption of an equal sex ratio in calves and yearlings (Figure 6.2). Irrespective of the sex, the relatively low numbers of calves and yearlings suggest a low recruitment rate (Figure 6.2).

6.3.2 Reproduction

The age of first reproduction is sensitive to nutritional condition and, therefore, highly variable. The proportion of females calving as two-year-olds (conceiving as one-year-olds) ranges between 4-12% (Table 6.5). However, female bison typically enter oestrus as two-year-olds, and give birth to their first calf at three years (Table 6.5). Mature females in some populations reproduce each year (Rutberg 1984; Shaw and Carter 1989; Wolff 1998), although in other populations mature females may not breed in some years (Fuller 1962; Green 1990; Halloran 1968; Soper 1941; Van Vuren and Bray 1986; Wolfe *et al.* 1999). This is particularly true of females breeding as two- to four-year-olds (Green 1990). Fuller (1962) noted that for wood bison in the Hays Camp area of WBNP, 21% of the females more than three years old at the time of parturition were lactating, but non-pregnant, while the same was true for 9% of the females in the Lake Claire area of the park. This proportion may vary within the same population at different densities of bison and other ungulate species relative to forage conditions (Halloran 1968; Shaw and Carter 1989). The young born to females following a year of not breeding were larger and more fecund than the young of females who bred the previous year (Green and Rothstein 1991). Females continue to breed until more than 16 years of age (Green 1990). Bison are typically monoparous, with twinning reported only occasionally (Reynolds *et al.* 2003).

Male bison maintained on supplemental feed are physiologically capable of breeding as early as 16 months of age (Helbig *et al.* 2007), and those not receiving diet supplements may breed at two to three years old (Maher and Byers 1987). However, males generally do not breed until they are five or six years old and large enough to compete with older and more experienced bulls (Fuller 1960; Komers *et al.* 1994; Meagher 1973; Rothstein and Griswold 1991).

The age of first successful reproduction may be modified by disease in bison of the Jackson, Yellowstone and GWBE populations. More than 90% of the first pregnancies were lost in brucellosis infected captive female bison (Davis *et al.* 1990; 1991). In free-ranging bison, the impact of brucellosis on the age of first successful reproduction will vary with the proportion of first time breeders in the population, the proportion of those breeders infected with brucellosis, and the severity of the infection (Bradley and Wilmshurst 2005). Diseases may also modify reproductive performance of older females. At WBNP, both tuberculosis (BTB) and brucellosis may impact the reproductive success of females of all age classes within select population segments (Joly and Messier 2004; 2005). In two population segments of wood bison at WBNP, infection with brucellosis or BTB alone did not impact pregnancy status, but infection with both diseases reduced the probability of pregnancy by 30% (Joly and Messier 2005). In a third population segment, infection with BTB alone reduced the probability of pregnancy by 75% (Joly and Messier 2005).

6.3.3 Mortality factors and survival

Proximate causes of mortality in contemporary wood bison herds include wolf predation and the exotic diseases brucellosis and BTB (Fuller 1962; Calef 1984; Carbyn *et al.* 1993; Joly and Messier 2001, 2004; 2005; Wilson *et al.* 1995 in Bradley and Wilmshurst 2005). In addition, some wood bison succumb to irregular outbreaks of anthrax (*Bacillus anthracis*) (Gates *et al.*

Table 6.3 *Ratios of select age classes:100 females among plains and wood bison populations.*

Subspecies	Location	Period of Observation	Adult		Sub-adult		Sub-adult		Reference
			Male	Female	Male	Female	Yearling	Calves	
Plains bison	Henry Mountains, UT	July or September weighted average 1977–1983	54	100			43	53	Van Vuren and Bray 1986
Wood bison	Slave River, NWT	Summer 1978	32	100	4	1	7	35	Van Camp and Calef 1987
	Mackenzie Bison Sanctuary, NWT	July 1993	78	100					Gates *et al.* 1995
	Mackenzie Bison Sanctuary, NWT	July, unweighted average 1984–1998		100			22	41	Larter *et al.* 2000
	Mink Lake, NWT	July, unweighted average 1989–1998		100			30	51	Larter *et al.* 2000
	Wood Buffalo (Delta Area), AB	Spring unweighted average 1989–1996		100			20	36	Carbyn *et al.* 1998

1995). Wallows may serve as focal areas for anthrax spores, and more frequent wallowing by adult males may contribute to greater mortality among adult males than adult females during outbreaks of the disease (Gates *et al.* 1995). Bison have died falling into hot pools and bogs. Accidental drowning of whole herds of bison by falling through thin ice in spring and fall has been reported (Roe 1970; Gates *et al.* 1991). Once bison break through lake or river ice, they are generally unable to haul themselves out and become trapped (Carbyn *et al.* 1993).

Droughts and severe winters, alone or in combination, have led to episodic over-winter mortality in the absence of wolf predation in plains bison of the YNP central herd (Cheville *et al.* 1998; Green *et al.* 1997). Episodic droughts reduce late growing season forage quality and increase the probability of wildland fires that reduce the amount of winter forage available (Frank and McNaughton 1992). Simulations indicate that over-winter survival of YNP northern range bison is most strongly influenced

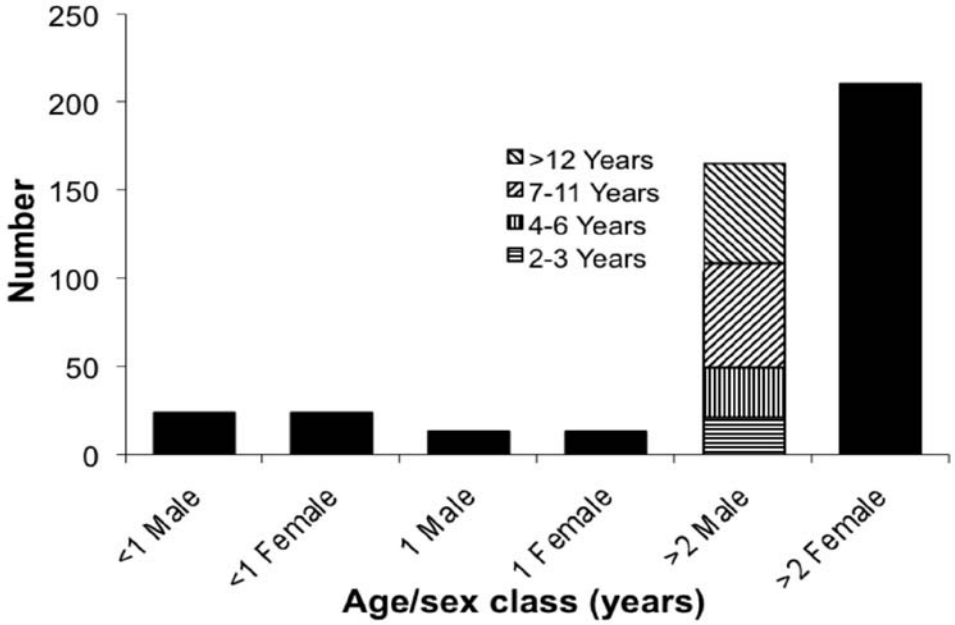


Figure 6.2 *Age and sex class structure of wood bison at Mackenzie Bison Sanctuary, Northwest Territories, assuming an equal sex ratio among calves and yearlings (Gates et al. 1995).*

Table 6.4 *Age-specific reproductive rates (%) of female plains and wood bison at select locations. Ages are female ages at time of birth of offspring (so, a female reported as pregnant at one year by necropsy is shown as giving birth at two years, her second birthday).*

Subspecies	Location	Age			Reference
		2 years	>2 years	>3 years	
Plains bison	Wichita Mountains, OK	13	52	67	Halloran 1968
	Wichita Mountains, OK	12	72		Shaw and Carter 1989
	Fort Niobrara, NB			83	Wolff 1998
	Henry Mountains, UT		52	62	Van Vuren and Bray 1986
	Antelope Island, UT			46	Wolfe *et al.* 1999
	National Bison Range, MT			86	Rutberg 1986
	Konza Prairie, KS			66 – 79	Towne 1999
	Badlands, SD	4		67	Berger and Cunningham 1994
	Wind Cave, SD	5		80	Green 1990, Green and Rothstein 1991
	Yellowstone – Northern Herd, WY/MT			40	Kirkpatrick *et al.* 1996
	Yellowstone – Central Herd, WY			52	Kirkpatrick *et al.* 1996
	Yellowstone – mixed, WY			73	Pac and Frey 1991
	Yellowstone – mixed, WY			79	Meyer and Meagher 1995
Wood bison	Wood Buffalo – Hays Camp, NWT	4		53	Fuller 1962
	Wood Buffalo – Lake Claire, AB	12		76	Fuller 1962
	Wood Buffalo, NWT and AB		76* 70**		Joly and Messier 2004
	Wood Buffalo, NWT and AB			43	Carbyn *et al.* 1993
	Mackenzie Bison Sanctuary, NWT		70		Gates and Larter 1990

* no disease ** infected with brucellosis and bovine tuberculosis

by winter severity and the area of wildland fires (Turner *et al.* 1994; Wallace *et al.* 2004).

Survival of calves to six months is more than 90% in plains bison herds in protected areas, or those that are only lighted hunted in the absence of predators and diseases (Table 6.5). The survival rate for the first six months of life in the presence of wolves at WBNP was 47% (Table 6.5; Bradley and Wilmshurst 2005). At the SRL survival rates for the first six months of life increased from 6% to 30% coincident with a decline in wolf abundance (Table 6.3; Calef 1984). Survival through the first year of life, in the presence of wolves, has been estimated at 10% and 41% for bison at WBNP (Table 6.5; Carbyn *et al.* 1993; Fuller 1962). Calf survival through the first year of life was 95% for an increasing herd at the MBS, when wolf abundance was low (Table 6.5; Calef 1984). There are highly variable estimates on survival patterns in the first year of life (Table 6.5).

Adult survival rates in disease-free, protected, or lightly hunted, populations of plains bison are more than 95% for sexes combined or females only (Table 6.5). Survival rates for both sexes in increasing populations have averaged 75% for wood bison at the MBS, and 95% for the Jackson plains bison herd (Table 6.5; Larter *et al.* 2000; USFWS-NPS 2007). At WBNP, bison infected with both brucellosis and BTB experience lower survival rates than do those infected with only one of the two diseases, or not infected at all (Table 6.5; Bradley and Wilmshurst 2005; Joly and Messier 2001; 2004; 2005).

Table 6.5 *Age-specific survival rates (%) of plains and wood bison at select locations (mm = male; ff = females).*

Subspecies	Location and Years	Age			Comment	Reference
		<6 months %	<1 year %	Adult %		
Plains bison	Henry Mountains, UT	93		96		Van Vuren and Bray 1986
	Badlands, SD			98		Berger and Cunningham 1994
	Jackson, WY			95	Females only. Increasing population.	USFWS and NPS 2007
	Wind Cave, SD	99			1 of 153 calves born died	Green and Rothstein 1991
Wood bison	Wood Buffalo, NWT and AB		<10			Fuller 1962
	Wood Buffalo, NWT and AB		41		Calculated from life table	Carbyn *et al.* 1993
	Wood Buffalo, NWT and AB			92 (mm) 94 (ff)	One or no diseases. Average of Wilson *et al.* 1995 and Joly and Messier 2001	Bradley and Wilmshurst 2005
	Wood Buffalo, NWT and AB			<85 (mm) <87 (ff)	Both diseases	Joly and Messier 2001, Wilson *et al.* 1995 in Bradley and Wilmshurst 2005
	Wood Buffalo, NWT and AB	47	33			Bradley and Wilmshurst 2005
	Mackenzie Bison Sanctuary, NWT		95		Increasing population. Few wolves.	Calef 1984
	Mackenzie Bison Sanctuary, NWT			75	Increasing population. Ad. Female range 67–100: Adult male range 67–100	Larter *et al.* 2000
	Slave River Lowlands, NWT 1974–1976	6				Calef 1976 in Calef 1984
	Slave River Lowlands, NWT 1976–1978	30			Following wolf decline	Van Camp 1978 in Calef 1984

6.3.4 Population growth rates

The rate of increase of a population is influenced by sex ratio and age structure, forage and habitat availability and quality, immigration and emigration combined with reproductive and mortality rates. The highest rates of increase occur in captive bison herds, in the absence of predators, where the sex ratio is skewed towards reproductive age females, some supplemental feeding occurs, and most, or all, of the population is rounded up annually and "surplus" bison removed. The Tallgrass Prairie Preserve (Oklahoma) population attained a rate of increase of about 50% under such conditions (R. Hamilton, personal communication).

The maximum exponential rate of increase (r_m) is the rate at which a population with a stable age structure will grow when resources are not limiting (Caughley 1977). The observed exponential rate of population growth over time ($\hat{r}$) may approximate r_m for populations introduced into areas where resources are abundant (Caughley 1977). The observed rate of growth may be expected to deviate from r_m over time as a population increases, and per capita resources become limiting. The length of time for a population to double in size may be calculated as (natural log (ln) of 2)/ $\hat{r}$ (Johnson 1994).

Plains bison re-introduced to the NBR in 1909 were permitted to increase without management intervention for 14 years (Roelle 1977 in Fredin 1984). The observed exponential rate of growth of the population in this period, with a starting population of 37, was $\hat{r}$ = 0.2053 (Figure 6.3). The population grew at a rate of 20.5% each year, with a doubling time of 3.4 years, or, given the birth-pulse characteristic of bison, it would realistically double every four years. The northern Yellowstone plains bison herd was intensively managed in the early 20th century, with supplemental feed provided in winter (Meagher 1973). Numbers increased from 21 in 1902 to 239 in 1915, after which bison were removed from the herd (Meagher 1973). The observed exponential rate of increase for the northern Yellowstone herd for this 14-year period was $\hat{r}$ = 0.1787. The population doubling time at this rate of increase was four years.

Plains bison, allowed to become free ranging in the Jackson Valley, Wyoming in 1969, experienced minimal management intervention until 1980, when these animals began utilising supplemental forage intended for elk at the NER (USFWS-NPS 2007). Limited numbers of plains bison were killed by agency personnel or licensed hunters between 1980 and 2002 (USFWS-NPS 2007). Plains bison numbers have been estimated annually by staff of GTNP; S. Cain; personal communication). The observed exponential population growth rate for the 33-year period from 1969 to 2002 was 0.129 (Figure 6.4). The observed exponential rate of increase for the Jackson herd for the 14-year period from 1980 to 1993, with a starting population size of 37, was $\hat{r}$ = 0.1197. At these rates of increase, a population would double every six years.

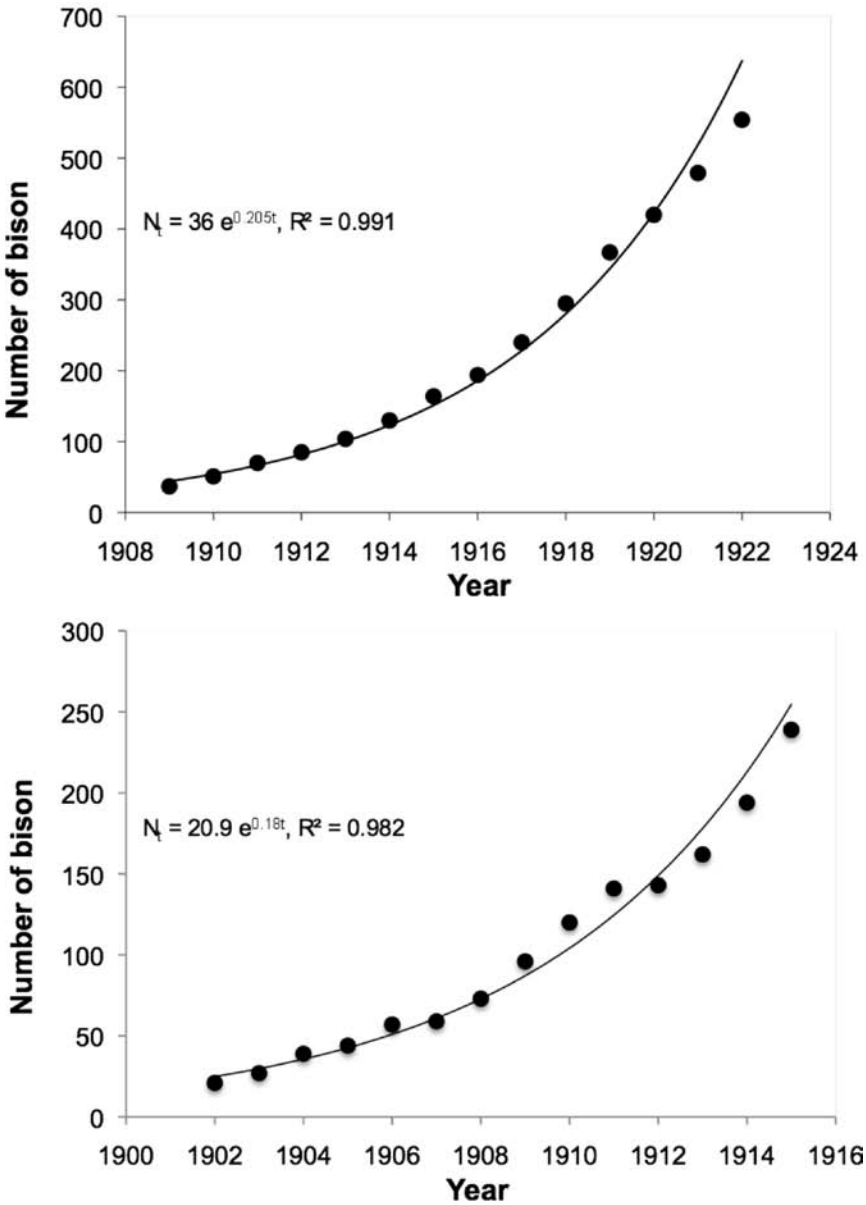
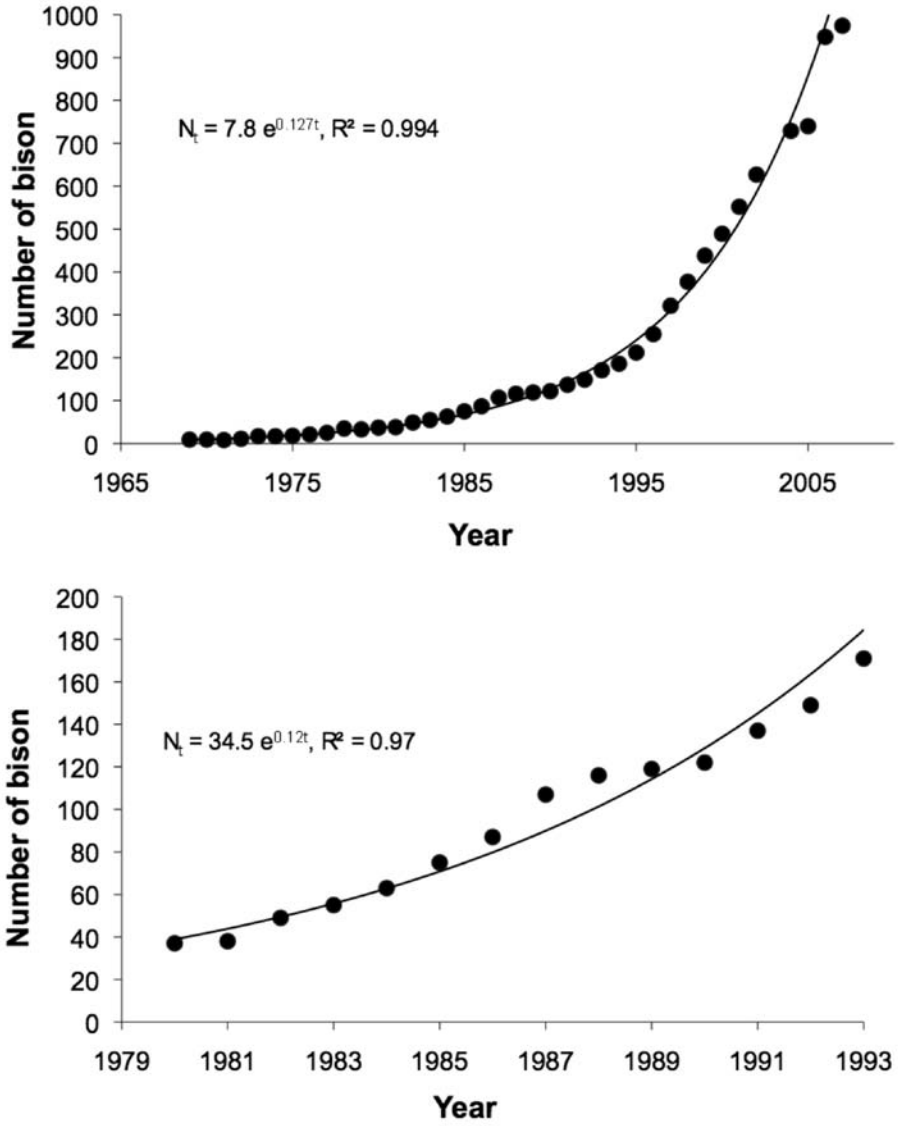


Figure 6.3 *Growth of the National Bison Range plains bison population between 1909 and 1922 (14 years) starting with 37 bison (upper panel), and the northern Yellowstone National Park population between 1902 and 1915 (14 years) starting with 21 bison (lower panel).*

Figure 6.4 *Growth of the Jackson Valley plains bison population in Wyoming between 1969 and 2007 (39 years) starting with 9 bison (upper panel) and between 1980 and 1993 (14 years) starting with 37 bison (lower panel).*

The highest rate of increase reported for a bison population under natural conditions was for the Mackenzie population in the Northwest Territories. It increased at a maximum exponential rate of 0.26, and averaged an annual exponential rate of 0.21 during the first three decades following its establishment (Calef 1984; Gates and Larter 1990).



Chapter 7 Numerical and Geographic Status

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7.1 Introduction

The "Great Contraction", a term used by Flores (1996) to describe the destruction of bison in North America, has been chronicled by numerous authors (Dary 1974; Isenberg 2000; Reynolds *et al.*; 2003; Roe 1970) and was summarised in Chapter 2 of this document. Fewer than 300 wood bison and perhaps only 200 plains bison remained at the turn of the 19th Century. The numerical recovery of plains bison began with the efforts of private citizens in the U.S. and Canada to save a few remaining animals (Freese *et al.* 2007). Governments later became involved in the conservation of plains and wood bison. Protective legislation was implemented first in Canada in 1877 (Gates *et al.* 2001). The first legislation providing specific protection for bison in the U.S. was the National Park Protective Act (Lacey Act) signed on 7 May 1894 by President Cleveland (Boyd and Gates 2006). It imposed a jail sentence and fine for anyone found guilty of killing game in Yellowstone National Park, the range of the last free-ranging plains bison.

Between 1900 and 1970, modest progress was made, increasing the number and populations of bison, largely in public herds. Then in the mid-1980s, the commercial bison industry began to prosper (Freese *et al.* 2007; Renecker *et al.* 1989); the number of bison in North America increased rapidly to more than 430,000, the vast majority of which are under private ownership (Boyd and Gates 2006; Freese *et al.* 2007). However, numerical progress alone cannot be equated with the security of bison as a wildlife species. Conditions under which privately owned bison are raised are commonly motivated by market objectives and there are no regulations or government-supported guidelines requiring private owners to contribute to bison conservation. Domestic bison (those raised for captive commercial propagation) may be subject to small population effects, selection for domestication and market traits including docility, growth performance, conformation and carcass composition, and intentional or unmanaged introgression of cattle genes (Freese *et al.* 2007). Although some private owners exercise their legal property right to manage bison for conservation of the species and/or for their ecological role, the conservation practices of such owners are a matter of personal choice, with no guarantee of persisting beyond the owner's interest in the herd. Currently there are no well-developed regulatory or market-based incentives for managing private commercial herds for species conservation (e.g., independent conservation management certification). Unless effective private-sector incentives are developed, bison populations managed in the public interest as wildlife represent the most secure opportunity for their conservation, adaptation in the evolutionary sense, and viability of bison as an ecologically interactive species in the long term.

Some North American aboriginal communities and individuals also own bison herds. As with other private bison populations, the management of Native-owned bison is not necessarily consistent with conservation policies. Management practices vary from intensive management for commercial production to semi free-ranging herds hunted for subsistence and retention of culture.

It was beyond the scope of this status report to evaluate the management of individual privately owned herds for their conservation value, whether owned by aboriginal or non-aboriginal people. The IUCN Bison Specialist Group acknowledges the important opportunity that Aboriginal Governments, the Intertribal Bison Cooperative, and the Native American Fish and Wildlife Society have to develop guidelines for enhancing the conservation value of herds managed by aboriginal peoples. Similarly, the commercial industry could play a role by providing standards and guidelines and developing incentive-based programmes, such as independent formal certification, for conservation management.

Contemporary conservation is focussed on ensuring long-term persistence and maintaining the potential for ecological adaptation through the effects of natural selection operating in viable populations in the wild (Soulé 1987; IUCN 2003; Secretariat of the Convention on Biological Diversity 1992). Viability relates to the capacity of a population to maintain itself without significant demographic or genetic manipulation by people for the foreseeable future (Soulé 1987). In wild populations, limiting factors, such as predation, resource limitation and mate competition, contribute to maintaining the wild character, genetic diversity, and heritable traits that enable a species to adapt to and survive in a natural setting without human interference (Knowles *et al.* 1998). Therefore, viable wild populations, subject to the full range of natural limiting factors, are of pre-eminent importance to the long-term conservation, security and continued evolution of bison as a wildlife species. We consider the three conservation biology principles proposed by Shaffer and Stein (2000), resiliency, representation, and redundancy, to be relevant for evaluating the geographic and

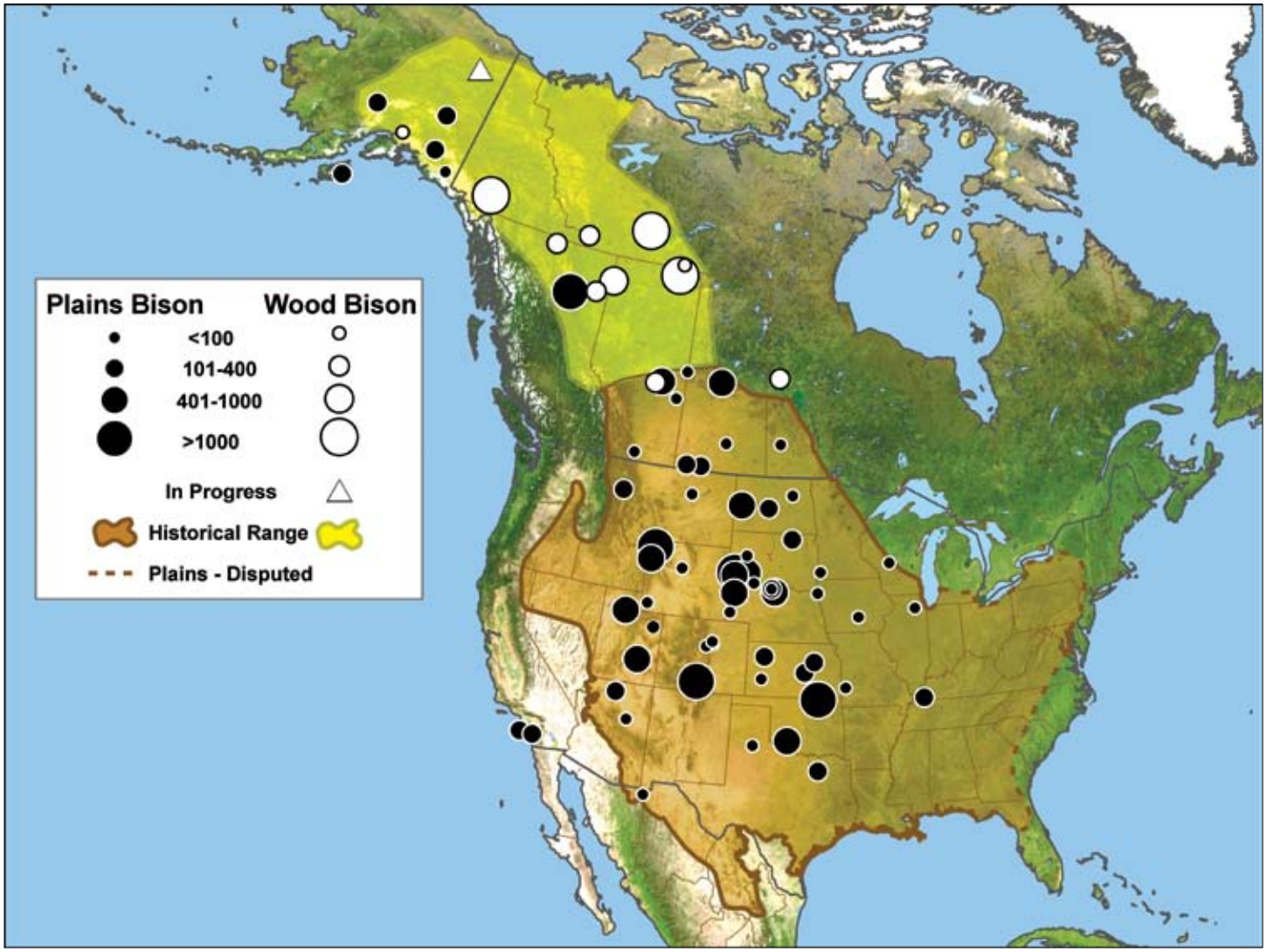

Figure 7.1 *Locations and size classes of bison conservation herds in North America. Historic ranges of wood and plains bison were based on Stephenson et al. (2001) and Sanderson et al. (2008), respectively.*

numerical status of bison. Beyond viability, resiliency refers to the need to preserve individual populations large enough to have a high probability of persisting for extended periods in the presence of minimal management, and which preserve genetic diversity and the potential for adaptation to changing conditions (minimum of 1,000 bison; Gross and Wang 2005). Representation reflects the need to preserve populations of a species across the fullest array of environments in which it occurred originally. Redundancy refers to the need to preserve a sufficient number of large populations to safeguard against local catastrophes.

Here, we provide a summary of the status of wood bison and plains bison populations managed by national or state/provincial public governments and non-governmental organisations whose primary mission is nature conservation. For simplicity, these populations are referred to as "conservation herds". Information on the number of herds and bison under captive commercial propagation is also included. Display herds in zoos were not enumerated. The following seven criteria were considered for reviewing the status of conservation herds: numerical status; geographic status; population size class distribution; opportunity for mate competition among mature males; presence of wolves; the presence or absence of diseases that could affect conservation status (see chapter 5); and presence, or likely presence, of cattle genes based on analysis or stocking history.

7.2 Numerical Status

Numerical status refers to the number of bison and number of populations in North America in conservation herds. Where possible, the reported number of bison in each conservation herd was verified with herd managers in 2008, but the numbers reported here may differ from the actual numbers of animals present because not all herds were surveyed recently, census techniques may not account for every animal, herds are not always managed to achieve a consistent target number, and herd size and productivity vary annually.

Sixty-two plains bison and 11 wood bison conservation herds were enumerated (Figure 7.1 and Appendix A). Although the number of plains bison conservation herds has steadily increased over time, the number of individuals in conservation herds has changed little since 1930 (Freese *et al.* 2007). In 2008, we estimated there were 20,504 plains bison and 10,871 wood bison in conservation herds. Among plains bison there were 9,227 breeding age females (two years old and older), 4,121 mature males (seven years old and older) and 1,230 subadult males (four to six years old). Among wood bison there were 4,892 breeding age females, 2,609 mature males and 652 subadult males.

Since conservation efforts began in the early 1900s, wood bison numbers have fluctuated independently of the number of conservation herds (Figure 7.2). Peak abundance occurred

Figure 7.2 *Numbers of herds and individual plains bison (upper panel) and wood bison (lower panel) in North America, 1890-2008. Sources for wood bison data: Novakowski 1978; Wood Bison Recovery Team 1987; Reynolds and Hawley 1987; Van Camp 1989; Larter et al. 2000; Gates et al. 2001; www.nwtwildlife.com/NWTwildlife/bison/woodbuffalopark.htm accessed 15 January 2009, and 2008/2009 data from agencies. Plains bison data follow Freese et al. 2007 and current status data from agencies.*

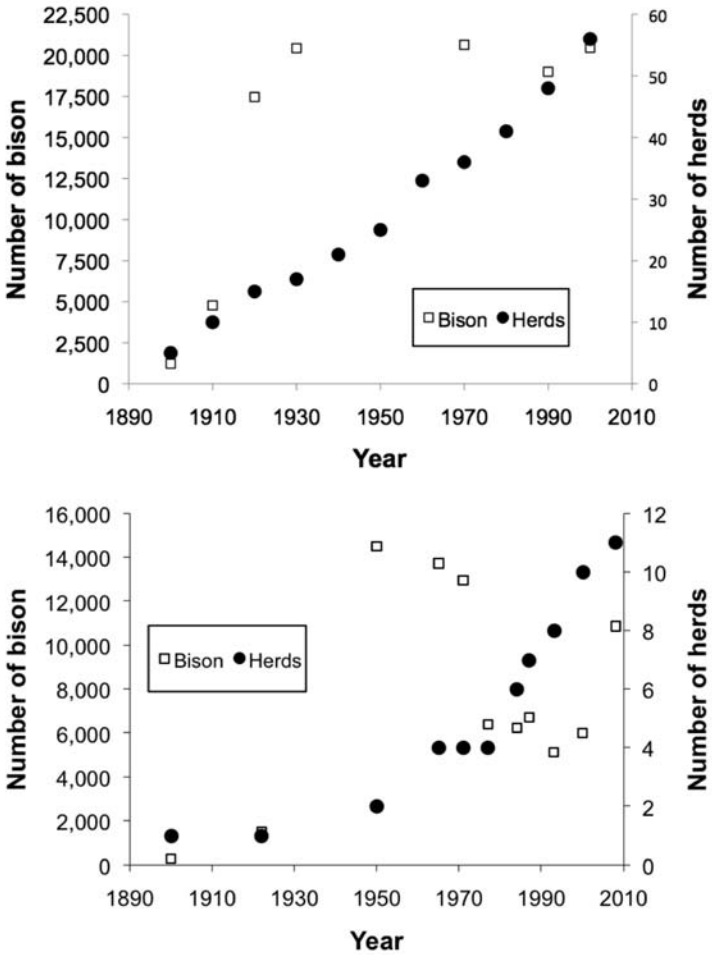

Plate 7.1 *Wood bison near the northern extent of their range in the Yukon, Canada. Photo: Tom Jung.*

from the 1940s to early 1970s following the introduction of more than 6,000 plains bison into Wood Buffalo National Park (WBNP) in the late 1920s. The number of bison in the Greater Wood Buffalo National Park area declined after 1971 when predator management ceased (Carbyn *et al.* 1993). The number of wood bison conservation herds has increased to 11. However, there are still more bison in the WBNP and Snake River Lowlands (SRL) metapopulation (6,141 animals), which is infected with bovine tuberculosis (BTB) and brucellosis, than in the nine disease-free reintroduced populations (4,730 animals).

The number of bison under commercial propagation has outnumbered those in conservation herds since about 1970 (Freese *et al.* 2007). In 2006, there were 195,728 bison on 1,898 farms reporting in the Canadian National Census (Statistics Canada, www.statcan.gc.ca/daily-quotidien/080125/t080125b-eng.htm, accessed 4 December 2008). The U.S. Department of Agriculture's 2007 Census of Agriculture reported 198,234 bison on 4,499 farms (http://www.agcensus.usda.gov/, accessed 10 February 2008). Thus, based on these numbers, there are nearly 400,000 privately owned bison on around 6,400 farms in Canada and the U.S.

7.3 Geographic Status

The original range of bison extended from lowland meadows in interior Alaska to desert grasslands in Mexico, and included areas as far east as New York and as far west as California (List *et al.* 2007; Reynolds *et al.* 2003). The original range of American bison spanned an area estimated by Sanderson *et al.* (2008) to be 9.4 million km^2, and encompassed 22 major habitat types (derived by Sanderson *et al.* 2008 by combining some of the eco-region classes mapped by Ricketts *et al.* 1999). In assessing geographic status of bison in conservation herds, we considered three criteria: representation of subspecies

Plate 7.2 *Plains bison near the southern extent of their range near Janos, Chihuahua, Mexico. Photo: Rurik List.*

populations within their original range and in major habitat types, and the geographic area occupied by, or potentially available to, individual conservation herds.

Representation within and outside their original range: A displaced population of a subspecies within the original range of another subspecies may occupy habitat otherwise available for the recovery and conservation of the indigenous form. Eighty-seven percent of 62 plains bison conservation herds were located within the original range of plains bison (Figures 7.1 and 7.3). Eight plains bison herds residing in California, northern British Columbia, and Alaska were distinctly outside plains bison original range. Those in Alaska and northern British Columbia occur in the original range of wood bison. Nine of 11 wood bison herds were within original range. The two wood bison conservation populations outside the original range include one free-ranging herd in the Inter-Lake region of Manitoba (originally the range of plains bison) and a fenced herd in central Alberta. The latter wood bison population is Canada's national conservation breeding herd at Elk Island National Park, which also supports a separate herd of plains bison.

Representation in major habitat types: Eighteen major habitat types occur within the original range of plains bison (Figure 7.4). At least one conservation herd is represented in 14 (78%) of them and 10 (56%) major habitat types hold two or more conservation herds. At least one wood bison conservation herd is represented in four (57%) of seven major habitat types in their original range, and four habitat types have two or more herds. With the exception of WBNP and the adjacent SRL bison herds, geographic separation or management of other populations precludes inter-population movements.

Available area: The area available for a herd represents the potential for supporting a large resilient population and opportunities for bison to behave as a "landscape species", interacting with spatially variable resources and a variety of other native species. On small pastures, bison may be unable to segregate into social units (mature bulls, maternal and non-maternal herds) or to move in relation to resource depletion and abundance gradients. In addition, the larger the area available, the greater the number of bison that can be supported sustainably. Landscape area is an important factor in considering the conservation status of bison.

The area of range available to bison conservation herds was classified into four categories (metric conversions are approximate): small areas (less than 20 km^2; 5,000 acres); medium areas (more than 20 km^2 and less than 200 km^2; more

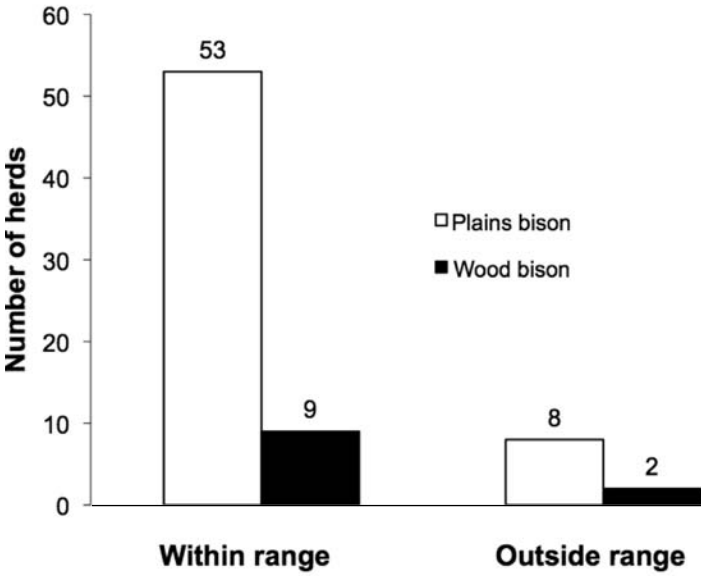

Figure 7.3 *Numbers of plains and wood bison populations within and outside their original range.*

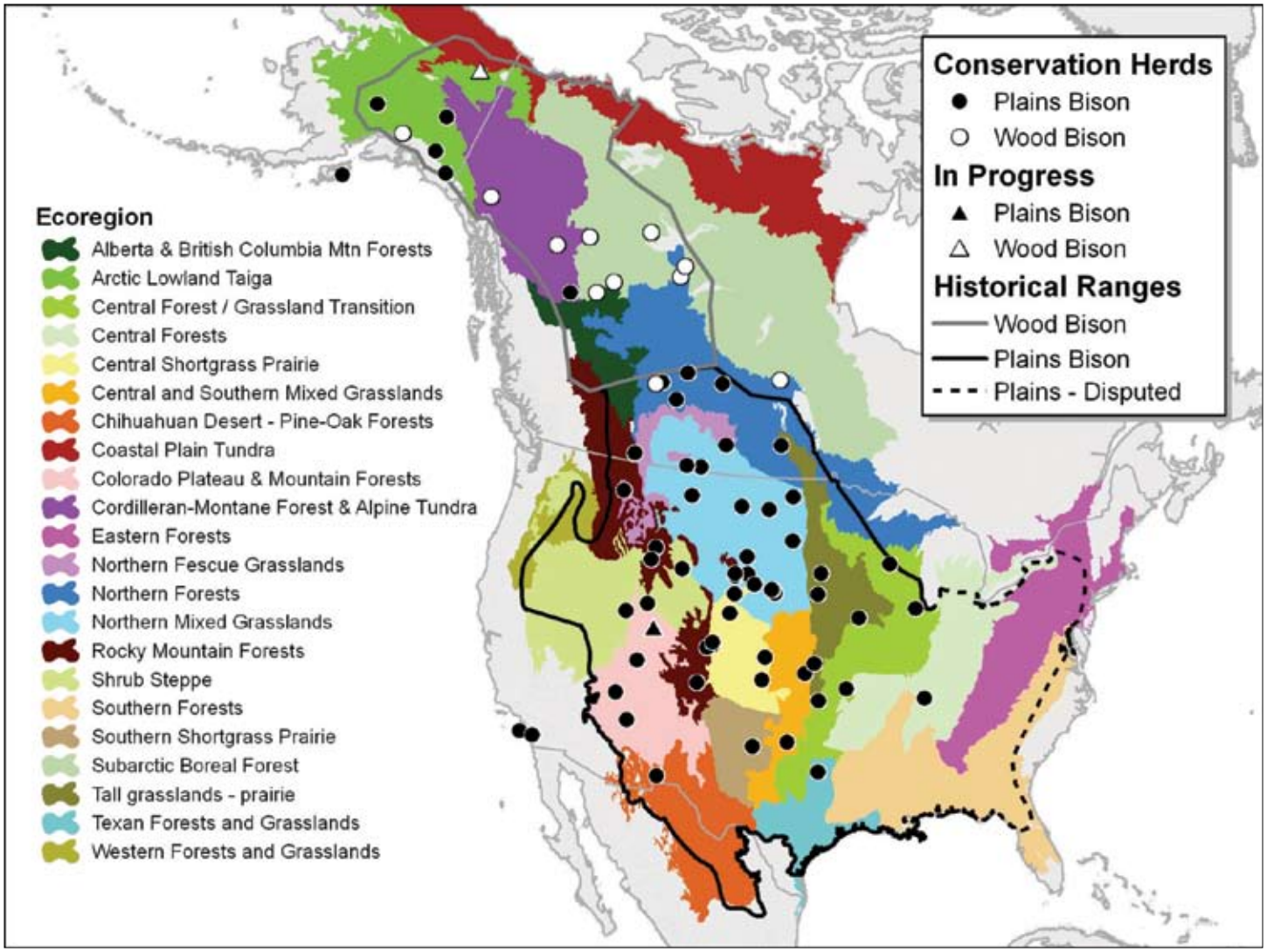

Figure 7.4 *Representation of plains and wood bison conservation herds in original ranges and major habitat types in North America. Habitat types were based on Sanderson et al. (2008).*

than 5,000 acres and less than 50,000 acres); large areas (more than 200 km^2 and less than 2,000 km^2; more than 5,000 acres and less than 500,000 acres); and very large areas (more than 2,000 km^2; more than 500,000 acres). About half of plains bison conservation herds occur on small ranges and only 10% of herds are on very large ranges (Figure 7.5). In contrast, 37% of wood bison herds occur on very large ranges and none occur on small ranges.

7.4 Population Size Distribution

Using a simulation model, Gross and Wang (2005) demonstrated that a minimum population of about 400 animals was needed to retain 90% of selectively neutral variation with a 90% probability for 200 years. Allelic diversity was more sensitive to management treatments than average heterozygosity. On average, a high proportion of alleles with an initial frequency of less than 0.05 were lost when herds had fewer than 400 animals. Differences in generation time accounted for about 75% of variation in retained heterozygosity for populations of 200-800 bison. As population size approached 1,000, the effects of population management on genetic variation were small. Therefore, we considered populations exceeding 1,000 to be more resilient than smaller populations.

Sanderson *et al.* (2008) defined the following size classes for ranking contributions of bison herds to ecological restoration: small contribution, fewer than 400 animals; modest contribution, 400-1,000 animals; large contribution, 1,000-5,000 animals; exceptional contribution, more than 5,000 animals. The frequency distribution of conservation population size (Figures 7.1 and 7.6) illustrates that small populations (fewer than 400 animals) are the most common population size class among both plains and wood bison (74% and 55%, respectively). Five plains bison and three wood bison herds exceed 1,000 animals. Only two populations have encompassed 5,000 animals within their recent range of size variability (Greater Yellowstone Area and Greater Wood Buffalo Park area).

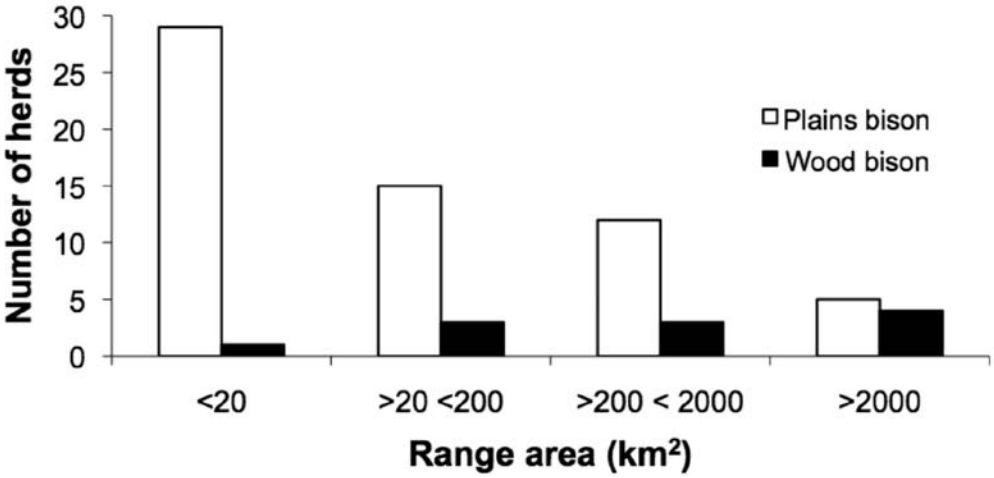

Figure 7.5 *Area classes of ranges available for existing bison conservation herds.*

7.5 Mate Competition

The sex and age structure of small populations are sometimes manipulated to reduce the risk of escapes, remove aggressive animals, compensate for unequal mating by males, alter fecundity, or to increase the rate of population increase. A common practice for both small conservation herds and commercial herds is to remove males before they become morphologically and behaviourally mature (six to seven years old and older), when they may become dangerous to people or other animals and property (e.g., fences). Furthermore, the sex ratio may be manipulated to maintain only sufficient young males to ensure fecundity (e.g. 10 males: 100 females). In contrast, in non-manipulated wild herds the mature male: female ratio can exceed 50:100 (Gates *et al.* 1995) and mate competition among males is assured.

The bison is a polygynous species in which mature males (six or seven years old) compete vigorously for mating opportunities (Komers *et al.* 1992). In the absence of mature males, juvenile and subadult males are capable of breeding successfully, but there is little competition among them for mating opportunities (Komers *et al.* 1994a,b). We considered that the presence of two or more mature males indicates the potential for mate competition. Sixteen percent of plains bison conservation herds did not contain mature males. In contrast, two or more mature males were maintained in all wood bison conservation herds, thus providing opportunity for mate competition.

7.6 Presence of Wolves

Key species, such as bison, have a disproportionate influence on the patterns of occurrence, distribution, and density of other species. Where present, bison influence the structure, composition, and stability of plant (Campbell *et al.* 1994; Knapp *et al.* 1999) and animal communities (Bogan 1997; Roe 1970; Truett *et al.* 2001). Grazers like bison also enhance mineral availability and nutrient cycling through faeces and urine deposition, and carcass decomposition (Augustine and Frank 2001; Towne 2000; Wallis DeVries *et al.* 1998). The presence of wolves, the only effective predator of bison (aside from humans), is an indicator that the maximum number of interactions is possible between bison and other species in an ecosystem. If wolves are present we assumed that all other natural limiting factors would likely be present in the ecosystem. Wolves are associated with only 10% of plains bison conservation herds (6 of 62) in contrast to 82% of wood bison herds (9 of 11).

7.7 Presence of Reportable Diseases

Although diseases may limit bison population growth and productivity they are unlikely to cause extirpation. However, the presence of diseases reportable under federal or state/provincial statutes may lead to management interventions that impact conservation (Chapter 5). The type of intervention varies with the disease and jurisdiction (Chapter 5). For example, captive conservation herds that test positive for BTB or brucellosis would normally be depopulated, while less serious interventions (such as the use of

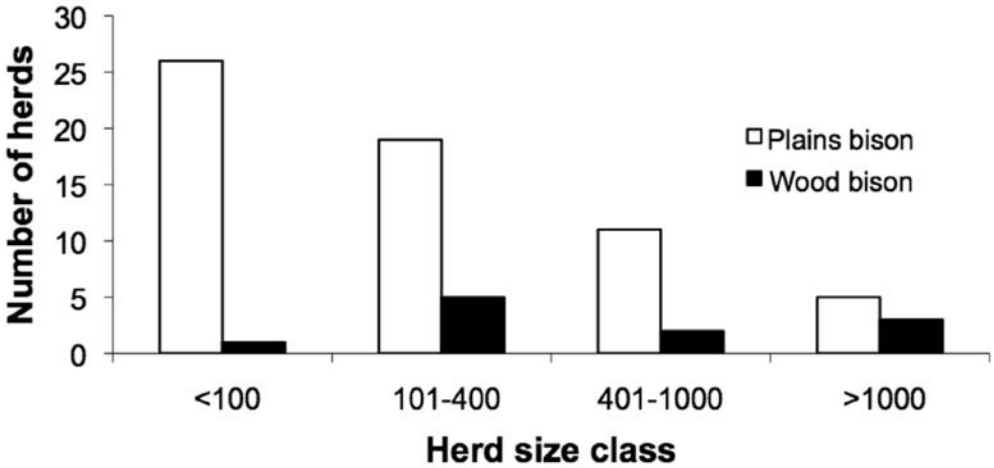

Figure 7.6 *Number of bison conservation herds in four size classes.*

Plate 7.3 *Male plains bison sparring. Photo: Dwight Lutsey.*

control areas) may be applied for infected wild populations in large wilderness areas. The presence of reportable diseases may preclude translocations. Management interventions are possible to control some diseases (anthrax, BVD, JD). Reportable diseases were present in 5 of 62 (8%) of plains bison herds and 3 of 11 (27%) wood bison herds.

7.8 Cattle Gene Introgression

The molecular legacy of historic hybridisation between bison and cattle is a serious challenge for bison conservation today (Halbert and Derr 2007). Forced hybridisation has left a legacy of cattle DNA that is widespread among contemporary bison populations (Chapter 4). The implications for bison conservation are just beginning to be understood and appropriate interventions considered. Available technology allows testing of populations for the presence of markers for the cattle genome and mitochondrial DNA (MtDNA), but all conservations herds have not yet been tested (Figure 7.7). Among those tested, introgression was demonstrated in seven plains bison conservation herds, but none of eight wood bison herds. Based on stocking sources, introgression is likely in 17 plains bison herds and no wood bison herds.

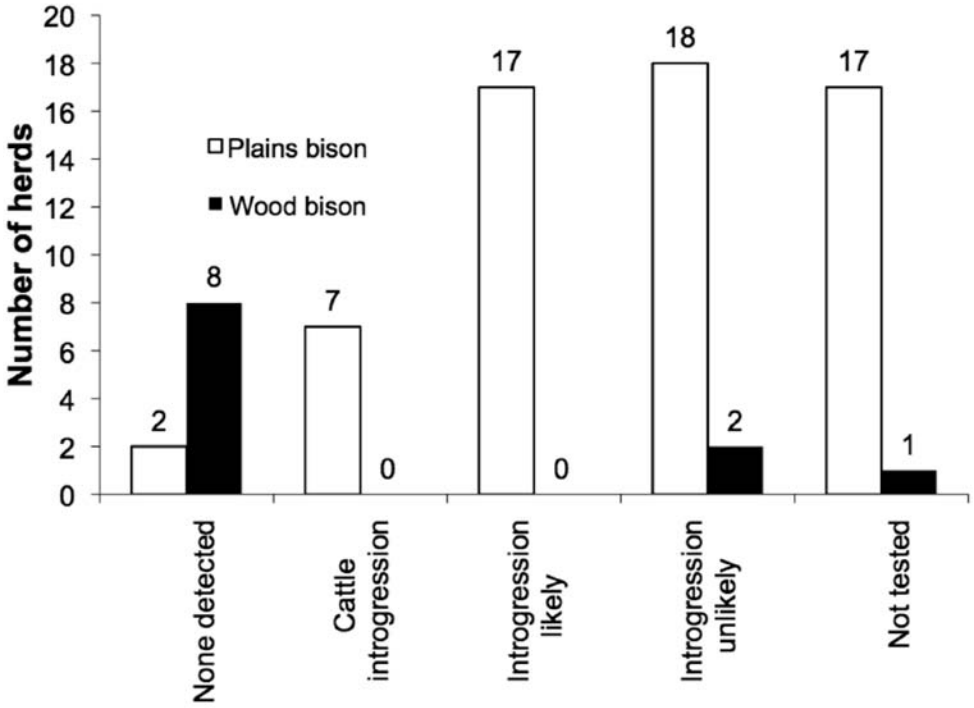

Figure 7.7 *Results of tests for cattle gene introgression in conservation herds.*

7.9 Conclusions

Originally, the American bison ranged from northern Mexico to Alaska. Plains bison occurred from Northern Mexico to central Alberta and wood bison occurred from central Alberta to Alaska. The continental population underwent a dramatic decline during the 19th century, caused by overhunting, but has since partially recovered. Approximately 93% of the continental population is managed for private commercial propagation; very few of these herds are managed primarily for species conservation, and none are managed in the public interest for conservation. Bison currently occupy less than 1% of their original range, and conservation herds occupy a small fraction of that 1%. The number of conservation herds has increased since 1930, but the numbers of individuals in populations managed primarily for conservation has changed little since then. There are 62 plains bison and 11 wood bison conservation herds (managed for conservation in the public interest). Conservation herds are typically small (fewer than 400 animals) and populations are widely dispersed with only one situation that provides geographic conditions for natural movements between population units. The current number of large populations is five plains bison and three wood bison herds. The estimated number of breeding females in conservation populations is 9,227 plains bison and 4,892 wood bison. Their current range is restricted by land use and wildlife

management policies in the south, and by wildlife and reportable disease management policies in the north.

Among North American nations, the species is most limited in Mexico, where an international trans-boundary wild herd recently occurred, but is now limited by management to a private ranch in New Mexico (U.S.), where they are classified as livestock. Several increasing herds or new projects (American Prairie Reserve, Montana; Broken Kettle Grassland Reserve, Iowa; San Luis Valley, Colorado; PANP, Saskatchewan, Canada; Janos Grassland, Chihuahua, Mexico and adjacent New Mexico; Yukon Flats, Minto Flats, and lower Innoko River areas in Alaska) have the potential to develop resilient populations on large landscapes thereby advancing the long-term security of bison as wildlife.

The American bison nearly qualifies for listing as Vulnerable C2a(i) under IUCN criteria and is currently listed as Near Threatened on the IUCN Red List in light of its dependence on ongoing conservation programmes and a very limited number of large resilient populations in the wild (Gates and Aune 2008). Future progress on the conservation and recovery of the American bison will depend on significant changes in its legal status and management as wildlife by federal and state/provincial agencies, harmonisation of policies and activities among agencies at multiple levels, cooperation with landed non-profit organisations, and possibly through the creation of voluntary formal conservation standards for private commercial herds and populations managed by Native American governments.

Chapter 8 Legal Status, Policy Issues and Listings

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8.1 Introduction

The bison is an iconic North American wildlife species that symbolises the wild and open western prairie and boreal forest landscapes of the recent past. Although their decline, and subsequent recovery, is frequently recounted in conservation circles, the ecological recovery of "wild" bison was never really considered, and consequently their restoration has never been fully accomplished (Sanderson *et al.* 2008). Most plains bison in North America are found on farms and ranches (about 400,000) while relatively few (about 30,000) are located on provincial/state, federal, and non-profit conservation reserves (see Chapter 7). Few populations are distributed broadly on native landscapes in suitable habitat, and most do not enjoy equal legal or policy status when compared to other important wildlife species such as elk (*Cervus elaphus*), deer (*Odocoileus* spp.) or pronghorn (*Antilocapra americana*). Wood bison are managed more commonly as wildlife within their historic range than plains bison, but suffer from fragmented distribution and disease issues that complicate their management.

The purpose of this chapter is to evaluate the historic and current legal status of bison in North America and identify legal and policy obstacles relevant to conservation efforts for this species. Due to a historical paradigm that viewed bison as livestock, and past conservation measures that treated them in a manner similar to livestock, bison have not achieved a legal or policy status commensurate with a premier keystone herbivore native to prairie ecosystems. During the great restoration period of wildlife management, bison were routinely classified and managed by state/provincial and federal agencies across North America as a form of livestock, while other wildlife were classed and managed as free-roaming wild animals consistent with wild landscapes.

8.2 History of Protection and Conservation

8.2.1 Early legal and policy efforts by governments to protect plains and wood bison

8.2.1.1 Early policy development in the United States

Outcries during the 19th Century to halt the destruction of bison in the U.S. were largely ignored. In 1820, Major Stephens expressed concern about the excessive killing of plains bison and advocated a law to prevent wanton slaughter (Dary 1989). In 1843, John J. Audubon issued warnings against the slaughter of bison (Dary 1989). Despite their pleas, no conservation policy or protective legislation was enacted for several more decades. Numerous bills to protect plains bison were introduced by members of the U.S. Congress between 1871 and 1876; none was passed into law. Although there were no successful federal interventions to halt the slaughter, several states enacted legislation on their own. Between 1864 and 1872, the states of Idaho, Wyoming, and Montana implemented statutes to reduce the killing of game, including bison. Although these laws reflected deep concern for the conservation of wildlife, they were largely ineffective owing to limited enforcement. In 1872, President Ulysses S. Grant established Yellowstone National Park to protect all resources, including bison, within its borders. 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 May 1894, providing the means necessary to halt the extirpation of the last free-ranging plains bison population in North America (Gates *et al.* 2005). Despite these efforts, by 1902, fewer than 25 free-ranging plains bison remained, and these were located in the remote Pelican Valley of Yellowstone National Park (YNP) (Meagher 1973). A few wood bison may have persisted into the 20th Century in Alaska, but were soon extirpated (Stephenson *et al.* 2001).

8.2.1.2 Early policy development in Canada

In Canada, early conservation efforts began in 1877 with the passing of the Buffalo Protection Act (Hewitt 1921). In 1883, the Ordinance for the Protection of Game was passed, but it was not effective owing to poor enforcement (Ogilvie 1979). Plains bison were extirpated from the wild in Canada by the 1880s (COSEWIC 2004), but wood bison persisted in a small population in what is now Wood Buffalo National Park (WBNP). 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 first significant contribution by the Government of Canada was made in 1907 when it purchased the privately owned Pablo-Allard herd in Montana. The government of Canada enacted the Unorganised Territories Game Preservation Act in 1894, partly as a response

to the decline of wood bison. The 1922 Orders in Council under the Forest Reserves and Parks Act established WBNP in an attempt to save wood bison from extinction (Boyd 2003; Gates *et al.* 2001a; 2001b; Soper 1941).

8.2.1.3 Policy development in Mexico

Historically, bison were present in five states in northern Mexico, but until recently existed in the wild only in the borderlands between the Janos region of Chihuahua and south-western New Mexico (List *et al.* 2007). Mexico first included bison on its red-list of endangered species in 1994. The most recent version (SEMARNAT 2002) specifically lists bison in the Janos-Hildago herd as "endangered wildlife". Although the population is afforded legal protection in Mexico, it is considered livestock when it ranges into New Mexico. See section 8.5.5.3 for more details on this herd.

Bison conservation in Mexico has primarily been implemented through federal programmes; status has not yet been established under state legislation. The National Ministry of Environment (SEMARNAT 2002) managed bison for many years. Recently the responsibility for priority species, including bison, was transferred to the National Commission of Protected Natural Areas. The Institute of Ecology of the National University of Mexico is advocating legal protection of the herd in both countries, including protection under international treaties on migratory wildlife species between Mexico and the U.S. The IUCN Bison Specialist Group (BSG) strongly encourages this protective action and other efforts to restore plains bison to the Chihuahuan Desert grasslands.

8.2.2 Plains bison conservation by the private sector

Private sector conservation efforts can be categorised into two non-exclusive groups: 1) private citizens interested primarily in commercial production of bison and secondarily in bison conservation; and 2) private conservation groups interested in conserving bison as wildlife. The former do not typically have formal constitutions mandating conservation, while the latter institutions typically do. Legislation, regulations, rules, and policies affecting captive herds owned by these sectors are similar to domestic livestock, focusing on transport, trade, export, import, animal health, and use of public grazing lands.

Notably, Turner Enterprises has been involved in the development of production herds on 14 large ranches in the U.S., the largest number of plains bison owned and managed by a single owner. Bison are managed with low management inputs similar to many public conservation herds. Notably, the Castle Rock herd on Vermejo Park Ranch in New Mexico is derived from stock translocated during the 1930s from YNP and showing no evidence of cattle gene introgression. Although some privately owned herds may be valuable for conservation, there is no precedent for assessing their long-term contribution to conservation of bison as wildlife. Recently, the Wildlife Conservation Society developed an evaluation matrix that helps identify the key characteristics and possible management adjustments that would be necessary for privately owned herds to contribute to bison conservation (Sanderson *et al.* 2008). This matrix is still evolving and was recently tested among a small producer group to refine and improve its application. Population and genetic management guidelines presented earlier in this document may also be useful for guiding private producers toward managing their herds in support of conservation. However, a system for certifying herds for conservation management would be required to ensure that guidelines are followed.

Several non-governmental organisations (NGO), particularly The Nature Conservancy (TNC), the Nature Conservancy of Canada (NCC), American Prairie Foundation (APF), and the World Wildlife Fund (WWF) have been active in developing conservation herds. More information on their initiatives can be found in section 8.5.5.4.

8.2.3 Conservation efforts by tribes and First Nations

Many North American Native Peoples have strong cultural, spiritual, and symbolic relationships with bison (Notzke 1994; Zontek 2007). Some tribes believe that because the animals once sustained their Indian way of life, they, in turn, must help the bison to sustain their place on the earth. The conservation of wild bison includes the intangible values these tribes hold for bison. Values vary greatly between tribes, and in some cases, even between members of the same tribe. Some tribal people believe that the status of the bison reflects the treatment of North American Indians. Interest in preserving the cultural significance of bison, and in restoring cultural connections to the species, can be important incentives for Native governments and communities to participate in bison conservation (Notzke 1994; Zontek 2007).

Some tribal bison managers consider all bison as wild animals regardless of the source of stock, genetic introgression from cattle, or domestication history. This can be the basis for conflict with conservation biologists who apply biological criteria when evaluating the conservation merit of a herd. Tribal governments commonly operate under challenging circumstances. Political views can vary between succeeding tribal administrations, creating unstable policies that can affect bison management and conservation practices. Numerous Native Tribes own or influence the management of a significant land base that has the potential to sustain large bison herds. However, there has yet to be a systematic survey of the number of herds or the distribution of bison under Native management—a task of sufficient magnitude and complexity to exceed the scope of this review.

The potential for tribes to participate in bison restoration is improving with the development of tribal game and fish

administrations, and the increasing capacity to implement modern wildlife management for wildlife on tribal lands. Some tribes have developed independent bison projects. Others have joined the Intertribal Bison Cooperative (ITBC) to obtain guidance and support. The ITBC was formed in 1990 with the mission to restore bison to Indian Nations in a manner that is compatible with their spiritual and cultural beliefs and practices (ITBC website: http://www.itbcbison.com/). In cooperation with the Native American Fish and Wildlife Society, the ITBC was able to secure U.S. congressional support for bison restoration in 1991. In 1992, tribal representatives met and the ITBC became an officially recognised tribal organisation in the U.S. The ITBC is a non-profit 501(c)(3) organisation governed by a Board of Directors comprised of a tribal representative from each member tribe. Currently there are 57 member tribes that collectively manage more than 15,000 bison. The role of ITBC is to act as a facilitator for education and training, developing market strategies, coordinating transfer of bison from federal ownership to tribal lands, and providing technical assistance to tribal members to encourage sound management. The ITBC does not have a presence in Canada, nor is there an equivalent organisation there. A summary of tribal bison conservation initiatives is in section 8.5.5.5.

8.3 Important Policy and Regulatory Considerations

8.3.1 Legal status and listings of bison

8.3.1.1 International and global status

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is a multilateral agreement among nations to ensure that international trade in specimens of wild animals and plants does not threaten their survival. Species listed in Appendix I are those threatened with extinction, while species listed under Appendix II might soon be if trade is not controlled. Wood bison were transferred from CITES Appendix I to Appendix II in 1997 based on Canada's ability to satisfy the "precautionary measures" of Resolution Conf. 9.24 (Annex 4, paragraphs B.2.b.i and ii). Although bison are in demand for trade, they are managed according to the requirements of Article IV. It was determined that Canada maintains appropriate enforcement controls to prevent the unauthorised taking of wild bison for commercial farming, and that the transfer to Appendix II was consistent with the goals of the government's recovery plan, and would not hamper progress toward the recovery of wood bison in the wild within their original range. Import and export of wood bison is regulated under permit by CITES authorities within member nations. Plains bison are not listed under CITES (http://www.cites.org/).

American bison were recently listed as "Near Threatened" in the IUCN Red List of Threatened Species™ (Gates and Aune 2008). A taxon is Near Threatened when it has been evaluated against the criteria, but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for, or is likely to qualify for, a threatened category in the near future. No distinction is made between wood and plains bison in the World Conservation Union (IUCN) Red Book.

NatureServe is a non-profit conservation organisation and international network of biological inventories known as natural heritage programmes or conservation data centres operating in all 50 U.S. states, Canada, Latin America and the Caribbean. It assigned an overall conservation status rank to American bison of G4 (Apparently Secure), meaning they are globally common (more than 100 occurrences) generally widespread, but may be rare in parts of their range, and although they are secure in their global range, there may be a concern for their security in the long term (NatureServe 2006). The wood bison is ranked by NatureServe as G4T2Q, where "T" refers to it being an intraspecific taxon (trinomial), "2" means imperilled, and "Q" refers to questionable taxonomy. The plains bison is ranked as G4TU, where "U" means currently unrankable due to a lack of information or substantially conflicting information about status or trends.

8.3.1.2 Status in North America

The wood bison was designated by Canada as "Endangered" in 1978. Owing to progress made towards recovery, it was down listed to "Threatened" in 1988. This designation was re-evaluated and affirmed in May 2000. The wood bison is protected under the Canadian Species at Risk Act (2003), but hunting is allowed in Alberta, the Northwest Territories, and the Yukon, subject to conservation strategies and management regulation. In June 1970, the wood bison was listed under the U.S. Endangered Species Act (ESA) as "Endangered in Canada" to reflect its status in Canada at that time. Canada and the U.S. are undertaking efforts to harmonise the national listings of this subspecies (Gates *et al.* 2001b). A recent petition to down list wood bison from endangered to threatened in the U.S. was submitted and the decision is under 90-day review by the U.S. Fish and Wildlife Service (USFWS).

Although plains bison are currently not listed in the U.S. or Canada under species at risk of extinction legislation, consideration of a listing status is being undertaken (COSEWIC 2004). In 2004, COSEWIC recommended designating plains bison as Threatened under the Species at Risk Act in Canada (Wilson and Zittlau 2004). The proposed change was listed for comment on the public registry in 2005. Criticism ensued from commercial bison producers concerned with the impact on their industry and international trade, and there

was a lack of support by Agriculture and Agri-Food Canada and the provincial governments. In July 2006, The Federal Minister of the Environment recommended that plains bison not be listed because of potential economic implications for the Canadian bison industry (http://canadagazette.gc.ca/partII/2005/20050727/html/si72-e.html).

There are several potential complications that would accompany the process of listing plains bison in North America. One complication regarding the legal status of bison is the issue of hybridisation with cattle. There is considerable uncertainty concerning if, and how, endangered species status should be applied to hybrids in Canada and the U.S. (Boyd and Gates 2006; Campton and Kaeding, 2005). Hybrids are exempt from the Endangered Species Act (ESA) when propagated in captivity, and when they are the progeny from one listed and one non-listed parent (O'Brien and Mayr 1991). A second complication is the consideration of commercial bison production in evaluating the numerical status of this species. A third complication is the legal distinction and status of wild and captive bison should listing be considered for the wild form (Boyd 2003).

Bison often enjoy protected status in Canadian and U.S. national parks as a result of the legal status of the habitat. The Canadian National Parks Act protects bison and their habitat in national parks. In Canada, provincial and territorial governments can also use the federal Wildlife Trade Act to control the movement of bison across their borders. In the U.S., enabling legislation attached to each national park when it was established, typically protect bison as wildlife unless they are not considered native to the region. Where they are not considered native to a region, or are known to be cattle hybrids, national parks often consider them invasive and may consider removal or eradication.

The United Stated Forest Service (USFS) classifies the American Bison as "Not Sensitive in Region 2 and Not of Concern" by its Species Conservation Program assessment (USDA Forest Service 2009). The rationale for this classification is that populations and habitats are currently stable or increasing. This USFS review suggests that while the species may warrant restoration as an ecological keystone species, it does not warrant sensitive status.

Conservation and restoration programmes for American bison are confounded by socioeconomic challenges resulting from the confusing legal status for this species. The legal status of bison ranges from domestic livestock to wildlife among various federal, state, and provincial jurisdictions across North America (Table 8.1). The legal recognition of bison as wildlife is often impeded by their historic, or in many cases dual, classification as domestic livestock. Where they have attained their status as wildlife, they are routinely managed within fenced preserves where some, if not all, natural selective processes are curtailed. Ten states in the U.S., four provinces in Canada, and one state in Mexico classify bison as wildlife (Table 8.1). All other states and provinces within their original range designate bison solely as domestic livestock. Plains bison are designated and managed as wildlife in Alaska, Arizona, Utah, Montana, Wyoming, British Columbia, Alberta, Saskatchewan, and Chihuahua. Four other states consider bison as wildlife, but do not have free ranging populations to manage; Idaho (extreme rarity), Missouri (extirpated), New Mexico (no longer occurring), and Texas (extirpated). Plains bison are listed and managed as wildlife, but are considered extirpated, in Alberta and Manitoba. Wild bison are preserved, as a public trust resource, managed to protect natural selection processes, and hunted as free roaming wildlife in Alaska, Arizona, Utah, Montana, Wyoming, British Columbia, Alberta, and Saskatchewan. Wood bison are designated and managed as wildlife under provincial statutes in Manitoba, Alberta, British Columbia, Yukon, and the Northwest Territories. Wood bison enjoy protected status in all of these provinces. There are legal restrictions on hunting and other activities such as capture and harassment. Subsistence hunting by aboriginal peoples is allowed under strict regulation in Northwest Territories and Yukon.

Under Mexican law, wildlife belongs to the nation. However, Mexico has only recently developed a wildlife conservation and management system that entitles a landowner to be registered in the programme (*Unidades de Manejo y Aprovechamiento)* and to receive the benefits of harvest and commercial use of wildlife. This programme has doubled the landscape available for wildlife protection in Mexico. In 1995, the federal government established a bureau managed by the Secretary of the Environment. Within this organisation is a department for the administration of wildlife conservation programmes. In 2007, the conservation of threatened species is becoming the responsibility of the National System of Protected Natural Areas.

There is only a limited state or local wildlife management infrastructure to support federal wildlife conservation efforts in Mexico. Local communities are only now beginning to accept and appreciate the value of free-ranging wildlife on landscapes that they own and manage. Until a broader legal and policy infrastructure is established, federal law and policy will continue to direct wildlife management conservation in Mexico. Federal policy is primarily aimed at developing partnerships with landowners and cooperatively identifies conservation measures acceptable to individual landowners. In addition, federal conservation law and policy drives the protection of land to establish "Natural Protected Areas" to conserve species associated with those landscapes. Public interest has increased in developing wildlife programmes for economic and conservation purposes. Interest in conservation

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Table 8.1 *Current legal status of plains and wood bison (Excluding portions of bison range where large landscapes are no longer available).*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
United States	Yes	Yes	Plains bison petitioned under ESA but denied; Managed as captive wildlife on USFWS Refuges; USFS R-2 classifies bison as not sensitive; Managed as wildlife (captive or free-ranging) in several National Parks. Recent petition to downlist wood bison to "Threatened" is under 90-day review.	No comprehensive strategy; Activity limited to and fragmented among NGOs, very few states, National Parks and USFWS Refuge System.	NEPA; National Refuge Act; Each National Park has its own organic legislation-Interpreted by each Park Superintendent; Wood bison are listed as Endangered under ESA; Animal Health Protection Act (7#U. S.C. 8301 et seq.).	No	Absence of strategic planning; Multiple jurisdictions and coordination of agencies; Management in captivity under refuge policy; Disease transmission to livestock; Limited involvement and interest by many state wildlife agencies; Confused regulatory status in many states.
Alaska	Yes	Yes	4 introduced plains bison herds are "Wildlife"; One plains bison herd on Popof Island; Maintain a hunting programme by permit only.	Long-term goals being established for wild wood bison in State Wildlife Action Plan (SWAP) and reintroduction programmes; Management planning for the 4 introduced plains bison herds.	ESA 10(J) status for wood bison - Minto Flats introduction; Title 16 in Alaska state statutes designates bison as wildlife; Delta Bison Mgt. Plan; Wood bison Conservation Plan in progress; Livestock manages captive bison under Title 3 in Alaska state statutes. Domestic bison governed under same rules as domestic cattle.	Yes; Yukon and Minto Flats Wood Bison Restoration is underway.	Plains bison outside their original range; Aboriginal hunting rights; USFWS interpretations of legal status of wood bison under ESA.
Arizona	Yes	Yes	Bison are wildlife, specifically big game, and are managed by AGFD on two state wildlife areas (House Rock and Raymond Ranch).	Yes, in SWAP.	Title 12, R12-4-401 Game and Fish Commission Rules for Live Wildlife; R-12-4-406 Restricted Live Wildlife Section B9.d exempts restrictions on possessing captive bison (permit not required to possess); A.R.S 17-101 A22 defines wildlife and 101B defines bison as a game animal.	No	Arizona is at the edge of bison original range; Current strategic plan limits conservation to two existing populations; House Rock population hybridised with cattle; Agriculture and forestry conflicts.
Colorado	No	Yes	Bison are exempt from the requirements of wildlife commission regulations. Today, captive herds are designated as livestock. Conservation herds exist in two Denver City parks, one USFWS Refuge and one TNC preserve.	Yes; On Two USFWS Refuges and one TNC preserve.	Chapter 11, Section 406-8 Wildlife, Parks and Unregulated Wildlife; Wildlife Commission Regulation #1103 exempts bison from all wildlife commission regulations, as domestic animals	No	Agriculture and forestry conflicts; Regulatory status.

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Idaho	Yes	Yes	Identified as S1 species in wildlife commission status report. S1= critically imperilled species at high risk because of extreme rarity.	No	Livestock regulations chapter 210 section 01.a; Not mentioned in SWAP.	No	Disease Status in YNP; Agriculture and forestry conflicts; Regulatory status.
Illinois	No	Yes	Considered extirpated in Illinois.	No	Managed as livestock under state statute Chapter 225 part 650/1; Not mentioned in SWAP.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land; Regulatory status.
Iowa	No	Yes	Considered extirpated in Iowa; Found only on one small National Wildlife Refuge.	Yes; Only on one National Wildlife Refuge.	Managed as livestock under state animal health statutes. Bison statutes combined with those of cattle; Not mentioned anywhere in wildlife regulations or wildlife conservation strategies.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land; Regulatory status.
Kansas	No	Yes	Considered extirpated prior to 1900; Designated domestic under beef rules; State wildlife department manages bison on two small game ranges; TNC has two additional preserves.	Yes; Only on TNC and state preserves	Identified in SWAP as not meeting criteria for species of greatest conservation need; Chapter 60 section 4001 in livestock regulations.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land; Regulatory status.
Louisiana	No	Yes	All bison are considered livestock.	No	Louisiana Code of regulations 7: XXI.11705; No mention of bison in SWAP or in wildlife regulations.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land; Regulatory status.
Minnesota	No	Yes	Wild bison are considered extirpated in MN; Found only on a couple of small preserves	No	Minnesota statutes for livestock (17A.03); Bison not mentioned in SWAP.	No	Agriculture and forestry conflicts; Regulatory status.
Missouri	Yes	Yes	Wild bison are considered extirpated in Missouri.	No	Identified as class 1 wildlife in title 3 Code of State Regulations (CSR) 10; Identified as livestock in title 2 CSR 30.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land.

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Montana	Yes	Yes	Game animal status; Tier 1 species in SWAP; Species in need of management in YNP; Managed in habitats adjacent to YNP. On NBR; Ownership of NBR is in dispute; American Prairie Reserve (APF).	Yes in SWAP; National Bison-Refuge Plan; Yellowstone Interagency Bison Management Plan; APF Bison Reintroduction and Conservation Plan.	Montana Environmental Policy Act (Montana Code Annotated (MCA) 75-1-102); Legislative authority to manage wild bison in Montana (MCA 81-2-120; MCA 87-2-130); SWAP; Interagency Bison Management Plan-EIS, 2000.	Yes; Charles M. Russell Refuge Plan	Agriculture and forestry conflicts; Disease status in YNP.
Nebraska	No	Yes	Wild bison are considered extirpated in the state; Bison are defined as livestock; Found only on several small preserves.	Yes; Only on National Wildlife Refuge and TNC preserves.	Bison found only in the Department of Agriculture regulations. Title 23 and 54; Section 54 defines the required health regulations for cattle and bison;	No; Possibly tribal efforts.	Agriculture and forestry conflicts.
New Mexico	Yes	Yes	Classified as game animals in 1978; Identified in wildlife database as "apparently no longer occurring" but not identified as extirpated or extinct; Included in SWAP.	Yes	Title 17-2-3 New Mexico Administrative Code (NMSA) 1978 classifies bison as game animals except where raised in captivity for commercial purposes; Title 19 (Wildlife) chapter 31 describes the legal weapons for taking of bison yet there are no hunting regulations for bison (19.31.10.16); Title 19 Chapter 26 describes livestock (and names bison) as domestic animals raised on a ranch (19.26.2.7); Title 21 (agriculture and ranching) has many references toward management of bison.	No	Agriculture and forestry conflicts; Lack of suitable habitat.
North Dakota	No	Yes	Classed as non-traditional livestock; Bison are found only in Theodore Roosevelt National Park and managed as domestic livestock outside the National Park.	Yes; Only on two federal and one TNC preserves.	Unable to find any reference to bison in agriculture regulations (Title 4) or wildlife regulations (Title 20).	No	Agriculture and forestry conflicts; Regulatory status.

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Nevada	No	Yes	Wild bison are considered extirpated in Nevada and are not classified by the Nevada Dept. of Wildlife; Bison are classified by Nevada Dept. of Agriculture.	No	Bison not referenced in wildlife regulations (Nevada Administrative Code (NAC) 502, 503 or 504); Regulations note that possession of bison does not require a permit; Regulations pertaining to domestic bison are described in NAC 571.	No	Agriculture and forestry conflicts; Regulatory status.
Oklahoma	No	Yes	Classified as domesticated animals; Protected on two preserves (one federal and one private).	Only for Wichita Mountains National Wildlife Refuge and TNC preserve.	There are no references to bison in the Game and Fish regulations in Title 29; Title 800-25-25-3 lists species of wildlife exempt from wildlife permits or license; Regulations pertaining to domestic bison are described in Title 2 (Agriculture) and Title 4 (Animals) of Oklahoma Code.	No	Agriculture and forestry conflicts; Small parcels of public or private conservation land; Regulatory status.
South Dakota	Yes, partially	Yes	Identified as "Wildlife" only in the confines of National Park System; Bison are contained within Custer State Park.	Yes; Only within the State and National Park System and one TNC preserve.	South Dakota statutes Title 41 do not mention bison anywhere in the wildlife regulations; State laws identify bison as livestock.	No	Status of bison is livestock outside the National Park System; Management under captivity; Agriculture and forestry conflicts; Regulatory status.
Texas	Yes	Yes	Texas Parks and Wildlife Department considers wild bison extirpated; Found only in Caprock State Park and on one TNC preserve.	Only within one state park and one TNC preserve.	No longer considered a game animal in Texas - Parks and Wildlife Code Chapter 43; Texas Agriculture Code (chap. 2.005) recognises bison as wild animals indigenous to the state but can be raised for commercial purposes to preserve the species.	No	Agriculture conflicts; Small parcels of public or private conservation land; Regulatory status.
Utah	Yes	Yes	Free roaming populations are found in the Henry Mountains and on Antelope Island; Utah just completed a reintroduction to the Book Cliffs.	Herd management plan being developed for the Henry Mountains population and Book Cliffs.	Wild bison are managed under regulations in Title 23 of Utah Code; Regulations pertaining to domestic bison are described in Title 4 of Utah Code.	Yes; Recent introduction to Book Cliffs.	Agriculture conflicts.

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Wyoming	Yes, partially	Yes	"Wildlife" within national forest and national parks of Park and Teton counties in the GYA; Are classified as domestic animals in the remainder of the state.	Yes, in NER and GTNP Management Plan and EIS; Yellowstone population conserved though Interagency Bison Management Plan with Montana	WY (Wyoming Fish and Game Commission regulation) 11-6-32 vi classifies bison as livestock unless otherwise designated by Livestock Board and Wildlife Commission; WY 23-1-302 xxvi gives authority to designate individual bison or herds as wildlife; Management Plan and EIS for bison and elk on NER and Grand Teton National Park.	Yes; Northern Arapaho re-introduction to the Wind River Reservation.	Status of bison outside of designated areas in statute (Park and Teton Counties); Disease status of YNP and Jackson-Grand Teton bison; Agriculture and forestry conflicts; Regulatory status outside of Parks.
Canada	Yes	Yes	The General Status of Species for plains bison is Sensitive; Plains bison petitioned for endangered status denied-Current Status Threatened; Wood bison are listed as Threatened; Both subspecies are managed as native wildlife on some Canadian Parks and in some provinces	No, plains bison; Yes, wood bison, in National Recovery Plan.	1996 Accord for the Protection of Species at Risk in Canada; Species at Risk Act, 2002; COSEWIC designated plains bison threatened in May 2004; Wood bison were classified as endangered in 1978 moved up to Threatened in 1988 (COSEWIC); Canada National Parks Act (2001); Wood bison are on The Recovery of Nationally Endangered Wildlife (RENEW) priority list.	Yes, in Banff National Park, Waterton Lakes National Park, Grasslands National Park for plains bison; National Recovery Plan for wood bison.	Absence of strategic planning for plains bison; Multiple jurisdictions and coordination of agencies; Agriculture and forestry conflicts; Disease transmission to cattle: Diseased status of some existing wild bison; Management in captivity
Alberta	Yes for wood bison; No for plains bison.	Yes	Consider plains bison as extirpated; Plains bison are not listed under the Alberta Wildlife Act; Plains bison listed at risk in 2000 status report; Lists wood bison as endangered in the Hay-Zama wood bison protection area in NW Alberta.	No for plains bison; Yes for wood bison, with National Recovery Plan.	1985 Policy for the Management of Threatened Wildlife in Alberta; Alberta Wildlife Act (1998) 2000 Status of Alberta Wild Species.	Yes; in Banff and Waterton National Parks.	Legal status of plains bison is "livestock"; Agricultural and forestry conflicts; Conservation status of hybrid bison in WBNP.
British Columbia	Yes	Yes	For plains bison the General Status of Species=Sensitive. General Class is "Big Game" and "Wildlife"; Listed as Vulnerable; Wood bison are on the Provincial Red List-Imperiled subspecies.	No for plains bison; Yes –for wood bison, with National Recovery Plan	British Columbia Wildlife Act (1996) General Status of Species in Canada (CESCC 2001); Provincial Blue List and Provincial Red List (British Columbia Conservation Data Centre 2000).	No for plains bison; Wood bison under National Recovery Plan.	Agricultural and forestry conflicts; Plains bison outside their original range.

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Manitoba	Yes for wood bison; No for plains bison.	Yes	Provincial Heritage Status-S1-Susceptible to Extirpation; Listed as "at Risk" by CESCC; Plains bison are not listed as "Wildlife" but are classed as Livestock; Wood bison are protected in the Chitek Lake area.	No for plains bison; Yes for wood bison, with National Recovery Plan.	Manitoba Wildlife Act (2004); Manitoba Agriculture, Food and Rural Initiatives (2003).	No for plains bison; Wood bison under National Recovery Plan.	Status of plains bison as "livestock"; Agricultural and forestry conflicts.
Sas-katche-wan	Yes	Yes	Provincial Heritage status - S3=Vulnerable; CESCC status as "may be at risk"; Bison are "Wildlife" but there are no open hunting seasons; Department of National Defense offers protection due to prohibition of trespass except by Cold Lake First Nations; First Nations have aboriginal hunting rights; protected in Buffalo Pound Provincial Park, Prince Albert and Grasslands National Parks; Nature Conservancy of Canada (NCC) Old Man on His Back Conservation Area.	No for plains bison except in National or Provincial Parks; Yes for wood bison, with National Recovery Plan.	Saskatchewan Wildlife Act (1998); The Wildlife Regulations, 1981; Saskatchewan Game Farm Policy 1998 includes captive bison; Range Access Agreement between CLFN and DND (2002); Saskatchewan Parks Act (1997); Cooperative Inter-Jurisdiction Plains Bison Management Strategy.	Plains bison in Grasslands National Park; Wood bison under National Recovery Plan.	Agriculture and forestry conflicts; Limited suitable habitat.
Northwest Territories	Yes	Yes	Both plains and wood bison are "Wildlife"; Wood bison are designated as in danger of becoming extinct; Some regulated hunting of wood bison is allowed in designated herds; Importation of plains bison prohibited.	Yes, wood bison in National Recovery Plan; Bison harvest is regulated under a co-management process; Hook Lake is managed under a specific Hook Lake Recovery Plan.	Northwest Territories Wildlife Act (1964) designated wood bison a protected species; Agency policies prevent plains bison ranches or introduction to the wild.	No	Conservation status of hybrid plains/ woods bison in WBNP.
Yukon	Yes	Yes	Both plains and wood bison are "Wildlife"; Wood bison are a protected species; Importation of plains bison prohibited.	Yes, wood bison in National Recovery Plan; Bison are managed on a sustained yield basis under a cooperative management plan.	Yukon Wildlife Act (2002); Agency policies prevent plains bison ranches or introduction to the wild.	No	

Table 8.1 *(continued)*

Country/ State Province	Animal Classification		Protected and/or Wildlife Status	Long Term Conservation Goal	Key Statutes or Policies Affecting Conservation	Proposals for Restoration	Major Legislative and/or Policy Obstacles
	Wildlife	Domestic					
Mexico	Yes	Yes	Appeared as extirpated in 1994; In 2002 red-list Janos bison were listed as endangered.	Not officially, however non-governmental conservation is emerging and proposing a long-term vision for conservation preserves.	Secretaria de Desarrollo Social, 1994-NOM-059-ECOL-1994. Secretaria de Medio Ambiente y Recursos Naturales-NOM-059-ECOL-2001.	Yes, Developing a National Recovery Plan.	Agriculture conflicts; Lack of suitable habitats: Small properties available; Economic and market obstacles; Lack of public interest: A developing wildlife conservation programme; Varied status of the Janos bison at the international border with New Mexico
Tribal and First Nations	Yes	Yes	Varies by tribe or First Nation; Most tribes with strong cultural histories protect bison for tribal use; The Intertribal Bison Cooperative has 57 member tribes that are actively pursuing bison management for cultural and commercial interests.	Yes, depending upon tribal conservation programmes; Some tribes are developing advanced game codes and sophisticated species restoration and management plans.	Varies but generally determined by Tribal Council and managed by Tribal Fish and Game Commissions; Intertribal Bison Cooperative was formed to encourage the restoration of bison; Cultural consideration is primary driver for legal and policy considerations by each tribe.	Yes	Variability of tribal government structure and function; Agriculture conflicts; Variable wildlife conservation and management infrastructure.

and protection of the Janos-Hildago bison herd is an example of this rising conservation interest. Bison in this specific population are protected by endangered species status under federal law. All other bison in Mexico are privately owned and maintained on fenced private property.

Over 93% of the bison in North America are privately owned and managed for commercial production (Chapter 7). Bison can be kept as domestic livestock in all of the U.S. These bison are privately owned and typically managed for meat production or breeding. In Alberta, Saskatchewan, and Manitoba, where bison are regulated as livestock, individuals in the private sector may own bison. In British Columbia, bison may be produced commercially, but a game-farming license is required. Commercial herds owned by individuals, corporations, or NGOs are managed independently, subject to market forces, and regulations governing animal health and trade. In the Yukon and Northwest Territories, existing policy prevents the establishment of plains bison ranches or their introduction into the wild. There is no unified conservation effort or regulatory framework that encourages or facilitates conservation of commercial bison as wildlife at national, state or provincial levels. The “laundering” of wild animals through captive-breeding operations and farms has not been detected in Canada or the U.S

8.3.2 Disease status

Early in the history of bison restoration, diseases were not considered very important and restoration efforts proceeded with limited concern for the transfer of pathogens. As a result of significant failures to guard against disease transfer and control during translocation, bison restoration projects today have to overcome some historic baggage.

With the development of an extensive and aggressive domestic animal disease control programme in North America during the mid to late 1900s, the implications of diseases to wildlife restoration has increased (Friend 2006). Furthermore, with the successful restoration of many wildlife species, and the subsequent increase in their distribution, these same diseases are now very important to the wildlife community (Wobeser 1994). Finally, increased globalisation and the high mobility of society are increasing the likelihood of pathogen transfer across continents, thereby increasing the vigilance of disease control programmes (Friend 2006). As a result, efforts to conduct bison restoration will have to consider the significance of diseases in restoration projects. For a comprehensive review of diseases significant to bison conservation, the reader should refer to Chapter 5 of this document. Unfortunately, disease issues often trump conservation interests, especially when the conservation actions are likely to come in direct conflict with powerful agricultural industries. This will necessitate the careful selection of source

stock, extensive testing and screening of source herds, health monitoring of herds, and regulatory involvement in the process of translocation (Table 8.2).

Successful restoration projects will need to navigate the animal health regulatory process necessary to permit translocation of bison and to accomplish the eventual establishment of healthy conservation herds in North America (see Chapter 5). The key disease categories that need to be considered in bison restoration are: Foreign Animal Disease (FAD) events, regulatory diseases (across international boundaries and within country jurisdictions), and diseases of significance to livestock, but not regulated. A foreign animal disease will cause significant impact to bison restoration and agricultural activities in any jurisdiction. A significant response network is already available to address FADs within countries, states, and provinces. This response network typically involves federal, state, and provincial agriculture, wildlife, and public health agencies. Any such event involving source bison, or on a restoration landscape, would halt a restoration project and stop movement of individuals from an infected source stock. A bison conservation effort is at risk when a bovine FAD arrives in any country, and a subsequent federal response is required to immediately stop movement of all affected animals. Regulatory diseases on the other hand are typically more manageable, with regulatory steps required to allow movement after health standards are met. Although they are significant, there are established protocols to test, manage, and even control many of these diseases. Each disease has its own characteristics and subsequently the challenges of disease testing, management and control vary. There have been many historic efforts, some successful and some not, to control and eliminate these types of diseases in bison. This historic record is a good place to go to see what works and what does not.

The science behind wildlife disease issues is improving, but more work is needed (Friend 2006). Considerable research is needed to establish quarantine and testing protocols required to ensure the safe movement of animals. To be certain that restoration projects will not introduce new diseases, or exacerbate existing diseases, it is important to accurately and reliably establish the health background of source herds and of the wild and domestic animals within restoration areas. There will be many agricultural interests examining bison restoration efforts, so during a restoration project, utmost attention should be given to communicating the health prevention measures taken, and testing information obtained. It is likely that agricultural conflicts will be one of the major impediments to restoration, but embracing modern approaches, with careful monitoring of population health and integrating regulatory health officials into the projects from the beginning, can mitigate most disease issues. Restoration efforts should establish and maintain regular communication with state, provincial, and federal animal health regulators and other appropriate public health agencies. General communications should also be established with key animal health organisations, such as the U.S. Animal Health Association or Wildlife Disease Association, to ensure that the best health information is being openly discussed and shared with affected groups and individuals.

Restoration projects that involve international transport of bison are subject to additional legal and policy considerations. For example, increased animal disease regulations due to any discovery and control of bovine spongiform encephalopathy (BSE) across the U.S.–Canadian or U.S.–Mexican borders will undoubtedly complicate trans-boundary movement of bison (APHIS, USDA 2007). Until these restrictions are eased there will be limited opportunity for international movement of bison despite any evidence that this disease actually exists in American bison. Restoration planning will need to include a thorough search of current international border restrictions related to disease control. Early discussions with animal health regulators will be essential to identify any disease regulations and specific testing requirements for transport of bison across an international boundary.

Table 8.2 *Some diseases that will or may have implications to bison restoration.*

Disease	Restoration is Prevented	Significant Impediment	Medium Impediment	Locally Significant
Any FAD*	X			
Anthrax	X			
Bovine Tuberculosis	X			
BSE**	X			
Brucellosis		X		
MCF***		X		
JD****			X	
Respiratory Diseases (e.g. BVD, IBR, BRSV, PI3, Bacterial)			X	X
Endoparasites				X
Ectoparasites				X
Other Bacterial/Viral infections				X

* Foreign animal disease ** Bovine spongiform encephalopathy
*** Malignant catarrhal fever ****Johne's disease.

8.4 Legal and Policy Obstacles Hindering Conservation of Bison

Bison conservation and restoration intersects directly with many laws, rules, and policies within a complex social-economic-ecological matrix. Isenberg (2000) detailed the historical relationships of social and economic change to preservation of the bison at the turn of the century. Bison were caught in a vortex of social, economic, and ecological change on the Great Plains, and were nearly exterminated (Isenberg 2000). These changes remain the central themes for an ongoing modern Great Plains drama. The continued expansion of the human population (except in rural areas of the Great Plains, where it is declining), the dominant use of prairie grazing lands for domestic livestock, and the conversion of native prairie to cropland, have led to persistent competition between wild bison and humans for primary use of grassland habitats. However, intermixed among these agricultural and urbanising landscapes are relatively intact islands of suitable prairie habitat with potential for bison restoration. These remaining intact landscapes are typically a mix of private and public land and are characterised by a mosaic of land ownership, land management regimes, socio-economic interests and land use policies. Excluding disease status of bison (see above section), we have identified six principle obstacles that are major impediments to conservation of bison within this social-economic-ecological landscape. Although there are many other minor obstacles, most of these are site specific in nature and can be addressed without efforts to shape law/policy or public attitudes in a range wide scale.

The most significant legal and policy obstacles to wild bison restoration are indirectly derived from socio-economic concerns and persistent historical paradigms of bison management. The greatest impediment is social intolerance for a large grazing bovid that is perceived to compete with other interests adjacent to, or within, prospective prairie landscapes suitable for bison restoration. As a species, the biology, behavioural plasticity, and wide ecological scope of bison provide unlimited opportunity for restoration efforts with a high probability of success in recolonising available grassland habitats.

8.4.1.1.1 Confusing legal classification and status

There are relatively few states and provinces where conservation bison herds are legally classified as wildlife (see Table 8.1). Other states/provinces have mixed status for bison and there is some confusion relative to the legal authority or policies of other bison herds. Many states/provinces within the original range of bison have classified bison as domestic livestock and management authority is vested within agricultural agencies. In addition, many conservation herds are managed by federal agencies, such as the National Park Service (NPS) or U.S. Fish and Wildlife Service (USFWS) Refuge System, adding a federal layer of laws and policies upon bison. This confusing legal classification and status increases the difficulties in conserving the species in a comprehensive manner.

Privately owned bison herds do not enjoy legal status as wildlife. Some bison owned by private producers may have conservation value (e.g., good genetics), but management is principally production oriented. Several privately owned bison herds managed by NGOs are managed in an ecologically relevant manner, but are also not legally classified as wildlife. In Alaska, wood bison were not considered native wildlife for many years by the USFWS, but plains bison herds were established by the State of Alaska and managed as wildlife. Federally owned bison herds are typically managed as wildlife, although behind high fences, but they are usually not recognised as native wildlife by state authorities. This confusion in the legal status of bison is probably the single most important obstacle impeding ecological restoration and hindering a nationwide conservation strategy for this species.

8.4.1.1.2 Historical management policies

Adding to the confused legal status of bison is the consistent policy of establishing and managing bison behind high fences by state and federal agencies. This management paradigm, established in the early 1900s to protect the species, has persisted, further confusing the management policy framework and public attitude toward bison as a wildlife species. This confusing management approach to bison is not consistent with other wildlife and has produced the second most significant obstacle to ecological restoration. Few agencies or members of the public identify bison as native wildlife deserving the same status as other free-ranging wildlife. A public recognition for the need to manage bison as wildlife, in an ecologically sensitive way, is essential to successful restoration. Ecological restoration of bison will be hindered until this management paradigm shifts and social tolerance is developed to allow free-ranging bison on native prairie habitats.

8.4.1.1.3 Complex partnerships needed to manage large landscapes

Bison populations managed on public lands are considered as the core of the wild herds being managed to conserve the species for the future (Boyd 2003; Knowles *et al.* 1997). However, few public land management agencies have a sufficient land base to manage bison populations in a manner that allows for natural selection processes. Bison need large landscapes to allow natural movements and express appropriate ecological function. Unfortunately, most wild bison are being managed as small populations on relatively small areas by single agencies or tribes. Forging the partnerships to manage populations across multiple jurisdictions on large landscapes seems to limit existing conservation efforts. Building partnerships to manage wild bison, as a public trust resource by a coalition of private and public interests, while theoretically feasible, has been limited in practice.

The problems of governance and scale have been well discussed in the literature (Westley and Miller 2003; Wilke *et al.* 2008). There typically is a wide range of actors associated with the conservation of large landscapes and species with large spatial needs such as bison. It is easy to underestimate the complexity of ownership patterns on large landscapes and to miss identifying key actors on this conservation stage. Furthermore, different kinds of actors will have different rights, interests, and capacities, and will need to be approached in different ways (Wilke *et al.* 2008). The challenge of forming complex partnerships at the appropriate scale is formidable and often discourages efforts to consider large-scale initiatives.

8.4.1.1.4 Defining the social and economic value of wild bison

Many legal and policy changes necessary for the ecological restoration of bison are linked to social and economic factors. Agencies and conservationists need to identify the economic, social, and ecological benefits of restoring wild free-ranging bison, while protecting existing cultural and economic interests (Geist 2006). The value of restoring wild bison must be expressed in a manner that does not necessarily diminish the economic value of existing livestock and commercial bison markets managed under an agricultural paradigm. This may take creative approaches involving policy adjustments and paradigm shifts among cooperating agencies/private sectors that optimise complimentary land use strategies and mitigate identified conflicts. This process could be supported by tax incentives, payment for environmental services, ecotourism, incentives for landowner cooperation (e.g., Colorado's Ranching for Wildlife Program), extension services, and training for a new generation of landowners and managers.

8.4.1.1.5 Coordination of policies, rules, and regulations by government

Coordination of management policies, rules, and regulations (or the lack thereof) by various governments has also hindered bison conservation efforts. Because no single government agency owns or manages sufficiently large blocks of land to sustain free-ranging bison, cooperation between agencies is needed for restoration and conservation planning and implementation. Many agencies' missions are not readily compatible with cooperative management strategies needed for conservation of bison at large scales. Furthermore, many land management agencies have directed missions and goals that may not immediately support the types of policy changes required to manage for the conservation of bison. In addition to coordination among government agencies there is often a compelling need to coordinate with and among Tribal and private lands influenced by other policies and management objectives.

8.4.1.1.6 Agricultural conflicts among mixed land ownership

The most significant conflicts associated with restoring wild free-ranging bison are likely to be with agricultural neighbours living near conservation reserves. Establishing free-ranging wild bison herds in North America will undoubtedly lead to conflicts from crop damage, forage competition with livestock, mixing with livestock, possible interbreeding with cattle, disease issues, and damaging private property. These agricultural conflicts are not entirely uncommon with other large herbivores.

These six policy obstacles are quite common across international, state/provincial, and public/private jurisdictional boundaries within the original range of bison. Bison restoration must occur at sufficiently large landscape scales that few, if any, individual agencies will be able to implement an effective management programme on their own. Coordination of agency missions to conserve wild bison must in the long run be a negotiated process to ensure joint conservation goals can be established and implemented within the legal framework. In addition, conservation goals must be established to encourage privately owned populations of wild bison (as defined elsewhere in this document) to be managed over the course of many years in a manner that allows ranchers to build new markets that provide economic benefits for conserving the characteristics of ancestral bison herds.

Other obstacles to restoration include: long time scales, institutional resistance, funding, and conservation mission creep. Most large-scale conservation projects for long-lived mammals need to play out across long time scales. It is easy for conservation partners to fatigue, and for shifting political and social climates to make extended time scales problematic. Institutional resistance is inevitable within and among the cooperating agencies and private sector partners involved in a bison restoration project. Within agencies and organisations there is likely to be some internal resistance to various aspects of the project, so care will be needed to build reasonable consensus. Although many agency or private groups may support the concept of restoration, there is a fundamental need for funding and contribution from all critical partners. Finally, with every conservation programme, the implementation can creep off target or move beyond intended goals. This has a tendency to dismantle social and political support for a project by creating a different type of management or objective than was originally identified and agreed upon by stakeholders. For example as landscapes become larger, and some measure of success is achieved, there may be a tendency to move the conservation focus. Conservation and restoration strategies and planning efforts need to clearly articulate the conservation goal and be able to measure progress and identify critical benchmarks for meeting those goals.

8.5 Overcoming Obstacles to the Ecological Restoration of Bison

8.5.1 Disease management considerations

Animal health and disease issues can present significant obstacles to bison restoration efforts. The presence of regulated diseases in bison can prevent the transport of bison across jurisdictional boundaries and limits access to sources of bison. Potentially important sources of genetically reputable bison for restoration from WBNP and YNP are deemed unsuitable because of their disease status. However, recent research efforts are exploring methods of quarantining bison from these sources to determine if disease free status can be established for animals passing through strict quarantine procedures (Nishi *et al.* 2002b; 2006). The use of effective quarantine to release these genetic sources of bison could be extremely helpful for enhancing access to a broader source gene pool for restoration.

Before animals can be translocated for restoration, each state or province and international border that would be crossed by bison will require specific health tests. When designing specific restoration projects, it is essential to contact State/Provincial or Federal Veterinarians so that required disease testing is a clearly articulated. Appropriate regulatory veterinarian(s) have the expertise to establish which disease(s) require screening, and which approved test protocols and diagnostic laboratories are acceptable/required for health clearance for specific jurisdictions. These health approvals need to be obtained *before* transporting any bison across jurisdictional lines. Good health monitoring of the source herd can provide important information to support the testing carried out prior to transport. A good health-monitoring programme will identify existing diseases circulating among the source herd, and include background information regarding the presence or absence of regulated diseases.

Infectious disease is an emerging threat that conservationists may be ill equipped to manage (Woodroffe 1999). Despite these limitations there are several disease management models across the globe that could help support disease management planning in bison (Osofsky *et al.* 2005). Through careful planning, and research of existing disease management models, this issue can be substantially reduced in scope and impact.

8.5.2 Legal status and policy considerations

In order to address obstacles to ecological restoration of bison, it is important to identify the strategic components of a continental conservation plan. The IUCN BSG has provided this strategic framework and associated technical guidelines for bison conservation to help agencies and the public accomplish ecologically relevant conservation projects. This framework can assist in resolving issues of international status and overcome legal/policy obstacles from a strategic perspective. While this continental wide strategy should be useful in advising some of the overarching legal and policy changes necessary to achieve conservation missions, federal state/provincial and local authorities will need to be involved, and supportive of significant local changes in policies, so that restoration projects can be accomplished.

For most bison restoration projects to advance, changes in laws and policy will be necessary, but they must be designed to encourage bison conservation in an ecologically relevant manner with due consideration of the potential socio-economic consequences to countries, state/provinces or local communities. Laws, rules, and policies of governments can impede conservation. However, they may be transformed into supportive frameworks if there is social acceptance and a high value associated with restoration goals. Comprehensive policies and laws need to be developed that promote ecosystem conservation, without being overly prescriptive. There will be a need for negotiation, compromise, and cooperation in the process of changing laws and policies. Such processes are interdisciplinary in nature, requiring integration of the disciplines of economics, law, ecology, and sociology to be successful (Wilkie *et al.* 2008).

8.5.2.1 Role of the non-governmental organisations

NGOs can play a key role advocating for the necessary changes to laws, rules, and policies that hinder restoration. NGOs can actively lobby for necessary legal/policy changes by federal, state or provincial governments to overcome identified obstacles. They can provide and secure or support government funding for conservation. Coalitions of NGOs and government agencies can be formed to advocate for specific conservation efforts. NGOs could also support the ecological, economic, cultural and spiritual interests of indigenous peoples with an interest in bison conservation. They can aid local community groups in negotiations and help these communities influence stewardship of natural resources in their area (Fraser *et al.* 2008). Finally, some NGOs could help to resolve international issues related to status and legal/policy obstacles associated with individual projects. While many agencies must operate within jurisdictional boundaries, NGOs can transcend these limitations and broker communication and cooperation among agencies.

The historic model of the American Bison Society (ABS), as a consortium of individuals and groups, is an example of how conservation organisations can play a powerful role in species restoration. The ABS advocated for the formation of bison preserves in the west and supported new wildlife policy and legislation to preserve a species at the brink of extinction. The Rocky Mountain Elk Foundation is an excellent example of a North American NGO employing land preservation and active advocacy to support conservation policies that create

suitable landscapes for wild elk. TNC is another conservation organisation that has worked effectively with private landowners and government to protect biodiversity and establish protected areas through the use of land purchase and easements. TNC has incorporated bison on several of these landscapes as a means of providing ecosystem services.

8.5.2.2 State/provincial and federal governance

It is vital that governments (both elected officials and government agencies) be engaged in policymaking and legislation that support bison conservation. Government agencies typically establish processes within their statutory authority to evaluate and approve appropriate policy changes, and recommend congressional and legislative changes, necessary to conduct conservation. It will be necessary to employ all of the instruments and processes of governments to modify policies or legal statutes affecting bison conservation at state, provincial, and federal levels. Government agencies can also direct public funding and staff resources to support implementation of a restoration project, and develop the necessary interagency agreements to achieve conservation goals. It is necessary that elected officials, as representatives of the people, approve relevant policies, and to develop a legislative framework that supports bison restoration, by empowering the appropriate agencies to implement management strategies for conserving bison as publicly owned wildlife. For example, opportunities for bison restoration could be increased by linking them to existing policies for land use planning for ecological integrity. This will require building public support for policy changes and acceptance by respective constituencies that these governments serve, by using, for example, extensive outreach, public advocacy and education. It will also require educating and influencing key politicians and government officials with critical decision making roles.

8.5.2.3 The private sector

There is substantial evidence of a massive change in land ownership and shifting economies taking place in the Great Plains and West, as well as some multiple-generation ranchers who are entrepreneurial and ready for change (Powers 2001). This shift in land ownership, economies, and visions brings opportunities to create a new paradigm for managing rangelands of high conservation value. Private landowners could have a strong voice influencing elected and agency officials of the need for policy changes that provide incentives for, and remove barriers to, bison conservation on private lands. Therefore, there is currently a substantial opportunity to engage landowners to petition government for change.

Privately owned bison managed on privately owned land typically present fewer regulatory obstacles than encountered in restoring wild bison. However, private herds are typically managed under a private property decision framework, which may not lead to a bison herd of conservation value. It is difficult to blend private property rights with the public trust framework for wildlife without negotiation and compromise. For effective cooperation, private owners of bison, or bison habitat, would have to be willing to sacrifice certain rights and submit to public review and scrutiny of operations. Government partners would also need to be sensitive to private property rights and the economic value of those rights for individuals or corporations willing to engage in bison conservation. Effective cooperation should include creative incentives, financial or other, to encourage the private entrepreneur to engage in bison conservation. For example, conservation easements compensate land-owners for transferring specific property rights. As noted earlier, a system for certifying producers who follow conservation guidelines in managing their bison herds may also provide an incentive.

To increase opportunities for large-scale conservation of bison, there is a need for federal and state policy programmes that foster the creation of private (for-profit or non-profit) protected areas (PPAs). PPAs are one of the fastest growing forms of land and biodiversity conservation in the world (Mitchell 2005). However, unlike Australia and many countries in southern Africa, the U.S. and Canadian federal governments and state and provincial governments do not generally have policies specifically supporting the creation of PPAs. The IUCN has developed guidelines for, and explored policies and programmes that support, the creation of PPAs (Dudley 2008). The danger is that private bison reserves may quickly shift away from a conservation mission and devolve to “private game farms” for privately owned wildlife, for which most states have policies and regulations. In addition, private nature reserves may be vulnerable to change of ownership and subsequent shifts in their mission unless clear legal instruments are in place to protect conservation values. Clear guidelines for management and accountability for the long-term security of private protected areas is essential (Dudley 2008).

8.5.2.4 Indigenous peoples

Many protected landscapes and seascapes would not exist without the deeply rooted cultural and spiritual values held by the people that originally inhabited these places and who often continue to care for them (Mallarach 2008). Mallarach (2008) points out that safeguarding the integrity of traditional cultural and spiritual interactions with nature is vital to the protection, maintenance, and evolution of protected areas. Hence, protected landscapes and seascapes are the tangible result of the interaction of people and nature over time. In recent years there have been many important developments in conservation and protection of important landscapes on

indigenous peoples' land (Dudley 2008). Within the original range of bison, there are extensive Native-owned grassland and mountain foothills landscapes suitable for bison restoration. These tribal lands present great opportunities to restore bison in a culturally sensitive way, protecting the rights and interests of traditional landowners. IUCN has identified basic principles of good governance as they relate to protected areas overlapping with indigenous peoples' traditional lands. In addition, there is one group, the ITBC, whose defining mission is restoration of bison. Cooperation of tribes and tribal organisations is essential to the conservation and restoration of bison in North America and should be encouraged. Governments and NGOs in North America should examine and then modify current policy and legislation to support the traditional and cultural interests of indigenous peoples relevant to bison restoration.

There is significant variation in jurisdictional powers over tribal landscapes, ranging from sovereignty over the land to co-management with other governments. It is important to understand indigenous peoples' rights and their level of authority over landscapes when designing restoration and conservation plans for bison. It is equally important to understand the cultural traditions and spiritual connections between indigenous people and bison. Some of this information is traditional knowledge that can only be acquired through conversation with elders and tribal leaders.

8.5.2.5 Local communities and economies

One key ingredient of successful bison conservation is active stakeholder participation in the development and implementation of conservation programmes. Stakeholders include all people or groups of people who are affected by, or can affect, the conservation programme. On public lands it is particularly important to have local support (individuals, adjacent landowners and communities) for policy changes and new legislation, and to avoid backlash from the types of regulatory protection that might be necessary for a successful conservation initiative (Merenlender *et al.* 2004). For landscapes with mixed jurisdiction (public and private), it will be necessary to engage stakeholders by developing critical relationships, building mutual understanding and designing an appropriate co-management framework.

Restoring bison to mixed-use landscapes will involve addressing conflicts with neighbouring landowners. These neighbours need some assurance that when conflicts arise they will be addressed as restoration projects are implemented. Comprehensive restoration and management plans will be required to clearly articulate population goals and to identify how agricultural conflicts are going to be resolved. Ranch land neighbours, living on agriculture lands near restoration projects, pose a great challenge, but may also provide a significant open-space buffer essential to the success of large-scale conservation efforts. Measures must be designed to appropriately manage the distribution of bison and address any trespass conflicts that arise. Other concepts to consider include the idea of wildlife damage insurance, economic incentives, and creative conservation-incentives to encourage and reward tolerance (Muchapondwa 2003).

Ecosystem services have been defined as *"the process by which the environment produces resources that we take for granted such as clean water, timber, pollination of plants, and habitat for fish and wildlife"* (Daly *et al.* 1997). Bison restoration and conservation programmes should consider assessing the value of ecosystem services associated with the development of a conservation strategy for bison. TNC has made significant investments in pursuing the valuation and marketing of ecosystem services as a conservation strategy and financing tool (Groves *et al.* 2008; Nelson *et al.* 2009). TNC, in collaboration with Stanford University and WWF, has developed a Natural Capital Project to better understand the economic values associated with natural systems (www.naturalcapitalproject.org). This project developed a tool known as InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) for quantifying ecosystem services for their inclusion in natural resource decision-making. They also established a "Swat Team" of ecosystem modellers and mappers who use InVEST to bring the valuation system into policy and decision-making for conservation projects (Groves *et al.* 2008). Approaches such as this may be useful in the valuation of ecosystem services associated with the conservation of large grassland landscapes and the role of bison as a keystone herbivore on those landscapes. We recommend further exploration of these emerging valuation tools and their application to the conservation and restoration of bison in North America.

In another novel programme, a coalition of NGOs, state and federal agencies, ranchers, and researchers has been developing a Pay-for-Environmental Services (PES) programme in Florida (Bohlen *et al.* 2009). This programme compensates cattle ranchers in Florida's northern everglades for providing water storage and nutrient retention on private lands. Key challenges to this programme include: identifying a buyer and defining the environmental service; agreeing upon approaches to quantify the service; reducing programme costs in light of current policies; and complex regulatory issues. Design of a PES programme requires navigating through a complex regulatory maze created by multiple state and federal agencies (Bohlen *et al.* 2009). This new model may provide an example for developing a PES on bison landscapes. In the case of bison restoration it will be challenging to meet the needs of multiple stakeholders, and to find the first entrepreneurial landowner willing start a new trend by participating.

Significant challenges lie ahead for the formulation of laws and policies about ecosystem services (Ruhl 2009). Some critical steps suggested by Ruhl (2009) include better definition of property rights, policies that prime the markets for ecosystem services, designing better governance institutions and instruments for these markets, and creative research to meet policy needs. Some governments are already engaged in this type of work, so interested readers are encouraged investigate programme and policy initiatives in their region (Freese et al. 2009). Furthermore, conservation organizations are encouraged to coordinate their activities with evolving government initiatives to more efficiently advance ecosystem-based conservation.

8.5.3 Coordination of agency missions, goals, regulations, and policies affecting bison conservation and restoration

There may be a need for new governance systems that will allow local communities, tribes, and governments to co-manage grassland reserves large enough to sustain bison. Political boundaries, agency policy, and legal jurisdictions need to be creatively blended to create a cooperative atmosphere for the successful establishment and co-management of new or expanded bison populations in the future. Accomplishing the coordination necessary to conduct effective conservation and ecological restoration will be formidable. However, the rewards for such effective coordination will go beyond the benefit of placing bison on the land, and could encourage much more opportunity to conserve other species associated with these landscapes.

It is likely that some type of standing co-management council or committee may be necessary to coordinate management of large landscapes with complex land ownership and affected local communities and economies. This committee should be structured and function to facilitate and maintain partnerships among the various government agencies, NGOs, landowners, and sportsmen or conservation groups that have interest in the project area. A co-management committee can encourage efficiencies in funding and coordinate restoration activities of the various stakeholders. A committee should include representatives from local stakeholders who are affected by the coordinated management effort. A recent announcement by the U.S. Department of the Interior (USDOI) of a new Bison Management Framework established a USDOI Bison Working Group to help coordinate bison management among the agencies. The working group provides an initial effort to coordinate many of the key federal agencies involved in bison conservation, but does not include non-government partners. This working group could become a new model for managing bison on multiple small-scale reserves as though it were one larger-scale population, creating an effective population of sufficient size to protect genetic and ecological integrity. In Montana (Northern Yellowstone Ecosystem) and Wyoming (Southern Yellowstone Ecosystem) interagency bison or bison/elk management plans were created that defined a co-management strategy transcending state and federal jurisdictional boundaries (See chapter 5). Public participation in these processes was achieved through numerous public meetings where stakeholders were provided opportunities to comment on and influence a proposed co-management design. Through this process, information was provided to the stakeholders, and some degree of acceptance for proposed decisions was negotiated. The establishment of the Sturgeon River Plains Bison Council in Saskatchewan is another co-management example developed by local stakeholders affected by bison management on neighbouring federal lands. These examples represent contrasting models of top down versus bottom up approaches to bison conservation. By combining local (bottom-up) and national (top-down) approaches, better forms of governance can evolve, natural resources may be more effectively managed, and livelihoods can be improved (Fraser et al. 2008).

Detailed project-specific planning for ecological restoration (see Chapter 10 of this document) should be completed by agencies, NGOs and private partners involved in the project area prior to implementing any bison conservation project. The successful completion of the environmental evaluations required under national, state or provincial environmental law will be critical to the advancement of any bison restoration project involving public land. These environmental evaluations will require a public involvement process and should gather input from all affected stakeholders in a meaningful process. In addition to public involvement significant public education and outreach should be developed and implemented during all phases of a restoration project.

Technical support from science groups, such as the IUCN Bison Specialist Group, can provide the necessary technical guidance for science based conservation strategies at the local, state/province and continental scale. Guidance from this technical group can identify best management practices, and recommend policy and legislative changes necessary to support sound conservation and restoration initiatives. Additional guidance for ecosystem restoration efforts can be found through other IUCN publications (Clewell *et al.* 2005; IUCN 1998; Chapter 10).

8.5.4 Recommendations

Some fundamental legal and policy changes recommended to enhance bison restoration include:

1) Where social acceptance for wild bison can be attained, establish the legal status of bison as a native wildlife species through working with state/provincial/federal jurisdictions.

2) Modify current policies that prevent partnerships and co-management among agencies, private sector, and tribes.

3) Develop outreach to state and federal land management agencies encouraging land management agencies to consider bison in agency planning and policy development.

4) Reform current policies governing suitable bison landscapes to protect the core habitat conservation values as defined in Sanderson *et al.* (2008) and this document. This is to protect the core value of these landscapes for future ecological restoration pending socio-economic shifts favourable to bison restoration.

5) Develop outreach materials identifying social and economic benefits and ecosystem services associated with restoration of bison and prairie conservation efforts for local communities, the private sector and governments.

6) Create a decision framework, suitable for private conservation efforts, that encourages restoration strategies with an ecological emphasis.

7) Create policies or economic and conservation incentives that reward private landowners who manage for biodiversity including bison.

8) Establish necessary state and federal regulations and legal instruments to support valuation and compensation for ecosystem services.

9) Work with animal health organisations (IUCN Wildlife Health Specialist Group) and regulatory agencies to encourage bison friendly health regulations.

10) Identify and support necessary research and monitoring to cultivate a science-based but adaptive process for ecological restoration of bison.

11) Encourage economic and power structures that support sustaining local communities and lifestyles.

12) Make efforts to reform policy and legislation that impede the interests and rights of indigenous people to manage bison in a culturally sensitive manner.

8.5.5 Recent initiatives to conserve and restore bison

Sanderson *et al.* (2008) present a collective vision for the ecological restoration of bison in North America. From a series of meetings with various conservation organisations, government agencies, indigenous groups, bison ranchers and private landowners a “Vermejo Statement” was jointly written that describes what ecological restoration of bison might look like. Five key attributes were identified in this statement that create both opportunities and challenges for bison restoration, such as large scale, long term, inclusive, fulfilling, and ambitious efforts. Sanderson *et al.* (2008) explored a shared vision for wild bison restoration with 20, 50, and 100-year timelines. Specific initiatives were not described, but a range-wide priority setting methodology resulted in a scorecard matrix with which to evaluate the conservation value of public and privately owned bison herds and a map of potential restoration areas. Significant changes in the landscape where bison once roamed are creating possibilities for bison restoration where few existed before (Freese *et al.* 2007; Sanderson *et al.* 2008).

8.5.5.1 United States

In the U.S., there are no specific federal efforts proposed to protect plains bison beyond the boundaries of existing national parks, monuments or wildlife refuges. The U.S. Forest Service (USFS) recently conducted an assessment of its management of national grasslands in Montana, North Dakota, Nebraska, South Dakota, and Wyoming and dismissed a proposed alternative to restore free-ranging bison (USDA Forest Service 2001).

The U.S. Secretary of the Interior recently announced a new management framework for improving the administration of the various bison herds on Federal Wildlife Refuges. The strategy will consider treating the various populations as a larger metapopulation, looking at ways to create and maintain gene flow, as well as protecting private alleles among these small populations by improving genetic management strategies. This framework also committed USDOI agencies to expanding herd size if possible, and building cooperation with partners for the conservation of bison. In addition, comprehensive refuge plans are being reviewed to consider the feasibility of attempting bison restoration on large refuge landscapes, such as the Charles M. Russell National Wildlife Refuge.

Utah just completed a reintroduction of bison into the Book Cliffs area of East Central Utah. This is a joint effort between the State of Utah Department of Wildlife Resources and the Ute Indian Tribe. Bison were moved onto this land from the Ute tribal bison herd and the Henry Mountains. These bison are legally classified as wildlife and will be managed as a valued wildlife resource in Utah. A herd management plan has been approved where hunting programmes will regulate bison population size and distribution.

Public interest in wood bison restoration in Alaska has grown, and there is widespread state, national, and international support for restoring one or more populations in the state. There is also support among local communities in the areas being considered for wood bison restoration. A Wood Bison Restoration Advisory Group comprised of representatives of various state and national interests has recommended that Alaska pursue the reintroduction of wood bison at the three sites, which include the Minto Flats, Yukon Flats, and lower Innoko/Yukon River areas in interior and western Alaska. These areas have sufficient habitat to support from 500 to 2,000 or more bison each, depending on the location. In 2008, wood bison were transported from Elk Island National Park (EINP) to a temporary holding facility in Alaska, where they are being quarantined for 2 years prior to release in the wild.

Alaska Department of Fish and Game and USFWS are developing a special rule that will designate wood bison in Alaska as a nonessential experimental population (NEP) under section 10(j) of the U.S. Endangered Species Act, which lists wood bison as endangered. The federal rule will remove many of the regulatory requirements that normally apply to endangered species, allowing a high degree of management flexibility and providing protection against possible regulatory burdens and effects on other land uses. NEP status will help maintain and enhance public support for wood bison restoration. An alternative proposal to delist bison from the ESA is being considered, which would obviate concerns by the oil and gas sector about impacts of a new listed species on development opportunities. Wood bison in Alaska will be legally classified as wildlife and, after populations reach levels that can support a sustainable harvest, their numbers will be regulated in part through a hunting programme as outlined in cooperative management plans that will be developed for each area prior to each reintroduction.

8.5.5.2 Canada

There have been several Canadian national park proposals and public discussions to include plains bison in their native species management plans. These include management plans for Banff, Waterton, and Grasslands national parks in Alberta and Saskatchewan (Boyd 2003; see also Chapter 7). Waterton park determined that there was insufficient landscape available for free-ranging bison within the park. Prince Albert and Grasslands national parks already have established plains bison herds. Bison in these herds are classified as federally managed wildlife and could be allowed to expand their range if coordinated management agreements can be negotiated with public and private landowners bordering these parks.

Canada has several large military reserves with suitable bison habitat. Restoration on military preserves is being discussed, but few detailed plans are currently available. Bison are protected on Department of National Defence Cold Lake/Primrose Air Weapons Range by virtue of prohibiting trespass, except for the Cold Lake First Nations, who can hunt with permission. Canadian Forces Base (CBF) Suffield is a 2,600 km^2 military reserve located in the Dry Mixed Grass Natural Sub-region of Alberta. It is used as a training area for military ground manoeuvres and it is a mostly intact native prairie landscape. CFB-Suffield has free-ranging populations of all indigenous large herbivores, except bison, for which the biological potential for restoration is highly favourable.

Canada's National Wood Bison Recovery Team was formed in 1973 and includes members from all relevant federal, provincial, and territorial governments, as well as academia. The draft national recovery strategy (H. Reynolds, personal communication, 1 March 2009) provides the following population and distribution objectives: 1) establish and maintain at least five genetically diverse populations of greater than 1,000 animals in each herd, 2) establish and maintain smaller free-ranging, disease-free herds where possible, and 3) establish and maintain at least two populations in each originally occupied ecological region.

8.5.5.3 Mexico

Since the original range of bison extended only a short distance in to the northern portion of Mexico, there are few suitable locations where they would be expected to successfully re-colonise available habitats in their former range. The large grasslands of the Janos-Casas Grande in north-western Mexico is the best location for bison conservation efforts, and a large biosphere reserve is proposed for this area to protect free-ranging plains bison.

A recent series of stakeholder and science workshops held in this boundary area have identified conservation needs and potential strategies for advancing bison recovery in this boundary area of Mexico, including reintroducing a plains bison conservation herd in Mexico. In November 2009, 23 plains bison were translocated from Wind Cave National Park in South Dakota to TNC's Rancho El Uno Ecological Reserve located in the Janos Biosphere Reserve in Chihuahua State. The project is part of a national programme for recovery of priority species in Mexico and an international collaboration on wildlife and habitat conservation in North America. The U.S. National Park Service donated the bison to The Working Group for Recovery of Bison in Mexico (El Grupo de Trabajo para la Recuperación del Bisonte en México), which is led by the National Commission of Protected Natural Areas (la Comisión Nacional de Áreas Naturales Protegidas). These bison are the foundation stock for a breeding herd that will be used to repopulate other areas, with the ultimate goal of restoring the ecological role of bison in the grasslands of northern Mexico. The bison will provide opportunities for ecological research and will serve as a focal species for educational outreach. Another potentially important area for the recovery of bison in Mexico is the Columbia Valley, in the State of Coahuila, where a privately owned herd moves over a very large area and is minimally managed. Bison were native to the state of Coahuila until the second half of the 19th Century.

8.5.5.4 Non-governmental organisations

TNC and NCC have played a lead role in North America in developing conservation programmes involving bison. TNC (eight herds) and NCC (one herd) already manage nine bison herds on grassland preserves in U.S. and Canada respectively. TNC is principally using bison as a native grazer and is considering adding bison to additional preserves in the U.S. and Canada. Specifically, the NCC is implementing a restoration strategy for the Old Man on His Back Conservation Area in Alberta, with a herd already established with bison from EINP (Freese *et al.* 2007).

In 2005, APF and WWF implemented a privately funded conservation effort restoring bison to the American Prairie Reserve in southern Phillips County, Montana. Plains bison were obtained from Wind Cave National Park. Under Montana regulations, they are currently classified as privately owned livestock, however, the Fish, Wildlife and Parks Commission has authority, under Montana law, to classify these bison as

Plate 8.1 Plains bison were reintroduced to the arid grasslands of the Janos Valley in northern Chihuahua State, Mexico in November 2009. The bison reside on Rancho El Uno Ecological Reserve, a property of The Nature Conservancy. Photo: Rurik List.

wildlife if APF agrees and if there is public support for such legal action. APF intends to purchase up to 405,000 hectares (one million acres) of land for a grassland preserve upon which wild bison would be allowed. In addition, the American Prairie Reserve leases adjacent BLM grazing allotments and recently modified these to change the class of livestock for these allotments from cattle to bison. Similarly, the USFWS has authority to establish bison on the Charles M. Russell Wildlife Refuge adjacent to the American Prairie Reserve. The combined efforts of these two agencies, and other conservation partners, could result in bison restoration on a very large native grassland habitat.

8.5.5.5 Tribal initiatives

Many tribal initiatives are also underway across North America. The ITBC was formed in 1990 and has 57 member tribes managing over 15,000 bison (http://www.itbcbison.com/index.php). Its stated goal is to restore bison to Indian Nations in a manner that is compatible with their spiritual and cultural beliefs and practices. Congress appropriated funding for tribal bison programmes in June of 1991, and has approved appropriations for ITBC annually since then. This action offered renewed hope that the sacred relationship between Indian people and the "Buffalo" might not only be saved, but would, in time, flourish.

Specific initiatives include the Cheyenne River Sioux Tribe, which has started an 8,900-hectare Tribal Wildlife Refuge. The Rosebud Sioux Tribe has officially endorsed "The Million Acre Project" developed by the Great Plains Restoration Council centred on the Pine Ridge Indian Reservation in South Dakota (Freese *et al.* 2007). Another potential initiative is identified in a strategic plan being developed by the Lower Brule Sioux Tribe in South Dakota (Lower Brule Sioux Tribe 10 year strategic plan; Lower Brule Sioux Department of Wildlife, Fish, and Recreation). The Wind River Reservation in Wyoming is working on a management plan that would restore wild free-ranging bison to available habitat on that tribal landscape. The Fort Belknap Reservation in Montana has requested Yellowstone bison from the state/federal quarantine facility. A comprehensive evaluation of the restoration potential of North American tribal/first nation's landscapes and continental conservation priority assessments for those landscapes has not been completed.

Chapter 9 Conservation Guidelines for Population, Genetic, and Disease Management

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9.1 Introduction and Principles

This chapter provides management and policy-relevant guidelines to foster bison conservation and full recovery. Conservation implies retaining desirable ecological, cultural, and genetic characteristics that currently exist, while full recovery implies a broader vision—bison populations inhabiting areas that permit full expression of natural behaviours and ecosystems functioning in ways similar to those of the past.

We focus on guidelines and principles that are broadly applicable, and we avoided highly specific, prescriptive recommendations. This approach requires managers and others to understand the basis for our guidelines, and to evaluate carefully how a guideline can best be implemented in a particular situation. We provide only brief reviews of the scientific basis for guidelines, and readers should refer to chapters four, five, and six in this volume for more comprehensive information on bison genetics, disease, and ecology.

A small set of overarching principles is the foundation for most of the guidelines in this chapter, and they provide a framework for developing and assessing conservation actions. These key principles are:

1) Maximize the number of bison in a population. Larger populations better retain natural variation, and are more resilient to 'surprises' or catastrophic events. Strive to achieve a 'maximum sustainable' rather than a 'minimum viable' population size.

2) Support and promote 'wild' conditions and behaviours. Where possible, provide an environment where bison are integral to community and ecosystem processes (Table 9.1). Behaviours and demographic processes should reflect natural selection, and active management interventions should be minimized. Wild bison herds use very large ranges.

Plate 9.1 *The bison is an interactive species. Here wolves are hunting and feeding on a plains bison they have killed and ravens are scavenging (middle photo). Top and middle photos: Douglas Smith, lower photo: Dwight Lutsey.*

Table 9.1 *Ecosystem processes that bison can strongly influence. See Hobbs (1996); Knapp et al. (1999); Larter and Allaire (2007); and Truett et al. (2001).*

Process	Description
Create patches	Grazing can produce a dynamic mosaic of vegetation patches that differ in seral stage and that differ due to variations in grazing intensity
Enhance nutrient cycling rates	Bison grazing can enhance nutrient turnover and change dominant system mode from detritus-decomposition to consumption-defecation
Enhance habitat quality	Bison grazing can increase habitat suitability for prairie dogs, pronghorn, and other species
Modify fire regimes	Bison consume fine fuels and create trails and trampled areas that reduce fire intensity and extent, and modify the effect of fire on vegetation heterogeneity
Create disturbances	Trampling and wallows create seedbeds for some species; localised tree stands that are not tightly clumped are susceptible to major damage by rubbing, horning, and thrashing of bison.
Stimulate primary production	Bison grazing removes senescent material from the sward and increases light penetration, nutrient availability, and growth
Disperse plant seeds	Bison transport seeds in leg fur and gut, and may enhance establishment (of native and exotic plants) via consumption, seed coat digestion, and defection in nutrient-rich media.
Maintain floral diversity	Bison grazing can result in greater grass and forb species diversity
Support carnivores and scavengers	Bison are prey to some large carnivores, and bison carcasses can contribute to supporting scavengers.

3) Preserve genetic integrity and health. Maintain bison lineages and carefully evaluate all movements of bison between populations. Consider potential genetic consequences of all management actions, especially for small herds.

4) Routine assessment is central to science-based conservation of bison. Routine monitoring and evaluation of demographic processes, herd composition, habitat, and associated ecological processes are central to evaluating herd health and management efficacy. Assessments are necessary to anticipate or respond to conservation needs and sound data is the basis for informed management.

The scientific basis and rational of principles for conserving bison is provided in the more detailed guidelines in this chapter and other chapters that review bison ecology, genetics, and ecological restoration.

9.2 Guidelines for Population and Genetic Management

The general goals for population and genetic management are to achieve and sustain a population with a healthy level of genetic variation and a sex and age composition typical of viable wild bison populations. Management actions needed to achieve these goals will vary with the size, history, and circumstances of each particular population. In this section, we articulate more specific management objectives, summarise background information relevant to our recommendations (see also Chapter 6), and provide both general and specific guidelines.

In bison, loss of genetic variation is a concern primarily when the number of actively breeding animals or the founding population size is small. Our best estimates are that bison populations can generally be considered “not small” (for genetic purposes) when they exceed about 1,000 animals, the population has approximately equal numbers of bulls and cows, and the size of the population is stable. For the purposes of this report, the genetic objective is to attain a 90% probability of retaining 90% of selectively neutral genetic variation for 200 years. This objective is less stringent than some published objectives, and thus our estimates for sustainable population sizes are smaller than those that result from estimates based on more conservative criteria (Reed *et al.* 2003; Soule *et al.* 1986). In all populations, the rate of loss of genetic diversity is directly related to how rapidly individuals in a population replace themselves (generation time) and to the size of the breeding population. Most guidelines for genetic management in this document can be understood in the context of just these two factors.

Most populations are not uniform, but have genetic variation related to the spatial substructure of the population (Manel *et al.* 2003). Demographic and genetic substructure occurs at a large geographical scale due to traditional use of particular parts of a range (e.g., breeding range fidelity, seasonal ranges, calving areas) by segments of a population (e.g., bison in YNP; Christianson *et al.* 2005; Gardipee 2007; Gogan *et al.* 2005; Halbert 2003; Olexa and Gogan 2007). Within herds, bison are thought to form family groups (i.e., matrilineal groups, mother cows with their preparturient daughters) and these family groups constitute fine-scale population structuring. These types of population structure are important because they increase the likelihood that animal removals without plans to explicitly accommodate substructures of cows could disproportionately impact a particular segment of the population and result in a greater loss of genetic diversity than necessary. Removal strategies should be designed to accommodate the potential spatial structure of herds, and institute procedures that ensure

animals are proportionately removed from different population segments. This could potentially be accomplished by removing animals from different parts of the range.

A variety of factors can lead to increased rates of genetic diversity loss. After accounting for population size, the most important factors are likely to be non-random mating (i.e., a few bulls are responsible for siring most calves), skewed sex ratios, and large variation in population size.

9.2.1 Guidelines that apply to most conservation herds

Very few conservation herds will persist without the need for some form of population control. Many guidelines in this chapter were included with the specific intent to support development of informed population management plans. Many of the following guidelines apply to most conservation herds, and are likely to be included in comprehensive management plans for conservation herds:

1) Maintain a sex ratio with neither sex constituting more than 60% of the population. Ideally, the adult sex ratio will be slightly female biased (e.g., 55 cows per 100 animals), reflecting observations that mortality rates of males tend to be slightly greater than those for females. Avoiding a high ratio of females to males helps ensure participation in mating and transfer of genetic diversity by a larger number of bulls. In large populations, mating competition will likely be sufficient when there are 20 or more mature bulls (six years old and older) per 100 cows. Maintaining mating behaviour, as noted above, calls for a more equal sex ratio.
2) Avoid removing a significant proportion of the population. For populations subjected to population control actions, culling should be on a yearly, or every other year, schedule, rather than periodically at longer intervals. We cannot offer a definitive definition of 'significant', as the effects of population fluctuations will be greater as population size diminishes and varies with other circumstances. As a general guideline, we suggest limiting removals of animals to less than 30% of the population;
3) Avoid disproportionate removal of matrilineal female groups (mother cows and their preparturient daughters). More specifically, attempt to retain the older cows matrilineal groups;
4) Remove animals from all spatial segments of the population;
5) Emulate natural mortality patterns—higher mortality/removal rates for juveniles and old age classes (more than 15 years);
6) In small populations, consider actions that reduce variation in the breeding success among individuals. This could be accomplished by reducing the opportunities for continued breeding by highly successful bulls.
7) Avoid human selection for market traits such as docility, carcass composition, body shape, or productivity, as such interventions contradict natural selection and conservation of genetic variability;
8) Routine supplemental feeding to increase productivity, or to support a population size that exceeds range carrying capacity, is discouraged for conservation herds;
9) Where practical, the full suite of natural limiting factors should be allowed to influence populations, including winter deprivation and predation. This will result in variable rates of reproduction and survival.

The need for active genetic management will vary with herd size, genetic composition, and management goals. In general, genetically diverse herds with more than 1,000 animals are unlikely to require active management to retain most of their genetic diversity for the next 200 years (Gross *et al.* 2006). Hedrick (2009) suggests a herd size of 2,000-3,000 to avoid inbreeding depression. In very small herds (fewer than about 250 animals), long-term genetic health will require occasional supplementation with genetic material from other herds. The exact number of animals needed to supplement a particular herd will vary with the genetic composition of the source and target herds, but a supplement of four to five breeding animals per decade should be sufficient for long-term herd genetic health (Wang 2004). In addition to the guidelines below, managers should follow the IUCN guidelines for translocation of wild animals between established herds, being especially careful about genetic purity (i.e., cattle genes and geographically appropriate sources of stock) and diseases (http://www.kew.org/conservation/RSGguidelines.html).

Active management to retain genetic variation (other than translocations) may be most important for intermediate-sized populations with about 250-750 animals because this is the size range where active management may prevent or greatly reduce the need for translocating animals to ensure long-term the genetic health of a herd (Gross *et al.* 2006). For conservation herds, the overall objective is to retain allelic diversity, which is the best indicator of the genetic resources available to the population. By contrast, genetic heterozygosity may be a better short-term indicator of the mating structure of the herd. In addition to the guidelines provided above, removal of young animals, prior to their first breeding, can significantly enhance the retention of genetic diversity (Gross *et al.* 2006). Removal of young animals to preserve genetic diversity may seem counterintuitive. Genetic material is lost only when animals in a population are replaced. Removal of young animals increases the length of the generation (replacement) interval, and this thereby prolongs the retention of genetic material.

9.2.2 Herd-level population and genetic management

For many conservation herds, the most frequent and contentious decisions will concern herd level management, especially population control. Key decisions address how many animals to maintain, which ones to remove, and how often to remove them, when to add animals, and where to source them. This section provides advice for active population management at the herd level—guidelines for establishing a new herd, maintaining the size of an existing herd, reducing the size of a herd that has become much too large, and how to deal with known genetic issues.

9.2.2.1 Soft release procedures

Bison may need to be moved to supplement an existing herd, or to establish a new herd. In such cases, the use of a "soft" release process should be considered in virtually all cases. Soft releases typically involve placing animals in a (usually large) holding facility prior to full release. Holding bison in a large pen may increase their tendency to remain in the area of release and establish some degree of site fidelity. American Prairie Foundation, for example, held bison for one month in a large corral prior to release on the American Prairie Reserve in Montana. An additional benefit of a soft release procedure is the effective quarantine and associated ability to monitor and more easily re-capture animals if any health issues become apparent.

9.2.3 Establishing a new herd

Establishing and maintaining related, isolated or semi-isolated herds (i.e., parental and one or more satellite herds) is critical to long-term species conservation in that multiple herds act to increase effective population size (N_e) and reduce the total loss of genetic variation over time (Lande and Barrowclough 1987). Furthermore, the maintenance of a unique genetic population in several small herds reduces the probability of accidental extinction, such as from a natural catastrophe by disease, and increases the opportunity for local adaptation (Franklin 1980; Lacy 1987). In theory, and under experimental conditions, several small groups (e.g., N_e about 50) may preserve more genetic diversity than a single herd with as many individuals as the smaller herds combined (Margan *et al.* 1998). Genetic drift within each related herd can be countered by the occasional movement of individuals between related herds (Mills and Allendorf 1996). Therefore, several moderately sized herds (i.e., more than 300 and fewer than 1,000 animals) of the same genetic stock can, if managed properly, act as a large metapopulation with an effective population size sufficient to impede genetic erosion (Lacy 1987). In this section, we articulate considerations for the establishment and maintenance of new bison herds from existing resources.

1. Source

Priority should be given to establishing satellite herds from extant conservation herds, within the respective original ranges for wood and plains bison, especially for those herds with unique genetic characteristics (Halbert 2003; Wilson and Strobeck 1999) and those which appear to be free of domestic cattle introgression (Ward *et al.* 1999; Halbert 2003; Halbert *et al.* 2005b). Beyond this, establishment of herds of mixed ancestry should be considered to maximise genetic diversity and the potential for adaptive response.

Although bison are likely to be more readily available from herds subjected to artificial selection and some level of domestication, we strongly recommend acquiring bison from "wild" herds not subjected to these influences.

2. Number of animals

Little specific information is available regarding appropriate foundation populations sizes. In general, a few (4-10) individuals should be sufficient to avoid very short-term inbreeding effects (Senner 1980). However, the loss of variation in such a small population will be substantial after the first few years (Nei *et al.* 1975) and additional bison should be imported over a period of several years to increase genetic variation. If the goal is to conserve or duplicate most of the genetic material in a source herd, many more animals are required. Shury *et al.* (2006) proposed a base of 200 "founder" animals to preserve most of the genetic variability in "re-established" wood bison herds.

3. Sex ratio

The initial imported bison should consist of approximately 50% of each sex, and the herd should be maintained with a balanced sex ratio to reduce inbreeding and maximise effective population size.

4. Breeding strategy

If a small number of bison are used to found a herd, and especially if additional bison are not brought into the new herd, breeding strategies to maximise the transfer of genetic diversity across generations should be considered (e.g., avoid excessive breeding by one or a few males). Appropriate genetic tools are available to accurately assign parentage in bison (Schnabel *et al.* 2000; Wilson *et al.* 2002), and these may be used to assist in captive breeding decisions by evaluating the breeding success of individual bulls and relatedness among calves.

5. Age composition and behaviour

Bison are social animals and the importance of social structure within a herd is critical to overall herd health and survival (McHugh 1958). We recommend establishing a new herd with both adult and sub-adult individuals to prevent disintegration of social structure and behavioural anomalies (e.g., foraging behaviour; Ralphs and Provenza 1999).

6. Maintenance number and growth rate

To minimise the loss of genetic variation and heterozygosity, and to maximise the probability of population survival, new herds should be allowed to grow as quickly as possible until the target herd size is attained (Nei *et al.* 1975). Bison herds can grow very quickly, doubling in size in as few as four years (see Chapter 6). Herds should then be maintained within an appropriate size range, which will likely be the maximum size possible within resource limits for herds with fewer than about 1,000 animals (Gross *et al.* 2006; Senner 1980). For small herds, fluctuations in population size can have a substantial negative impact on retention of genetic variation (Nei *et al.* 1975). Maintenance of population size is more important to population survival than is the founder population size and should, therefore, be given a high priority for small herds (Senner 1980).

7. Relationship between founders

Select unrelated individuals as founders for a new herd. Use appropriate genetic tools when available to establish relatedness between bison (Schnabel *et al.* 2000; Wilson *et al.* 2002).

8. Genetic variation and heterozygosity

Genetic evaluation should be carried out on the parental herd prior to establishment of a satellite herd, and repeated genetic evaluation of the satellite herd should be used to ensure that all the genetic variation from the parental herd are incorporated and maintained.

9. Disease

In general, do not use diseased bison to establish a new herd. Immune suppression in diseased individuals may lead to infection and spread of other diseases; further compromising herd establishment and health. One notable exception is the intentional creation of disease-free satellite herds from a diseased parental herd. In such cases, use extra precautions to prevent the spread of disease from bison to other wildlife during the initial disease elimination phase.

10. Monitoring success

Because it is expensive and time-consuming to establish bison herds, resources should be wisely invested to monitor bison herds and broader ecological effects of bison. Ideally, habitat characteristics should be monitored using a valid statistical process before bison are introduced. Herd composition, demographic parameters, and genetic structure, especially in the first few generations following herd establishment, should be monitored, along with ecosystem changes. Additional monitoring guidelines are provided below.

Trans-boundary transportation of bison to establish a new herd can introduce many administrative and regulatory considerations (Chapter 8). After an extended period of planning and negotiation, wood bison were transported from Canada to Alaska in 2008. Personnel with the relevant agencies may be consulted for advice on undertaking such an enterprise.

9.2.4 Maintaining or manipulating existing herd size

When a bison herd appears in need of intervention to restore or improve genetic health and population viability, the first and most important activity is to thoroughly evaluate the current condition of the herd to avoid premature, unnecessary, or even damaging management decisions. *There are no simple cookbook instructions that can be applied to any bison herd*. The following list of baseline evaluations will help ensure that decisions are well informed:

1. Determine the history of the herd to provide insight into current levels of genetic variation and population structure. Try to determine:

- Number and origin of herd founders;
- Number and origin of any bison introduced following herd foundation (transfers);
- Historic records on population size, especially with regard to substantial changes over time.

2. Evaluate current population parameters to establish baseline measurements for future comparison and to detect attributes that may lead to changes in social structure or genetic variation. Variables of interest include:

- Census population size
- Effective population size (N_e; will not be possible in all cases and requires knowledge of breeding structure)
- Rate and direction of population size changes (e.g., is the herd expanding or contracting)
- Sex ratio
- Age structure

3. Note any indications of inbreeding within the herd, such as:

- Unusual phenotypic characters within the herd, especially any that have recently appeared;
- Recent decrease in recruitment rates;
- High rates of morphologically abnormal or non-motile sperm among breeding-age bulls;
- Relatively low levels of heterozygosity as compared with previous measurements or other bison herds of similar size and history (e.g., Halbert 2003; Wilson and Strobeck 1999).

4. Assess potential health problems in the herd, including:

- Presence of transmissible diseases, especially those which may influence population dynamics (e.g., BTB, brucellosis, MCF);
- Presence of disease agents in livestock species on nearby (especially adjacent) properties (e.g., cattle with JD, sheep carrying MCF).

5. Evaluate the overall genetic constitution of the herd by measuring:

- Unique variation (rare or private alleles) and levels of heterozygosity in comparison to other bison herds (Halbert 2003; Halbert *et al.* 2004; Wilson and Strobeck 1999);
- Within-herd changes in heterozygosity and genetic variation between generations (Halbert *et al.* 2004);
- Current breeding structure of the herd (e.g. number of males contributing to calf crop each year, relatedness among calves, presence of genetic subpopulations);
- Existing levels of domestic cattle introgression in both the mitochondrial (Polziehn *et al.* 1995; Ward *et al.* 1999) and nuclear genomes (Halbert *et al.* 2005b).

Using the data collected from the above evaluations, informed and sensible management plans can be implemented to best fit the needs of the target herd. To further assist in this process, demographic and genetic data can be used to model the effects of various management alternatives prior to actually implementing a definitive management plan (Gross *et al.* 2006; Halbert *et al.* 2005a).

9.2.5 Transferring bison between herds

To maintain long-term herd health, it will be necessary in some cases to transfer bison between herds (Table 9.2). The decision to transfer bison between herds, however, must be made with extreme caution with the following considerations:

1. Necessity of movement

Is there actual evidence of loss of genetic diversity or inbreeding to necessitate the transfer? In bison and other mammalian species, well intended but uninformed management decisions to transfer individuals among isolated groups have resulted in detrimental and irreversible effects, especially related to genetic integrity and disease.

2. Domestic cattle introgression

As discussed in Chapter 4, few bison herds appear to be free from domestic cattle introgression (Halbert 2003; Halbert *et al.* 2005b; Polziehn *et al.* 1995; Ward *et al.* 1999). Therefore, it is essential to understand both the historic and genetic evidence of domestic cattle introgression in the recipient and potential donor herds before considering a transfer. If the two herds are related, and especially if one is a satellite of the other, the total effect on introgression levels due to transfer will be negligible. Care should be taken to prevent the introduction of bison of unknown origin, or questionable history, into conservation herds. Furthermore, given our current levels of understanding, bison should not be transferred into the few existing herds which appear to contain no domestic cattle introgression, with the possible exception of transfers between parental and satellite herds (Hedrick 2009).

Table 9.2 *Additional factors to be evaluated when considering transfers of bison between herds.*

Number	When possible, the number of imported bison should be based on prior modelling estimates to maximize improvements in heterozygosity and genetic diversity while minimizing dilution of the native bison germplasm.
Sex	Importing a few new males into a herd can have a large, positive and rapid genetic and demographic impact. The same overall effects can be obtained when importing females, although the process will be somewhat slower. In some cases, it may also be worthwhile to consider any known genetic uniqueness of the mitochondrial genome and Y chromosome. For instance, prior to importing bison into the Texas State bison herd, it was noted that this herd contained a unique bison mitochondrial haplotype not known to occur in other bison herds (Ward 2000; Ward et al. 1999). Therefore, importing males into this herd was favoured over importing females, in part to prevent dilution of the unique native bison mitochondrial haplotype (Halbert et al. 2005a).
Age	The most rapid infusion of germplasm will be obtained by importing breeding-age animals. It may be desirable to choose bison that have already produced offspring to avoid potential issues of sterility or offspring abnormalities. Despite planning, genetic incompatibilities between extant and imported bison may still influence contributions of the imported bison to the calf crop.
Quarantine	Consider a quarantine of newly imported bison prior to release, especially when the recipient herd is at a high risk of extinction. This allows for an easier adjustment of the imported bison to their new environment, as well as early detection and treatment/removal for latent diseases.
Mating regime	Decide whether imported bison should have exclusive mating privileges for one or more years or compete with other potential breeders for access to cows. "Exclusive" matings can be used to increase genetic and demographic impacts. A fully competitive mating regimen permits extant bison to contribute to the gene pool and provides some protection in case of genetic incompatibility between the donor and recipient herds.

3. Relationship between herds

Given the observed genetic distinctions among extant bison herds (Halbert 2003; Wilson and Strobeck 1999), dilution of unique genetic characters (alleles) within the recipient herd should be considered when evaluating potential donor herds (Halbert *et al.* 2005a). Ideally, bison should be transferred between satellite or related herds to reduce the loss of rare variants.

4. Health and disease

All attempts should be made to prevent the spread of disease between bison herds. Even if the recipient and donor herds host the same disease, transfers of bison should be discouraged since disease strain variants between herds can lead to differences in disease progression or effects. Potential donor herds should be thoroughly tested (see Chapter 5 and section above) to evaluate the presence of pathogens.

Once the above factors have been evaluated, there are various other features that may influence the demographic and genetic effects of the transfer, including the number, age, and sex of the imported bison as well as frequency (single or multiple introductions) and duration of the transfers (permanent vs. transient transfers, e.g., for short-term breeding). Each situation will differ and a comprehensive review is not possible here given the large number of potential management scenarios. However, the general guidelines in Table 9.3 should be considered.

Table 9.3 *Risk factors for disease.*

Disease Risk Factors	Disease Examples (not all-inclusive)
History of pathogen in the region	Anthrax, parasites
Proximity to potentially infected populations (wildlife or livestock)	MCF, Bovine tuberculosis, brucellosis, Johne's disease, bovine viral diarrhoea, foreign animal diseases (e.g., Foot-and-Mouth Disease)
Weather patterns and environmental suitability	Anthrax, parasites
Presence/abundance of mechanical or biological vector(s)	Anaplasmosis, bluetongue, pink eye
Population density (increased infectious contacts)	Most infectious diseases (e.g., brucellosis, tuberculosis)
Season	Diseases with unique transmission patterns (e.g., brucellosis, bluetongue)
Nutritional and other environmental stress	Infectious diseases which capitalise on depressed immunity (e.g., respiratory viruses)
Geographic location/ Climate	Hardy pathogens capable of surviving climate extremes

5. Number

The number of imported bison should be based on prior modelling estimates when possible, and should reflect the size of the population so that improvements in heterozygosity and genetic diversity are maximized with a minimum dilution of the native bison germplasm.

6. Sex

Importing a few males into a herd can have a large and rapid genetic and demographic impact. The same overall effects can be obtained when importing females, though the process will be somewhat slower. In some cases, it may also be worthwhile to consider any known genetic uniqueness of the mitochondrial genome and Y chromosome. For instance, prior to importing bison into the Texas State bison herd, it was noted that this herd contained a unique bison mitochondrial haplotype not known to occur in other bison herds (Ward et al 1999; Ward 2000). Therefore, importing males into this herd was favored over importing females, in part to prevent dilution of the unique native bison mitochondrial haplotype (Halbert et al. 2005a).

7. Age

Clearly the most rapid infusion of germplasm and improvement in herd viability will be obtained by importing breeding-age animals. In some cases, it may also be desirable to choose bison that have already produced offspring to avoid potential issues of sterility or offspring abnormalities. Even given the most well thought-out plans, however, genetic incompatibilities between native and imported bison may still influence the effectiveness of the imported bison in contributing to the calf crop.

8. Quarantine

A quarantine of newly imported bison should be considered prior to their release, especially when the recipient herd is at a high risk of extinction. Isolating the newly imported bison for some time will allow for an easier adjustment of the imported bison to their new environment and early detection and treatment/ removal of latent diseases.

9. Mating regime

Should the imported bison have exclusive mating privileges for one or more years or should they be included with all other potential breeders to compete for breeding rights? An "exclusive" mating regimen allows for larger potential genetic and demographic impacts. However, a "competitive" mating regimen permits native bison to continue to contribute to the gene pool each year and provides some protection in case of genetic incompatibility between the donor and recipient herds.

9.2.6 Recovering small or threatened herds

Small populations (N_e less than 50, or a census size of fewer than about 150 animals), or larger populations which have undergone a recent and significant decrease in population size, are especially vulnerable to a loss of genetic variation, decreased fitness, and, ultimately, extinction (Gilpin and Soulé 1986). Persistently small populations are additionally susceptible to inbreeding, which can lead to an overall loss of heterozygosity and increase in rare, and often detrimental, genetic traits.

If a large population has undergone a recent reduction (=population bottleneck) in a short period of time (e.g., fewer than three generations), and is allowed to subsequently increase in size rapidly and without culling, the resulting population will probably suffer only small reductions in allelic variation and heterozygosity (Nei *et al.* 1975). The same is not true of the bottleneck effect in small populations, where the loss of allelic variation and heterozygosity tends to be much higher; in this case, extra measures must be taken to maximise the transfer of genetic diversity and minimise the loss of heterozygosity across generations.

Several strategies can be used to alter the breeding strategy of a small herd to maximise recruitment rates and genetic diversity in the calf crops. For instance, attempts can be made to randomise breeding. Bison are naturally polygamous breeders, and it may be necessary or desirable to implement a controlled mating scheme to ensure that a maximum number of males are breeding with the available females, and to maximise the transmission of genetic variation across generations. If semen viability or other reproductive barriers are an issue, artificial insemination may also be considered.

In some cases, altering the breeding strategy of a herd may not be sufficient to reverse the effects of small population size (e.g., Halbert *et al.* 2005a). In these cases, it may be necessary to import bison from other herds to improve recruitment rates and increase genetic variation. As the effects of importing bison into a small herd can be irreversible and even detrimental, the ultimate decision to implement this strategy should be made only after careful consideration, and as a last resort (all issues discussed in section 9.6.2 should be considered). Furthermore, options to maximise demographic and genetic impact (e.g., importing several males vs. a few females) should be considered in threatened herds.

9.2.7 Recovering herds from germplasm introgression

If a bison herd has had an influx of germplasm (genetic material) from an outside source, including another bison herd or a related bovid species, the ability to recover the germplasm of the original herd depends on: 1) the ability to detect bison containing introgressed fragments, and 2) the number of generations since the original introgression event. For instance, if two distinct bison herds are accidentally mixed, parentage testing would allow for post-mating segregation of the two herds and their offspring provided that the bison from each herd are distinguishable (e.g., identification tags or sufficient genetic differences) and that a limited number of generations have passed (fewer than three). If more than a few generations have elapsed since the initial introgression event, the introgressed segments will become dispersed throughout the genome of the herd (hybrid swarm) and reconstitution of the original germplasm will not be possible (Allendorf *et al.* 2001). For example, low levels of domestic cattle introgression have been detected in many extant bison herds (Halbert 2003; Halbert *et al.* 2005b) and can be traced back to human-induced hybridisation of the two species over 100 years ago; in these cases, multiple domestic cattle fragments are dispersed so thoroughly throughout the genome that it is not possible to detect, much less remove, all introgressed fragments.

9.2.8 Herd size reduction

Bison have a high intrinsic reproductive rate and bison herds generally grow rapidly (see Chapter 6). Therefore, when resources are limited, bison herds often exceed the carrying capacity of their environment and begin to have negative impacts on other grazers and native plant species. As a result, most bison herds are subjected to some level of culling (=periodic removals) to maintain a suitable population size (Table 9.4). In extreme cases, it may be necessary to remove a large proportion of the population to meet management goals. For example, if bison have not been culled from a herd in several years, the herd may have nearly doubled in size, and it may threaten the survival of other species. In these cases, extreme caution should be taken to remove bison in a manner that will minimally influence herd and germplasm composition according to the following guidelines. Some discretion is needed in applying these guidelines. For example, it is important to avoid social disruption while simultaneously removing animals from all segments of the population. Managers must carefully evaluate their goals and the specific situation to achieve the best outcome (Table 9.4).

9.3 Behaviour: Mating System, Social Structure, and Movements

Bison behaviour is an index, or reflection, of the conditions experienced by individuals in a population, and behaviour is an emergent property of these conditions. For example, the intensity of competition for mates will be largely determined by population structure and density, and the ability of the herd to exploit environmental heterogeneity through foraging behaviours will be largely be determined by population density and habitat characteristics. Vertebrates exhibit a remarkable ability to modify behaviour, including territorial defence, mating system, or seasonal movement pattern, in response to environmental factors (Lott 1984). Here, we describe desirable behaviours related to social structure, mating, foraging, and movements. Unlike population or genetic composition, behaviours can only rarely be manipulated directly, and behavioural “adjustments” must be accomplished by modifying other factors.

Table 9.4 *Important considerations for culling bison herds. See section 9.2.8 for explanation.*

Genetic diversity	When removing a large proportion of a herd, the primary threat to long-term preservation of the herd is a loss of genetic diversity that can be very difficult, if not impossible, to restore. Therefore, thorough genetic evaluation (e.g., section 9.2.3), is necessary before, during, and after planned large-scale herd reductions. The primary genetic considerations should be the overall maintenance of mitochondrial and nuclear diversity, such that the genetic architecture of the herd is maintained during and after the reduction period. Routine examination of culled animals during the reduction period will allow for detection—and hopefully correction—of "biased" removals, such as removal of a sibship or multigenerational family groups. Preferential removal of related individuals can lead to losses in genetic diversity and effective population size and should be avoided (Frankham 1995).
Herd composition	If, prior to removals, the herd has the desired composition, bison should be removed proportionally from all age and sex classes to avoid disruption of social behaviours and demographic structure. If the current herd structure is substantially different from that desired (e.g. section 9.2), animals may be preferentially removed from certain classes. In the case of disproportional removals, particularly care should be taken to assess and mitigate the potential effects of removals on social structure and genetic diversity.
Population substructure	Population substructure is likely important in many bison populations (see section 9.2). The presence of distinct subpopulations should be carefully evaluated prior to large-scale herd reductions and accommodated in planned reductions.
Time scale	Bison should be removed at regular intervals (rather than large, occasional events) to minimise potentially irreversible impacts on social structure and genetic diversity The exact time period for removals will likely be different for each situation and will depend on such factors as total herd size, the total number of animals to be removed, and the resources available (e.g., facilities, manpower).
Assess effects of management actions	Before and after management actions are implemented, thorough genetic, health, and demographic monitoring is necessary to evaluate recovery efforts, and to detect the need for alternative management strategies. Small populations are especially sensitive to management changes, and comprehensive monitoring may be necessary for some time to ensure the recovery of such herds. Sections 9.2,1, 9.2.3, and 9.5.2 summarise information that should be monitored to detect changes in a timely manner. Especially for small herds, the overall health of the herd should be continuously monitored to detect and treat any heritable or transmissible diseases that may impede recovery efforts.

9.3.1 Social structure and spacing

Bison are inherently gregarious and there are many historical observations of huge bison herds roaming across North America. Despite the enormous size of some bison aggregations, astute observers consistently reported a definable population structure where cows, calves, and immature males formed mixed-sex groups, and where large bulls tended to form separate, much smaller groups throughout much of the year. Groups of bulls are typically smaller than cow-dominated or mixed groups, and bison bulls have frequently been observed alone (Allen 1876; Berger and Cunningham 1994; Meagher 1973; Melton *et al.* 1989). In winter, the general pattern is one of smaller mixed groups, with group size increasing to large aggregations that peak in size during the summer breeding season and then rapidly diminishing (Berger and Cunningham 1994; Hornaday 1889).

The fundamental social group in bison is thought to consist of matrilineal groups (Green *et al.* 1989), although the persistence of these groups in populations that differ in size and ecological circumstances is poorly documented (e.g., McHugh 1958). These general patterns provide a basis for social behavioural guidelines:

1) Bison herds should have the capacity to exhibit seasonal changes in group size;
2) Average herd sizes will usually be smaller in mountains or mixed terrain than in open prairie;
3) Old bulls will be observed alone or in small groups during much of the year;
4) Persistence of matrilineal groups should be facilitated and activities that divide matrilineal groups should be avoided;
5) Activities (roundups, harvest, visitor disruptions, and so on) that disrupt social groupings should be avoided. Where unavoidable, implement carefully to minimize disruptions.

9.3.2 Foraging and movements

Hornaday (1889) described a highly nomadic foraging strategy, where plains bison seemed to wander somewhat aimlessly until they located favourable grazing conditions. Bison then grazed until a need for water motivated further movement. More recent studies of bison foraging have shown that they actively select more nutritious forages, and forage in a highly efficient manner that satisfies their nutritional needs and that frequently compliments diet selection by sympatric herbivores (Coppock *et al.* 1983; Hudson and Frank 1987; Larter and Gates 1991; Singer and Norland 1994; Wallace *et al.* 1995). Spatial variation in forage is produced by natural gradients in soil moisture, soil nutrients, fire, other disturbances, including foraging by bison. After massive wildfires swept along the Alaska Highway in NE British Columbia and the SW Yukon Territory during the early 1980s, bison continued extensive use of recovering areas 15 years later (Larter *et al.* 2007). Bison serve as an ecosystem

engineer, both responding to, and creating, heterogeneity. Bison traditionally exploited broad- and fine-scale variation in forages, for example, sometimes migrating long distances in response to snowfall or drought.

Guidelines to help preserve desirable behavioural patterns are as follows:

1) Allow bison to respond to differences and changes in the distribution, quality, and quantity of forages by moving within, and between, ecosystems;
2) Provide herd ranges that include a broad variety of habitats so that bison can exploit short-term (seasonal) and long-term (annual, multi-year) heterogeneity in forages from patch to landscape scales;
3) Bison herds should have the ability to create and respond to spatial variation in forage quality, quantity, and distribution that is the result of underlying variation in resources necessary for plant growth, to variation resulting from herbivore foraging (by bison, prairie dogs, and other species), and to variation resulting from environmental disturbances such as fire and flood;
4) Balance the advantages of larger population size against a need to avoid permanent habitat damage.

These guidelines suggest that bison should have access to very large areas in which they can exploit natural heterogeneity in forage abundance and quality. Fences and other impediments to movement should be minimised.

9.3.3 Mating behaviour

Differential reproduction resulting from mate competition is an important evolutionary process and, as such, it is crucial to allow bison to express natural mating behaviours. The following guidelines for population management support this goal:

1) The sex ratio of a population should be nearly equal, and in no case should either sex constitute more than 60% of the population;
2) A population should include about 50 mature and reproductively active males for every 100 cows (Gates 1996, unpublished data; Gates *et al.* 2005; Komers *et al.* 1992);
3) Allow interaction and fighting between bulls.

The ratio of mature males to cows will generally be lower than the overall sex ratio because males (bulls) achieve sexual maturity at a greater age than females (cows) and the mortality rate of males is higher than for females.

9.3.4 Limiting factors and natural selection

Chapter 6 described factors that were historically responsible for seasonal and periodic fluctuations in the size and distribution of bison populations. These factors, and the population segments they tend to affect, are consistent with contemporary observations (Chapter 6; Gaillard *et al.* 1998).

General guidelines consistent with our understanding of "normal" demographic processes are:

1) Natural mortality rates should be highest for calves and the oldest age classes;
2) A "normal" range for calf survival is 40-90%, and calf survival should vary with winter severity, predation pressures, and forage availability;
3) Natural survival rates for prime-age adults will normally be about 95%;
4) Under good conditions (e.g., low density, mild winter, good forage production), pregnancy rates for three-year-old cows will be 70% or greater;
5) Under good conditions, pregnancy rates for prime-age cows (generally about 4-15 years old) will normally be 70-90% and some two-year-old cows (probably less than 5%) will produce calves;
6) Disease will generally lower reproductive performance.

9.4 Habitat and Biodiversity Management

Bison can, and usually will, significantly influence habitat and biological diversity, and bison are generally regarded as a foundation species and ecosystem engineers. This is especially true for ecosystems where bison are relatively abundant and range over large areas. Modern, small-horned bison have a long history as an integral part of two major ecosystems: the North American Great Plains (plains bison) and the sedge-meadow ecosystems of northern Canada and Alaska (wood bison).

Bison can profoundly affect ecosystem trophic structures, bio-geochemical cycling, species composition, and patterns of species diversity. Some major types of ecological processes that bison influence are summarised in Table 9.1, while a more detailed review is provided in Chapter 6.

Below we list guidelines for bison management that will help conserve biological diversity. Decisions on active bison management require knowledge of productivity, stocking rates, and movement patterns. Good sources of information for management of confined or semi-confined bison herds in western habitats are the USDA's Natural Resource Conservation Service (NRCS) and its Field Office Technical Guides (http://www.nrcs.usda.gov/technical/efotg/). These documents provide information on primary productivity, recommended stocking rates, animal conversion units, and other information relevant to range management. The NRCS guides, however, focus on obtaining the maximum sustained yield of livestock. There is no comparable resource for biologists managing northern bison. For

northern bison herds, managers should review relevant literature and consult with biologists in boreal regions that support wood or plains bison populations. To enhance and conserve regional biological diversity, bison managers will need to consider local and regional issues, cultural and economic issues, and land use patterns. For example, if the conservation of prairie dogs and other species associated with short vegetation structure is desired, plains bison stocking rates should be higher than those recommended by the NRCS field guides.

The following guidelines can help promote conservation of biodiversity to a higher degree than is achieved in most livestock production systems.

1) Promote the movement and distribution of bison across the landscape in as-natural-a-fashion as possible, including the existence of sub-herds;
2) Manage for a mosaic of seral conditions and grazing intensities across a landscape. If particular conditions or seral stages are regionally rare, they should be favoured through management. This may contrast with traditional livestock grazing management that attempts to impose relatively uniform grazing pressure across an entire management unit and avoid areas of "overgrazing";
3) Manage fire using the best available information on natural fire patterns for the region. Leave unburned areas as refugia for invertebrates and small mammals;
4) Restore and/or conserve prairie dogs and other grazers that interact with bison;
5) Where possible, restore or maintain native predators of bison, i.e., wolves and bears;
6) If mineral, food, or water supplements are necessary they should be provided in a way that creates habitat heterogeneity (as a point attractant rather than being distributed uniformly across the landscape);
7) Manage so that bison do not graze naturally inaccessible areas, for example isolated buttes and steep slopes, which increases landscape heterogeneity;
8) Leave carrion *in situ*.

9.5 Disease Guidelines: Considerations for Infected and Uninfected Herds

As all wildlife populations are hosts to a wide variety of natural pathogens, and these pathogens form an integral component of ecosystem health, we limit the focus of this section to:

- Pathogens that limit bison population recovery directly by reducing survival and/or reproduction, (demonstrating a bison population impact), and/or
- Pathogens that indirectly prevent bison recovery as they form threats to existing livestock and wildlife populations (e.g., so-called economic diseases).

In general, pathogens that fit the above categories are exotic (i.e., have spilled over from domestic livestock populations), such as bovine tuberculosis, brucellosis, bovine viral diarrhoea (BVD), and malignant catarrhal fever (MCF).

Wobeser (2002) outlined four general disease management philosophies: (1) prevention, (2) control, (3) eradication, and (4) the laissez-faire approach (do nothing). Preventative measures are those designed to inhibit the spread of disease to uninfected individuals or populations. For example, the Bison Control Area in the Northwest Territories is managed to prevent the movement of diseased bison from Wood Buffalo National Park (WBNP) to the Mackenzie Bison Sanctuary (Nishi *et al*. 2002c). Control measures reduce the frequency of occurrence or the effects of a disease within a population or contain the spread of the disease. Under this regime, a disease will normally persist indefinitely, requiring continued management. The Yellowstone National Park (YNP) cooperative bison management plan incorporates numerous control measures including test-and-slaughter of diseased bison, hazing of bison back into the park, vaccination, and radio telemetry of pregnant bison (NPS-USDOI 2000). Total eradication of a disease is difficult and, in some cases, may not be possible given current technology and resources. Test-and-slaughter programmes, in concert with vaccination, may eradicate a disease from a captive population (Nishi *et al.* 2002c); however, these techniques are difficult to apply to free-ranging wildlife (Wobeser 2002). In larger populations, or over larger areas, intensive management, emphasising treatment and vaccination, may be inappropriate, unsustainable, or simply impractical (Woodruff 1999). In these circumstances, managing population size, structure, area of occupancy, or the risk of contact between host species or adjacent populations, could offer alternatives to more intensive interventions. Depopulation (=eradication) of an infected herd is a potential option; however, there may be considerable logistical challenges and conservation and policy issues including genetic conservation or salvage, cascading ecological effects, and public opposition (Nishi *et al.* 2002c; Wobeser 2002). Selection of a disease management approach depends on the rationale for management, whether the disease is already present in a population, the availability of funding, and the likelihood of success (Wobeser 2002). Managers should also understand the ecology and pathology of the disease, the dynamics of the pathogen-host relationship (Bengis *et al.* 2002; Wobeser 2002) and the risk to adjacent uninfected host populations, including bison.

Our disease recommendations focus on four disease control strategies: prevention, surveillance, management, and research. We recommend development of a disease management plan under the umbrella of a restoration programme plan that is

consistent with conservation programme goals and incorporates the expert counsel of wildlife veterinarians, epidemiologists, and other disease specialists. Disease management plans should be developed in a local context and involve considerable stakeholder participation.

9.5.1 Prevention

Thorough efforts should be made to prevent the introduction of exotic diseases into existing and future free-ranging bison populations. Introduction of novel pathogens into bison populations could occur by contact with free-ranging wildlife or through contact with captive wildlife or livestock (herein referred to as "potential disease sources"). As a general strategy, managers should strive to maintain population attributes that reduce the likelihood of disease establishment, or an increase in disease prevalence should a pathogen be introduced (Table 9.5). For example, animal density may influence disease transmission and nutritional status of animals. Habitat conditions (e.g., marshy areas for bluetongue or dry conditions for anthrax) and the presence or absence of predators can influence disease establishment or prevalence.

A disease risk assessment should be conducted for existing and future free-ranging bison populations. This risk assessment should include components of disease surveillance (in both the potential disease source and the population at risk) to determine what potential pathogens are involved, contact potential (to determine risk of disease transmission), potential consequences of disease transmission, recommended strategies to mitigate disease risk, and collateral impacts of these actions. Preventive actions may include prevention of dispersal between infected and at risk populations, habitat modification, and maintaining optimal population density, as well as understanding the history of pertinent diseases within the region.

The development of a clinical infectious disease involves a complex interaction between the host (bison), the agent (pathogen), and the environment (habitat). Alterations to any one of these factors may influence the ability of a disease to be introduced or established within a given population. Therefore, a thorough understanding of the biology of the host, agent, and environment is necessary to minimise the risk of introducing or amplifying non-native diseases.

9.5.2 Surveillance

The first step in managing diseases in a population is to determine if a pathogen is present, and if no infected animals are detected, the probability that the disease is present, but at an undetectable level. Surveillance can also be used to determine the prevalence of a disease known to occur, and to monitor changes in its prevalence over time. Disease surveillance can be passive or active.

Passive, or opportunistic, surveillance would include disease testing of animals with clinical signs and/or those that are found dead or moribund. If a cause of death is not apparent, it may be prudent and informative to submit the entire carcass, where possible, for a full diagnostic necropsy to determine cause of death. Local management staff should be trained in basic necropsy techniques, and to correctly collect critical samples when it is not feasible to submit entire carcasses. Diagnostic evaluation is particularly important if human contact may have led to transmission of a zoonotic disease to an employee or a member of the public. If predators are present in the ecosystem, they may remove or compromise carcasses before they can be collected for investigation.

Active surveillance would include capturing animals and testing for diseases, or soliciting samples from hunters of hunted populations. Often, disease surveillance is performed by collecting serum from blood samples and testing these for antibodies to diseases of interest. It is important to remember that the presence of antibodies does not confirm disease in an animal, only exposure to the pathogen at some point in the past. However, one might infer that the pathogen of interest is present in a population based on positive serological results from individual animals. Additionally, most diagnostic tests have been developed for domestic livestock and their applicability in bison

Table 9.5 *Potential management techniques appropriate for management objectives to passively manage, control, or eradicate disease.*

Passive	Control	Eradication
Monitor herd for clinical signs of disease	All techniques under passive category	All techniques in passive and control categories
Implement movement restrictions from populations that are diseased or of unknown disease status	Manipulate population density to minimise spread of density-dependent diseases	Test and cull infected members of the population where scientifically founded and logistically feasible
Modify habitat to minimise congestion	Herd level treatment if feasible (rarely appropriate in free-ranging populations)	Combinations of vaccination, treatment or test and cull developed to rapidly eliminate disease
	Vaccination if available	Depopulation of host species followed by re-population with disease-free animals
	Implement temporal/ spatial separation between infected and susceptible populations (wildlife or livestock).	Elimination of bison from affected areas

may not have been validated. Testing faeces for parasites or pathogens, such as *Mycobacterium avium pseudotuberculosis* (Mptb), may also be beneficial. Active sampling allows estimation of the population-level prevalence of the disease (as it can have greater statistical value because it is likely to be more random than passive sampling), although passive surveillance as a disease detection strategy may be more suitable for protected populations. High priorities for disease surveillance, based on human, wildlife, and livestock health considerations could include anthrax, bovine tuberculosis, brucellosis, BVD, JD, and MCF, among others. Finally, while foreign animal diseases, such as foot-and-mouth (FMD) disease or heartwater, are not highly likely to affect American bison populations, they should be on the "watch" list of potential diseases, since introduction of diseases such as FMD to North America would have significant economic impacts.

Non-specific signs of disease should be monitored and investigated, even though diagnostics are required to determine cause (e.g., poor condition could be due to age or habitat condition, parasitism, or JD, among other causes; Table 9.6).

Table 9.6 *Non-specific clinical signs of disease.*

Loss of body condition	Abnormal behaviour
Abnormal exudates from body orifices	Isolation from the herd
Cloudy eyes	Abnormal loss of hair coat
Diarrhoea	Abortion
Abnormally poor hair coat	Lameness (multiple limb)
Somnolence	Abnormal interaction with humans
Unexpected/ abnormal mortality events	

9.5.3 Management

When a pathogen has been detected in a bison population, an evaluation should be made to determine if a disease management plan should be developed that is consistent with the goals for the bison population. Potential disease management objectives are: a) a passive approach where no actions, or at least no actions that manipulate animals, are taken to control the disease, b) a control strategy where actions are taken to limit disease prevalence, spread, or risk, or c) an eradication strategy where actions are taken to remove the disease from the population. All three strategies (Table 9.5) will likely involve monitoring disease prevalence (either actively or passively as defined above). Strategies used will also be influenced by the intensity of management within the herd. For example, management options, such as vaccination, would be more easily applied to a herd that is intensively managed with round-ups.

9.5.4 Research

Further research will be necessary to develop and implement tools for successful disease prevention, surveillance, and management. For example, many of the diagnostic tests commonly used in bison disease programmes were developed for use in the livestock industry and have not yet been validated in bison populations. Furthermore, key questions remain about the presence/absence and distribution of diseases in populations, and their potential effects on bison demography and genetics.

Research should be designed to meet the needs of local managers, so that results can be applied in more general contexts. A limited list of some of the key disease research themes include:

- Diagnostics (specific to bison, with high sensitivity and specificity to detect a disease);
- Vaccination/immunology;
- Role of genetics in disease resistance;
- Disease epidemiology (e.g., transmission, demography) and risk analysis (spread of disease among and between wild and domestic hosts);
- Identification of emerging disease threats to bison in North America;
- Pathology;
- Effect of disease on population growth and viability (both indirect and direct effects).

Where research is needed for a particular disease surveillance or management question, bison managers are encouraged to work with federal, state, university, and private researchers to meet this need. An adaptive management approach will be necessary, especially when information about a specific disease is scarce.

9.5.5 Stakeholder involvement

In summary, bison populations should be managed to prevent the introduction and spread of diseases that directly, or indirectly, impact bison recovery. However, bison disease management strategies have been, and continue to be, controversial because the apparent solution to the disease problems (or "cure") is often perceived to be worse than the disease itself. Extensive stakeholder involvement in disease management plans is absolutely critical to successful bison disease management; such management strategies have often failed without it. Typical stakeholders in bison disease

Plate 9.2 *Meeting of stakeholders at Vermejo Park Ranch, IUCN Bison Specialist Group. Photo: John Gross.*

management include state and federal agencies (animal health regulators, land management agencies, and wildlife agencies), landowners, livestock producers, conservation organisations, sportsmen's organisations, and native people groups and organisations.

9.6 Active Management: Handling, Herding, Infrastructure

Bison differ substantially from cattle and they often respond poorly to handling that would be routine for cattle. Bison should be treated as wildlife and handled infrequently or preferably, not at all. When handling is absolutely necessary, suitable precautions must be observed, for example, old bulls (and cows) can be very dangerous and difficult to handle. Handling facilities designed especially for bison are needed to ensure the safety of both the animals and people that work with them.

The overarching principle is that to preserve the true, wild nature of bison, active management, through herding or other interventions, should be minimised. Handling bison can result in changes to bison behaviour and lead to management-based selection that, over time, alters genetic composition of the herd (Lott 1998). These changes can be irreversible and detrimental to conserving or restoring a "wild" stock. The general guidelines on preserving normal bison behaviour below are only an introduction. An understanding of the concepts of bison behaviour, practical experience, and perhaps, special training is required to handle bison well. We recommend consulting known experts for advice. Bison handling presents a greater challenge than handling domestic stock and managing for "wild" behaviour is a relatively new concept.

9.6.1 Handling

"Sure, you can herd bison … anywhere they want to go."

When active management of bison is necessary, use "calm animal" techniques based on an approach that adjusts human behaviour to fit the natural response of the animal, rather than the other way around (Grandin and Johnson 2004; Roberts 1996). This approach simplifies handling "wild" animals, and it reduces the tendency for managers to inadvertently remove ecologically desirable traits over time by selective culling.

Guidelines for handling bison are predicated on exploiting their natural instincts (Lott 1991). Bison are strongly motivated by food, by threat of predation, and by the need to maintain social cohesion. Managers can exploit these tendencies: bison can be led with food, and lighter fencing is adequate if better foods are not detected across a fence. By appearing as a predator, managers can precipitate uncontrollable flight or even attack. Less aggressive techniques can be used to control bison movements while minimising risk and effort. Bison's herding "instincts" prevail and groups of bison can be motivated to move simply by motivating the lead cow. By the same token, disrupting the established "pecking order" or cow-calf bonds in a herd stresses bison and makes them harder to handle.

Social cohesion in bison has important implications for handling. In the wild, herds of bison found food and fended off predators better than lone animals, and social communication provides important clues when handling bison. Potential danger signals include postures such as tails up, intense staring, snorting and pawing, and "growling" (by bulls) (Lee 1990a). More subtle signals can advertise anxiety, intent to move away, or willingness to follow.

It is easier to lead than to drive bison (Lee 1990b). Once trained to come to vehicles for food, bison will readily follow a vehicle to different parts of their home range, or they can be gathered for processing. Food dispensed at corrals during annual processing can motivate bison to move on their own toward corrals at the appropriate time the next year.

Predator-related behaviours of bison that handlers can use to their benefit include:

1) A tendency to interpret a direct approach or staring as a threat;

2) A tendency to flee if approached too closely, too swiftly, or too directly;

3) A tendency to drift away if approached slowly and tangentially;

4) Reduced intensity of response with repeated harmless encounters.

Implications of bison being attracted by food include:

1) The difficulty of fencing them away from good-quality food;

2) A tendency for bison to seek out the highest-quality forages in their home ranges;

3) The power of food, when properly managed, to amplify desired behaviour and reduce undesired behaviour.

Ways in which social cohesion can affect handling include:

1) The strong tendency for social groups to follow the lead animal's response;

2) The difficulty of separating cows from their young calves during processing;

3) The stress and disorientation that accompany disruption of social groups;

4) The ease of translocating and moving animals if social groups remain intact.

9.6.2 Fencing

Motivated bison can easily cross or destroy fences generally effective at constraining cattle. Bison-proof fences can be expensive, and if not carefully designed, may hinder passage by other wildlife. Efforts to reduce a bison's motivation to breach fences can greatly reduce the costs of fencing required to contain animals, and reduce adverse effects on other species.

Appropriate fence designs vary with circumstance, and a detailed discussion is beyond the scope of this chapter. More detailed recommendations and evaluations should be consulted before any construction begins (e.g., Butterfield 1990a; 1990b; Gates 2006). In general, a three-strand barbed-wire fence can hold bison that have been trained to avoid fences and that are not strongly motivated to cross the fence. High-tensile wire is more commonly used to build new bison fences or to reinforce existing ones. Some prefer net-wire fences, but depending on design, they can be formidable barriers to other animals that need passage. Electric fences, high tensile or otherwise, greatly increase the barrier effect to bison, and also condition them to avoid fences in general.

The need to allow passage for other wildlife affects fence design where deer, pronghorn, elk, (or other large ungulates) are present. High tensile fences with the bottom wire at least 51 cm (20") off the ground and the top wire 107-132 cm (42"-52") off the ground will constrain bison under most circumstances, while still permitting deer and pronghorn to pass under the fence and most elk to jump over the fence (Karhu and Anderson 2003). A three-wire electric fence with the bottom and top wires 56 cm (22") and 107 cm (42") off the ground, respectively, offered better passage for deer, pronghorn, and elk than did two- or four-wire designs (Karhu and Anderson 2003). Gates (2006) provides additional details and recommendations that vary from those above (e.g., top wire 152 cm (60") above ground). Additional guidance should be obtained to ensure fencing meets the needs of any specific application.

Factors that can modify the effectiveness of fencing include:

1) Bison density; as density increases, more secure fencing may be required;

2) Deep snow-pack may require special design considerations;

3) Damage due to falling trees, big game, vandals, or bison;

4) Attractive food, or other objects, on the other side of a fence increases bison motivation to breach fences.

Factors that influence the effect of fences on deer, pronghorn, or elk include (Gates 2006):

1) Nutritional stress; adverse impacts increase during periods of nutritional stress;

2) Some fence designs (e.g., woven wire) have greater barrier effects than others;

3) Barrier effects that are only seasonal may not be evident when fences are built;

4) Poor designs may injure or kill animals or separate mothers from young;

5) Predators may kill big game more easily by chasing them against fences.

9.6.3 Corrals, pens, and chutes

Corrals and associated facilities for wild bison need to be more carefully designed and constructed than similar facilities for domestic livestock. Bison may not recognise standard fencing as a barrier. Young calves require special attention because they may run into solid gates or fences, although fences that are about 80% solid appear to prevent this (Lammers, personal communication). Fences and gates, with 30-40 cm (12"-16") planks spaced 10 cm (4") apart, effectively stop bison and can be easily climbed by wranglers. Open fences near the working chutes, even those that are very strong, often lead to injury and mortality. Totally solid fencing can be dangerous for people working animals from the ground if they need to escape crowded or charging animals.

Bison handling facilities must accommodate the strong social hierarchy and aggressive behaviours that bison exhibit.

Appropriate facilities usually include custom sized and constructed chutes and alleyways, crash gates, and chute crowding tubes. It is expensive to construct facilities safe for bison (and the people working with them), and we strongly recommend visiting facilities that have proven to be safe and effective. Highly credible facilities include those at YNP (Gardiner, Montana), the Baca Ranch (Colorado), Badlands National Park (South Dakota), and EINP (Alberta).

9.7 Modelling to Assess Bison Populations and Habitat

Computer models are routinely used to improve our understanding of bison population and disease dynamics, and to forecast probable genetic consequences resulting from particular management actions. In the future, we should expect even more widespread use of quantitative models, which can, and likely will, be used for a broad range of purposes. A detailed treatise on modelling is well beyond the scope of this plan. The main goals of this section are, therefore, to provide readers with the minimal background necessary to seriously consider the utility of using an existing model, or of constructing a new management-oriented model, and to provide sufficient insight to the modelling process, that they can reasonably evaluate the validity and usefulness of model results, or at least ask questions that will help resolve these issues.

For conservation purposes, population viability analysis (PVA) and population habitat viability assessment (PHVA) have become common, and important, approaches for assessing existing populations and for evaluating potential restoration or reintroduction projects. We restrict PVA and PHVA to analyses that employ quantitative modelling to assess the risk of extinction, or which attain a quantitative population threshold greater than extinction ("quasi-extinction", from Ginzburg *et al.* 1982; Burgman *et al.* 1992; Ralls *et al.* 2002). Other thresholds for evaluation could include attaining a specified level of inbreeding depression or allelic diversity, or estimating the likelihood that a proposed introduction plan will result in establishment. Conclusions drawn from expert panels, committees, and other source of opinions, in the absence of a quantitative model, do not constitute a PVA (Reed *et al.* 2002). PHVA is a much broader process than PVA, and includes evaluation of geographical, social, regulatory, and ecological considerations that may significantly affect a species. The PHVA process includes a broad range of stakeholders and leads to specific recommendations for conserving a species in the area considered (http://www.cbsg.org/cbsg/phva/index.asp). Viability analysis is important to bison conservation because so many bison populations are small and clearly at risk, and because we have a rich knowledge of factors necessary to conduct credible and insightful evaluations.

The small size of many bison herds has raised concerns about retention of genetic diversity, and these concerns motivated detailed simulations to evaluate effects of management actions on retention of genetic variation in bison herds (Gross *et al.* 2006; Halbert *et al.* 2005; Wilson and Zittlau 2004). Other modelling studies have focused on brucellosis dynamics and its control in bison (Dobson and Meagher 1996; Gross *et al.* 1998; 2002; Peterson *et al.* 1991; Treanor *et al*. 2007) and on illustrating population dynamics of bison (Brodie 2008). All wildlife models are ultimately limited by data availability, and model results can be misleading when forecasts are presented with an apparent precision that is not justified by the underlying model assumptions, structure, or the accuracy of model parameters (Ralls *et al.* 2002; Reed *et al.* 2002). In general, the most appropriate use of simulation model results is to evaluate the merits of alternative management actions, rather than to define an absolute threshold population size. In particular, minimum critical population sizes may be sensitive to small errors in parameter estimates, or to the functional structure of strong environmental perturbations.

9.7.1 Guidelines for using computer simulations

The first critical step is to clearly define the objectives of the modelling exercise. If the intent is to evaluate management actions, the best objectives are quantitative, specific, time-bound, and consist of "treatment" variables (e.g., number of founders, number or proportion removed) that can reasonably be simulated by a computer model. A good objective must include the likelihood of achieving the desired results, the quantitative value of a threshold, and a time horizon. For example, a bison PVA used the genetic objective to achieve a 90% probability of retaining 90% of currently observed selectively neutral genetic heterozygosity for 200 years (Gross *et al.* 2006).

Below, we list steps that will be required to construct a computer model to support bison conservation. A number of recent treatises provide more detailed information about this process (we especially recommend Burgman *et al.* 1993; Bessinger and Westphal 1998; Bessinger and McCullough 2002; Hilborn and Mangel 1997). Although we list steps sequentially, most modelling exercises are iterative and involve simultaneously working through a number of these tasks and revisiting them as more information or insight becomes available.

1. Clearly articulate the objectives of the modelling exercise. It is essential to clearly identify a small, discrete set of "treatments" and "responses".

- What management must be evaluated?
- What is the relevant time frame?
- What model outputs are to be evaluated?

2. Determine the required scope of model.

- Single or multiple species?
- Age or stage structured?
- One or more population units?
- Spatially homogeneous or with spatial structure?
- What is the geographical extent?
- Are animal-habitat feedbacks necessary?

3. Evaluate existing software and decide whether to use an existing programme or to construct a new model. Considerable time and money can be saved by using "off the shelf" software, such as RAMAS (http://www.ramas.com/software.htm), Vortex (Lacy 1993), ALEX (Possingham *et al.* 1992), or another modelling environment.

4. Collect necessary data and estimate model parameters. This can be a huge step. Data will be needed to estimate mean vital rates and realistic estimates of variance. Ecosystem or habitat models will require much additional information to determine carrying capacity and animal-ecosystem feedbacks. Most population-habitat models used for PVA will include catastrophes, estimates of variance in habitat carrying capacity, and specific assumptions on the form and process of density dependence.

5. Construct, calibrate, and run the model. Evaluate model results. Considerable effort may be required to understand and comprehensively evaluate model inputs, and to understand model results. Output from a simulation exercise usually includes huge quantities of data that will need to be reduced, summarised, and presented in an understandable form.

6. Package results in a digestible and understandable format. This is a vastly underappreciated problem, and it will be much easier if the model objectives were clear and concisely stated at the outset.

7. Ralls *et al.* (Table 25.4 in Ralls *et al.* 2002) provide a specific checklist for evaluating the quality of a PVA, and this checklist applies equally well to many additional conservation modelling exercises. They provide "yes-no" questions that focus on model objectives, model structure, data and parameter estimation, analysis of model outcomes, handling of model uncertainty, interpretation, and peer review. These criteria provide a sound framework for helping to ensure models are constructed and used in an appropriate fashion.

9.8 Conclusions

While many topics are addressed in this chapter, effective management of bison ultimately relies on the judicious application of common sense and good judgement. When bison have access to sufficient space and forage, and are left relatively undisturbed, they are more than fully capable of taking care of themselves. Nonetheless, most bison will not experience natural conditions that include wide-open spaces and intact predator communities, so we hope the guidelines provided will support science-based management programmes that lead to more effective conservation and restoration of bison. These guidelines focus on widespread common management issues—population management, disease, and genetic management. These guidelines and principles will ensure that key issues are addressed, and citations will help managers find more detailed information that may be necessary to accommodate specific situations.

Chapter 10 Guidelines for Ecological Restoration of Bison

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10.1 Introduction

During Pre-Columbia times, bison had the widest distribution of any large herbivore in North America, ranging from the arid grasslands of northern Mexico to the extensive meadow systems of Interior Alaska (Chapters 2 and 7). Following the arrival of Europeans, the species experienced unparalleled range contraction and collapse of populations in the wild, primarily during the late 19th Century (Isenberg 2000). Wild bison persisted in only two locations, south of Great Slave Lake in what is now Wood Buffalo National Park (about 300 individuals), and in the remote Pelican Valley in the Absaroka Mountains in the interior of Yellowstone National Park (YNP) (fewer than 30 individuals). The species was extirpated from the wild throughout the remainder of its original range. The American bison has achieved a remarkable numerical recovery, from approximately 500 at the end of the 19th Century to about half a million animals today, of which 93% now exist under captive commercial propagation (Chapter 7). However, Sanderson *et al.* (2008) estimate that bison occupy less than 1% of their original range.

Rarely do wildlife populations in North America achieve the full range of ecological interactions and social values existing prior to European settlement. The bison remains extirpated as wildlife and in the ecological sense from much of its original continental range. This is particularly true of the plains bison, for which few populations interact with the full suite of other native species and environmental limiting factors (Chapters 6 and 7). In the absence of committed action by governments (including aboriginal governments), conservation organisations, and perhaps the commercial bison industry, the conservation of bison as a wild species is far from secure. The main challenges were described in earlier chapters of this volume and are summarised by Freese *et al.* (2007). They include anthropogenic selection and other types of intensive management of captive herds, small population size effects, issues related to exotic diseases, introgression of cattle genes, management under simplified agricultural production systems, and associated with this, widespread ecological extinction as an interactive species.

Contemporary biological conservation is founded on the premise of maintaining the potential for ecological adaptation in viable populations in the wild (IUCN 2003; Secretariat of the Convention on Biological Diversity 1992; Soulé 1987), and maintaining interactive species (Soule *et al.* 2003). Viability relates to the capacity of a population to maintain itself without significant demographic or genetic manipulation by humans for the foreseeable future (Soulé 1987). For limiting factors, such as predation and seasonal resource limitation, adaptation requires interactions among species, between trophic levels, with physical elements of an ecosystem. These, and other interactions among individuals within a population (e.g., resource and mate competition), contribute to maintaining behavioural wildness, morphological and physiological adaptations, fitness, and genetic diversity. These factors enable a species to adapt, evolve, and persist in a natural setting without human support in the long term (Knowles *et al.* 1998).

Viable, wild populations of bison, subject to the full range of natural limiting factors, are of pre-eminent importance to the long-term conservation, global security, and continued evolution of the species as wildlife. However, the availability of extensive ecosystems capable of sustaining large, free-roaming, ecologically interactive bison populations is limited. This is particularly true in the original range of plains bison in the southern agriculture-dominated regions of the continent, given the historical post-European settlement patterns of industrial and post-industrial society. Social and political systems that provide space and environmental conditions where bison can continue to exist as wildlife and evolve as a species, are severely limited.

Innovative approaches need to be instigated in some locations to emulate, to the extent possible, the original ecological conditions, and to prevent domestication and small population-related deleterious effects such as those experienced by the European bison (Hartl and Pucek 1994; Prior 2005; Pucek *et al.* 2004). Currently, there is only one population of plains bison (YNP) and three populations of wood bison (Greater Wood Buffalo National Park, Mackenzie, and Nisling River) in North America that can be considered ecologically restored (thousands of individuals, large landscapes, all natural limiting factors present, minimal interference/management by humans).

The conservation of American bison as wildlife would be significantly enhanced by establishing additional large populations to achieve landscape scale ecological restoration. This will require effective collaboration among a variety of stakeholders, whereby local actions, based upon social and scientific information, are coordinated with wider goals for species and ecosystem conservation. The bison was an

ecologically dominant keystone species over much of its range. Thus the ecological integrity and diversity of ecosystems in which they occurred, whether defined historically or biologically, will depend on large-scale restoration of the bison.

10.2 Ecological Restoration

Ecological restoration provides a conceptual framework for bison restoration at medium to broad scales. It can be defined as the intentional process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed relative to a reference state or a trajectory through time (SERI and IUCN Commission on Ecosystem Management 2004). The goal of ecological restoration is an ecosystem that is resilient to perturbation, is self-sustaining with respect to structure, species composition and function, is integrated into large landscapes, and supporting sustainable human livelihoods. Many healthy ecosystems are a product of human endeavours over very long time periods. In many cases then, ecological restoration projects typically requires the participation of resource-dependant human communities, and have the potential to support ecologically sustainable economies in rural communities. Bison play important ecological roles (Chapter 6), as well as meaningful cultural and economic roles (Chapters 2 and 7). They are increasingly providing a viable alternative to grazing exotic domestic herbivores (Renecker *et al.* 1989).

Ecological restoration of bison: The re-establishment of a population of several thousand individuals of the appropriate sub-species, in an area of their original range, in which bison interact in ecologically significant ways with the fullest possible set of other native species and other biophysical elements of the landscape, and connect in meaningful ways with human communities, with minimal management interventions (adapted from Sanderson *et al.* 2008).

Sanderson *et al.* (2008) asserted that by sharing an inclusive, affirmative and specific vision and knowledge about bison and landscape conservation with a wide range of stakeholders, opportunities can be created to restore bison in ecologically effective herds roaming across extensive landscapes in all major habitats of their original range. Here we define the full, or ideal, ecological restoration of bison as the re-establishment of a population of several thousand individuals of the appropriate sub-species, in an area of original range, in which bison interact in ecologically significant ways with the fullest possible set of other native species and biophysical elements of the landscape, with minimal management interventions. This is not to say that populations smaller than several thousand bison do not contribute to bison conservation, or to restoration of ecological processes (e.g., grazing, soil disturbance, decomposition, nutrient cycling, predation, scavenging; Chapter 6). However, some processes, such as migration and natural selection, may be absent or not function as completely at smaller scales (Chapter 9). Sanderson *et al.* (2008) provide specific criteria for ranking the contribution of bison herds to ecological restoration.

10.2.1 Geographic potential for ecological restoration

The Wildlife Conservation Society hosted a workshop in May 2006 at Vermejo Park Ranch, New Mexico that involved 28 people, including bison specialists, indigenous groups, bison producers, conservation organisations, and government and private land managers, from throughout North America. Among other objectives, participants worked to draft a vision for ecological recovery of the American bison, to develop a consensus hypothesis on major habitat types within the original range that would be useful for representative conservation planning, and to map areas for potential ecological recovery over the next 20, 50, and 100 years (Sanderson *et al.* 2008; also see Chapter 7). The methods used to achieve these objectives were similar to those pioneered for jaguars (Sanderson *et al.* 2002) and subsequently applied to other species (e.g., Thorbjarnarson *et al.* 2006) under the title of "range-wide priority-setting".

A vision referred to as "The Vermejo Statement" was developed for the ecological future of the American bison (Sanderson *et al.* 2008):

"Over the next century, the ecological recovery of the North American bison will occur when multiple large herds move freely across extensive landscapes within all major habitats of their historic range, interacting in ecologically significant ways with the fullest possible set of other native species, and inspiring, sustaining and connecting human cultures.

This vision will be realised through a collaborative process engaging a broad range of public, private, and indigenous partners who contribute to bison recovery by:

- *Maintaining herds that meet the criteria for ecological recovery, as well as herds that contribute in some significant way to the overall vision, regardless of size,*
- *Managing herds for the long-term maintenance of health, genetic diversity, and integrity of the species,*
- *Restoring native ecosystems, ecological interactions, and species,*
- *Providing conservation incentives for bison producers, managers, and other stakeholders,*

"'Ecosystem' means a dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit" (Article 2 of the Convention on Biological Diversity).

- *Creating education, awareness and outreach programmes to public and policy-making constituencies,*
- *Building capacity among key stakeholder groups, and*
- *Working across international borders, where necessary."*

Participants in the Vermejo workshop were asked to map areas where "*ecological recovery might be possible*" over three time frames (20, 50, and 100 years), considering future trends in land use, economic development, demography, and climate. The resulting maps provide a subjective, visual hypothesis of the most promising places for ecological recovery (Sanderson *et al.* 2008). The maps illustrate that potential for ecological recovery exists throughout North America. Long-term opportunities are apparent across much of the original range of the plains bison, from private agricultural, state, and national grazing lands in northern Mexico and southern New Mexico, to the agriculture-dominated, mixed tenure landscapes of the Northern Great Plains. In northern regions of the continent, wood bison populations exceeding a thousand animals are already present in three large landscapes in Canada, and a new initiative will restore one or more populations in interior Alaska.

The kinds of large areas required to achieve ideal ecological restoration of bison are likely to be managed by several jurisdictions, and may also involve private landowners. Achieving agreement on restoring bison to such landscapes is challenging prospect, requiring principled, long-term development planning, soundly based on community-based conservation development praxis (see: Bopp and Bopp 2006, for practical guidelines for community development).

10.2.2 Principles for ecological restoration applicable to bison

Successful ecological restoration of bison as wildlife on multi-tenured landscapes requires careful assessment and collaborative planning. While some restoration projects will emerge from government and non-profit organisation initiatives, private landowners may initiate others. In many cases, assembling a sufficiently large landscape (tens or hundreds of thousands of hectares) for ecological restoration will require cooperation between public and private landowners.

The American Bison Specialist Group considered documents published by IUCN and the Society for Ecological Restoration Science and the Policy Working Group, and drew upon the professional and practical experiences of its members, and other participants, to develop the following guiding principles for agencies and non-profit conservation organisations interested in ecological restoration of bison:

1) Goals concerning the management of land, water, and living resources, including bison restoration, are a matter of societal choice.
2) Ecological restoration of bison is an interdisciplinary and inclusive undertaking requiring the involvement of all relevant sectors of society and scientific disciplines.
3) Planning and management of ecological restoration projects should be decentralised to the lowest appropriate level, as close as possible to the human community within a local ecosystem, and supported by the highest levels of government policy.
4) All forms of relevant information, including scientific, indigenous and local knowledge, and innovations and practices, should be considered in planning and implementing bison restoration.
5) Understanding and addressing economic drivers is imperative for successful ecological restoration of bison, including:
    a. Reducing market distortions that adversely affect conservation of bison as wildlife;
    b. Developing incentives to promote conservation of ecologically functioning bison populations and their sustainable uses; and
    c. To the extent possible, internalising the costs and benefits of managing bison as wildlife in an ecologically restored landscape.
6) Ecological restoration of bison should be undertaken at appropriate spatial and temporal scales, and should focus on restoring ecological structure, processes, functions, and interactions within a defined ecosystem.

"A functional conservation area maintains the focal species, communities, and/or systems, and their supporting ecological processes within their natural ranges of variability (i.e., the amount of fluctuation expected in biodiversity patterns and ecological processes under minimal or no influence from human activities)" (Poiani and Richter undated).

7) Restored bison populations should be managed, to the extent possible, as an integral component of, and within the ecological limits of, an ecosystem.

8) Conserving bison and conserving landscapes through restoration of ecologically functioning bison populations are inseparable.

9) Adopting a long-term perspective on ecological restoration of bison, and an inclusive process, will open up conversations and foster partnerships and political will that might not otherwise be possible.

10) Ecological restoration of bison should serve both biodiversity conservation and ecologically sustainable use, and involve fair and equitable sharing of benefits among stakeholders.

11) Ecological restoration of bison should be fully incorporated into national and state/provincial biodiversity conservation strategies.

12) Inter-sectoral and inter-jurisdictional communication at all levels (between nations, government ministries, management agencies, organisations, communities, etc.) improves awareness and multi-party cooperation.

The bison has been a utility species for many cultures and communities since people first arrived on the North American continent about 12,000 years ago, with the exception of a 100-year period between the great contraction of the species (*circa* 1880; Flores 1994) and recent commercialisation (*circa* 1980; Renecker *et al.* 1989). Its utility is reflected in the current predominance of animals managed for private commercial captive propagation (about 93%), and the fact that all large (more than 1,000 animals) free-roaming populations are hunted. The IUCN Policy on Sustainable Use of Wild Living Resources (http://cmsdata.iucn.org/downloads/2000_oct_sust_use_of_wild_living_resources.pdf) and the principles on sustainable use developed by the IUCN Sustainable Use Specialist Group (IUCN SUSG Technical Advisory Committee 2001) apply to the ecological restoration of bison. The IUCN Policy on Sustainable Use provides that conservation of biodiversity is central to the IUCN's mission, which is to influence, encourage, and assist societies to conserve the integrity and diversity of nature, and to ensure that any use of natural resources is equitable and ecologically sustainable. The Policy considers that both consumptive uses (harvesting of animals and plants) and non-consumptive uses (maintaining cultural and aesthetic values of biological diversity) are important components of a sustainable development agenda supporting human livelihoods, while, at the same time, contributing to conservation. In addition, the IUCN Re-introduction Specialist Group (1998) offered important considerations to ensure local stakeholder and agency support for wildlife restoration projects.

Principles for Sustainable Use of Living Resources (IUCN Sustainable Use Specialist Group 2001):

1. Sustainable use will most likely be achieved with consideration of socio-political, economic, biological and user factors at the community, sub-national, national, and international levels.

2. Sustainable use is enhanced by supportive incentives, policies, laws and institutions at all levels of governance, and by effective linkages between them.

3. Local communities, and other parties who have management responsibility for wild living natural resources, must be supported by recognised rights and the means to manage the resources.

4. The contribution and needs of those who manage wild living natural resources must be appropriately reflected in the allocation of the benefits from the use of those resources.

5. Adaptive management, relying on an iterative process of timely and transparent feedback from socio-economic, resource and ecological monitoring, is essential for sustainable use.

6. Sustainability of living wild resource use is enhanced if traditional/local knowledge is taken into account.

7. Sustainable use of wild living resources is enhanced if managerial jurisdictions match ecological and socio-economic scales.

8. Subsidies that distort markets, promote habitat alteration or destruction, and unsustainable use of natural resources should be eliminated.

10.3 The "Ecosystem Approach" for Designing Ecological Restoration of Bison

The Ecosystem Approach (Shepherd 2004) is a strategy for integrated management of land, water, and living resources that promotes conservation and sustainable use in an equitable way. It is the primary framework for action under the Convention on Biological Diversity. The Ecosystem Approach puts people, and their natural resource use practices, at the centre of decision-making. Because of this, it can be used to seek an appropriate balance between conservation and use of biological diversity in areas where there are many resource users combined with important natural values.

Planning and implementing ecological restoration of bison may involve multi-tenured landscapes and is a complex undertaking that requires assessing biophysical and social components, evaluating and engaging stakeholders, considering economic conditions, and cultivating long-term partnerships. Ecological restoration planning is a dynamic process, best achieved incrementally, with ample opportunities for iteration and feedback. The following elements provide guidance for agencies, organisations and individuals interested in designing ecological restoration projects.

10.3.1 Defining the biological landscape and objectives

Ecological restoration of bison considers the species as an interactive element of an ecologically functioning restoration area that provides the size and distribution of habitats necessary to support a restored bison population. Defining a biological landscape for this purpose involves determining the size and refining the boundary of the area, identifying the resource requirements of bison and other focal elements including their spatial needs, and mapping the distribution of habitat resources (Loucks *et al.* 2004). These tasks can be achieved by a variety of processes including expert-driven workshops and local working groups aided by technical experts. For example, the IUCN/SSC Conservation Breeding Specialist Group (CBSG) has extensive experience managing conservation planning workshops using its signature processes, the Conservation Action Management Plan and Population and Habitat Viability Assessment (PHVA), to assist groups in developing species level action plans (www.cbsg.org/cbsg). A Landscape Cumulative Effects Simulator (ALCES®; Forem Technologies; www.alces.ca) is another software tool that is rapidly gaining acceptance by industry, government, and the public as an effective simulation tool for exploring sustainable resource and landscape management alternatives.

Whatever the decision support system is used, common to each process is the need to have stakeholders (conservation groups, wildlife biologists, relevant government agencies, and local private and public land managers) involved. Agreements are typically required on the size and boundaries of the ecosystem and the potential biological capacity of the area to meet the needs of bison restoration and other conservation and community objectives.

"Conservation landscape" refers to a spatial plan for a priority area that meets fundamental conservation objectives while addressing other socio-economic needs (Loucks et al. 2004).

10.3.2 Defining the social landscape, the main stakeholders, and cultivating partnerships

Large-scale ecological restoration involves multiple levels of social complexity, and typically involves more than one jurisdiction. The geographic potential for ecological restoration of bison in North America is illustrated in a general sense by Sanderson *et al.* (2008). Priority areas may be considered as having the potential to become conservation landscapes (*sensu* Loucks *et al.* 2004) that have ecological and social potential for restoration of bison in the intermediate to long term. Careful assessment and understanding of social, economic, legal, and political conditions within candidate landscapes is an essential preparatory step for planning and implementing restoration projects (Loucks *et al.* 2004; The Nature Conservancy 2005), particularly where community support and involvement is required (Child and Lyman 2005).

The priority areas identified by Sanderson *et al.* (2008) represent, in the collective opinion of a group of experts, a hypothesis of where the most promising places for ecological recovery exist, considering future land use trends, economic forces, human demography, and climate. Understanding the regional social-ecological system in such target areas is an important feature of effective conservation planning (Driver *et al.* 2003). In addition to assessing the biophysical capability of a candidate area, detailed assessments are required to define the human community within the ecosystem boundaries. Social landscape analysis (Field *et al.* 2003) provides a tool for understanding and mapping the human landscape. It requires collecting, analysing and mapping human demographic and economic data, and information on land development and ownership patterns and trends. Social landscapes consist of the demographic patterns of people (location, density, age and gender structure, industry and employment patterns, and governance boundaries) in relation to land and resources.

The types of socioeconomic data relevant for ecological restoration planning will vary among locations across the continent. However, certain information is relevant for all landscapes. Detailed and current information on land use, including land use maps, is critical for assessing the impacts of habitat loss and trends. Development plans and targets for important resource sectors (agriculture, energy, and transportation) provide the basis for evaluating impacts of foreseeable change over time. Spatial information on land ownership and management authorities contribute to the identification of stakeholders and assessment of conservation potential.

Loucks *et al.* (2004) provided the following list of socioeconomic variables useful for conservation planning. The list should be reviewed and customised for each project in consultation with local managers:

1. **Current patterns of land and resource use:**
   - Major land and resource uses (including forest, water, wildlife use, agriculture, extraction);
   - Development plans and projected changes in land and resource use;
   - Existing zoning regulations;
   - Major existing and planned infrastructure (roads, dams, etc.);
   - Existing protected areas.
2. **Governance and land/resource ownership and management:**
   - Political boundaries (provinces, districts);
   - Land tenure (private, public, ancestral/communal areas);
   - Agencies responsible for management of land/resource areas (e.g., forest, agriculture departments).
3. **Population data:**
   - Human population density and growth;
   - Population centres;
   - Migration patterns (in- and out-migration);
   - Social characteristics: income, ethnicity, indigenous areas;
   - Economic data;
   - Economic growth and loss areas;
   - Land prices;
   - Potential values and opportunities for ecological services;
   - Potential for incorporating natural assets into the local economy.
4. **Additional factors that affect biodiversity and potential for bison restoration:**
   - Access (e.g. roads, rivers, energy corridors, etc.);
   - Trends in habitat conversion.

"Current conservation initiatives—parks, land conservation, regulatory programs—offer important contributions but provide solutions to only 10% of the problem. The remaining 90% exist at the interface of human populations and ecological systems" (Child and Lyman 2005).

Bison occupy a distinct iconic status as wildlife with both indigenous and non-indigenous North Americans. The cultural and historic significance of bison is particularly important to many Native North Americans (Stephenson *et al.* 2001; Wyckoff and Dalquest 1997). In recent decades, bison have increased in value as private property in the form of livestock (Chapter 7). In the grasslands of the continent, the cattle ranching culture and economy replaced a 10,000-year-old bison economy, and cattle ranching now occupies more than 95% of the Great Plains grasslands. The potential for restoration of plains bison at a meaningful ecological scale in this region therefore depends on support by people involved in this sector. Similarly, support from regulatory authorities, and harmonisation of policies and planning processes is necessary to ensure a feasible start, and sustainable outcomes of bison conservation projects.

To ignore or contradict cultural or local interests, or the authority of agencies, can generate unnecessary on-going resistance to conservation initiatives. An example of this is the concept of the "Buffalo Commons" or "re-bisoning" of the Great Plains proposed by Rutgers University geographers Frank and Deborah Popper (Popper and Popper 1987). The Popper's predicted economic and human population declines in the Great Plains, now borne out by current trends (Forrest *et al.* 2004). The idea of replacing the cattle ranching culture with a Buffalo Commons created a firestorm of protest among agriculture-based communities in the region, and continues to haunt discussions about bison conservation and ecological restoration. The general lesson learned from this case is that the ecological restoration of bison is not possible

Stakeholders are people who will be impacted by the decisions; they have the knowledge to make the best decisions, and the power to implement or block decisions.

anywhere without engaging stakeholders, their interests, mandates and aspirations, and developing local community and agency capacity to engage in sustainable ecological restoration.

Managing social-ecological systems requires an explicit approach that can serve as a vision for stakeholders (Knight *et al.* 2006). Conservation planners should avoid perceiving themselves as empiricists that operate outside, rather than within, social-ecological systems (Sayer and Campbell 2004). Clewell and Aronson (2006) discuss the major motivations or rationales for the restoration of ecosystems and their associated species. These include technocratic, biotic, heuristic, idealistic, and pragmatic rationales that often result in social conflicts. Restoration of bison and their native ecosystems is no exception, as a diversity of socioeconomic factors, from local to regional to international levels, is involved. Organisers wishing to initiate large scale ecological restoration projects are encouraged to become familiar with the theories and practices of community-based resource management (Child and Lyman 2005) and community development (Bopp and Bopp 2006), but more importantly, to include an experienced practitioner on the core development team.

Although bison restoration presents many challenges, it is important to remember that bison have historically provided many benefits to human societies and continue to do so today. In collaborative planning for ecological restoration, it is important to emphasise economic and social benefits, as well as those related to biodiversity conservation and ecosystem health.

Re-introduction: an attempt to re-establish bison in an area that was once part of its original range, but from which it was extirpated.

Re-enforcement/Supplementation/ Augmentation: Addition of individuals to an existing population of conspecifics.

Substitution: the introduction of a closely related species or sub-species, for subspecies that have become extinct in the wild and in captivity. The introduction occurs in suitable habitat within the extinct species or subspecies historical range (Seddon and Soorae 1999).

Source: IUCN Re-introduction Guidelines (Re-introduction Specialist Group 1998)

10.4 Guidelines for Planning and Implementing Ecological Restoration Projects for Bison

The IUCN Re-Introduction Specialist Group (1998) defines the purpose of a re-introduction in the following manner:

"The principle aim of a re-introduction should be to establish a viable, free-ranging population in the wild, of a species, subspecies or race, which has become globally or locally extinct, or extirpated, in the wild. It should be re-introduced within the species' former natural habitat and range and should require minimal long-term management."

Ecological restoration adds additional values to species' reintroduction projects. It has as its goal, an ecosystem that is resilient and self-sustaining with respect to structure, species composition and function, as well as being integrated into the larger landscape and supporting sustainable human livelihoods (SERI and IUCN Commission on Ecosystem Management 2004). The following guidelines for planning and implementing an ecological restoration project for bison were adapted from the IUCN Re-introduction Guidelines (IUCN 1998). They are also informed by other key documents on conservation and restoration planning (Loucks *et al.* 2004; The Nature Conservancy 2005), community based natural resource management (Child and Lyman 2005), and community development planning (Bopp and Bopp 2006). They address biological and socio-economic needs for restoring bison as an interactive species within a restored ecosystem:

10.4.1.1 Feasibility assessment

- Sites for ecological restoration of bison should be within the original range of the appropriate sub-species of bison;
- For a re-introduction, there should be no remnant population of bison in order to prevent disease propagation, social disruption, introduction of alien genes, or disruptions to logistics;
- In some circumstances, a re-introduction or reinforcement may have to be made into an area that is fenced or otherwise delimited, but it should be within the sub-species' original range and habitat;
- Ecological restoration may take place where the annual habitat and landscape requirements of more than 1,000 bison can be satisfied normally, without the need for supplementation, and a population of at least this number is likely to be sustained for the foreseeable future with minimum management intervention.
- The possibility of natural habitat change should be considered (e.g. forest succession, climate change);
- The effects of interactions of bison with other species in the ecosystem should be defined and considered in planning the restoration project;

- Legal, policy, political, and cultural constraints need to be evaluated to determine if mitigation is needed or possible;
- Determine if the factors causing decline can be eliminated or mitigated (e.g., diseases, over-hunting, over-collection, pollution, poisoning, competition with, or predation by, introduced species, habitat loss, adverse effects of earlier research or management programmes, competition with domestic livestock);
- Where the release site has been substantial degraded by human activity, a habitat restoration programme should be initiated before the reintroduction is carried out;
- A Population and Habitat Viability Assessment will aid in identifying significant environmental and population variables, and assessing their potential interactions, which can guide long-term population management;
- *A priori* agreement is desirable on population objectives, monitoring, and methods that will be used to manage population growth as the target population size is approached;
- Similarly, *a priori* agreement on range health objectives and range monitoring and management methods is desirable;
- Determine the availability of suitable stock, including subspecies or locally adapted forms, genetics (e.g. cattle genes), and absence of specific diseases of concern to conservation;
- A feasibility assessment should include determining if adequate funding is available to successfully complete the project.

10.4.1.2 Suitable release stock

- It is preferable that source animals come from wild populations, or captive stock that have been subjected to minimum management, such as selection for or against specific morphological traits;
- The source population should ideally be closely related genetically to the original native stock and show similar ecological characteristics (morphology, physiology, behaviour, habitat preferences) to the original sub-population;
- Use stock from a source population(s) that has tested negative for the presence of cattle gene markers, based on the best available technology;
- Stock must be guaranteed available on a regular and predictable basis, meeting specifications of the project protocol;
- Individuals should only be removed from a wild population after the effects of translocation on the donor population have been assessed and after it is certain that these effects will not be negative;
- If captive or artificially propagated stock is to be used, it must be from a population that has been soundly managed both demographically and genetically, according to the principles of contemporary conservation biology;
- Re-introductions should not be carried out merely because captive stocks exist, nor solely as a means of disposing of surplus stock;
- Prospective release stock, including stock that is a gift between governments, must be subjected to a thorough veterinary screening process for pathogens and exposure to pathogens before shipment from original source;
- If evidence of infection with any notable pathogen is found, the translocation should be stopped and a risk assessment conducted to determine the wisest action;
- Assess the presence of pathogens in wild and domestic species present in the re-introduction area;
- Minimise the risk of infection during transport by managing potential exposure to pathogens;
- Stock must meet all health regulations prescribed by the veterinary authorities of the recipient jurisdiction and adequate provisions must be made for quarantine if necessary;
- If vaccination is deemed appropriate prior to release this must be carried out allowing sufficient time for the required immunity to develop before the translocation.

10.4.1.3 Preparation and release

- Construct a multidisciplinary planning and management team(s) with access to expert technical advice for all phases of the programme;
- Establish short- and long-term goals and specific objectives, both for the bison population and for the habitat and biodiversity management, including success indicators and targets;
- Define monitoring programmes for evaluating how well goals and objectives are being met, and the adjustments that may be required. Each re-introduction should be a carefully designed experiment, with the capability to test methodology with scientifically collected data;
- Secure adequate funding for all phases of preparation and release;
- Monitor the health and survival of individuals;
- Secure appropriate veterinary expertise to ensure the health of released stock, including adequate quarantine arrangements, especially where stock is transported over long distances or crosses jurisdictional boundaries;
- Develop transport plans for delivery of stock to the site of reintroduction, with special emphasis on ways to minimise stress on the individuals during transport;
- Determine appropriate release strategies, including habituation of release stock to the project area, behavioural training, release techniques, and timing;
- Establish policies on interventions to manage parasites and pathogens;
- Establish, where necessary, a detailed containment programme that includes fence design and monitoring and protocols for dealing with escaped animals;

- Interventions (e.g., supplemental feeding, veterinary aid, horticultural aid) should only be undertaken if necessary to prevent catastrophic losses that risk extirpation, or a significant reduction in genetic diversity, particularly when the population is small;
- If fencing is required, use designs that allow for movement of other wildlife species (see Chapter 9 for specifications);
- Develop a conservation awareness programme for securing long-term support: professional training of individuals involved in the long-term programme, public relations through the mass media and in local community, and involvement, where possible, of local people in the programme.

10.4.1.4 Socio-economic and legal requirements

The IUCN Guidelines for Re-Introductions (IUCN 1998) also provide measures for addressing socio-economic and legal requirements of re-introduction programmes. They have been adapted here for ecological restoration projects involving bison. Considering that ecological restoration projects require long-term commitments of financial and political support:

- Socio-economic studies are needed to assess impacts, costs and benefits of the restoration programme to local human populations and governments;
- A thorough assessment of attitudes of local people towards the proposed project is necessary to develop and secure long-term conservation of the restored population;
- The restoration programme should be fully understood, accepted, and supported by local communities and affected government agencies;
- Where the security of the re-introduced population is at risk from human activities, measures should be taken to minimise these in the programme area;
- The policies of affected government agencies (at all levels) on restoration and bison management should be assessed. This will include evaluating existing municipal, provincial, national, and international legislation and regulations, and if necessary negotiating new measures;
- Restoration projects must take place with the full permission and involvement of all relevant government agencies. This is particularly important in restoration programmes involving multi-tenure landscapes, such as in border areas, in areas involving more than one state, or where a re-introduced population can expand into other jurisdictions or onto adjacent private lands;
- As with other species of large herbivore (e.g. moose and elk), bison pose small, but manageable, risks of personal injury and property damage. These risks should be minimised and adequate provision made for awareness and, if necessary, compensation;
- If projects are situated adjacent to international or state boundaries, provisions should be made for monitoring or managing bison crossing the boundaries;
- Measures for managing escaped or emigrating bison should be agreed to *a priori* with owners of adjacent lands;
- Approval by relevant government agencies and landowners, and coordination with national and international conservation organisations are necessary.

10.4.1.5 Monitoring, evaluation, and adaptation

The implementation of an ecological restoration project does not guarantee its objectives will be attained or its goals achieved. Outcomes of restoration projects involving complex systems can be unpredictable. Restored ecosystems are dynamic and require evaluation over many years. In large landscapes, a bison population may not mature demographically for 30 years or more following release from management control or following reintroduction (Gates *et al.* 2005; Larter *et al.* 2000). Environmental factors, such as sporadic drought, severe winters or predation effects, contribute to uncertainty of outcomes. Maintaining support for an ecological restoration project in the long term requires continuous evaluation of performance measures (indicators) that represent the ecological infrastructure and functioning of the ecosystem, and others that represent human community needs about sustaining culture and economy. Respect for both local and science-based knowledge, coupled with participatory processes, ensures the full and equitable engagement of the communities, and that the indicators selected, data collected, and decisions made, meet the needs of agencies and local communities.

The following guidelines for monitoring, evaluation and adaptation are offered:

- Post-release monitoring of a significant sample of individual bison is necessary to evaluate individual survival, health, reproduction, and movements, and to assess the causes and significance of unanticipated losses (e.g., copper or selenium toxicity, behavioural naivety to predators) during the initial years of a project;
- Demographic, ecological and behavioural studies of the population should be undertaken over the long term to monitor changes in population and distribution patterns;
- Habitat protection or restoration may be necessary to support population and biodiversity restoration goals;
- Publicity and documentation should be incorporated into every restoration project because published accounts are important for maintaining long-term support of a project. Regular public information releases and publications in scientific and popular literature are useful instruments;
- Monitoring all the costs and a full range of benefits (monetary and non-monetary) to provide documentation that shows the impacts of the project and that funding support is justified;

- Implement adaptive management procedures as needed. Adaptive management, as a restoration strategy, is essential because what happens at one stage in restoration informs or dictates what needs to happen next;
- Capacity building should be informed by results of the monitoring programme and targeted toward the highest priorities and weakest aspects of management.

10.5 Summary

The next 10-20 years present opportunities for conserving American bison as a wild species and restoring it as an important ecological presence in many North American ecosystems. Taking an ecosystem approach, which puts people and their natural resource use practices at the centre of decision-making, offers a paradigm for balancing the sometimes competing demands of bison conservation, the use of bison and biological diversity by people, and sustaining human communities in areas where there are many resource users combined with important natural values. To achieve ecological restoration at broad scales (large herds roaming across vast landscapes, at numerous locations) will require flexible approaches that can be adapted to a variety of legal and socio-economic conditions. Assembling large landscapes for conservation herds will typically involve several land tenure holders, potentially including public agencies, tribal governments, non-profit private organisations, and for-profit corporations or individual entrepreneurs. Diverse mandates, interests, and incentives will influence how stakeholders choose to manage land and wildlife, including bison. Creative new approaches are needed for forging enduring partnerships among land tenure holders for cooperative undertakings. Strategies may range from top-down government programmes to bottom-up market-based or cultural-based initiatives. Progress towards large-scale restoration will require a much more supportive framework of government policies and significant investment by both public and private sectors. Awareness and substantial public support are necessary at both the local level where restoration occurs, and among national constituencies for whom the bison is an iconic component of North America's natural and cultural heritage. For ecological restoration of bison to be successful, careful assessment and understanding of biophysical, social, economic, legal, and political conditions are required for planning and implementation. This is particularly true where both community and agency support and involvement are required. This chapter provided guidelines for planning and implementing an ecological restoration project for bison, including feasibility assessment, selection of stock, preparation and release methods, assessing socio-economic and legal requirements, monitoring, evaluation, and adaptation.

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Appendix A North American conservation herds of bison and their managing authorities

Plains bison

State/Province	Site	Jurisdiction	Managing Authority
AB (Alberta)	Canadian Forces Base Wainwright	Federal-Canada	Department of National Defence
AB	Elk Island National Park	Federal-Canada	Parks Canada Agency
AB/SK (Saskatchewan)	Primrose Lake Air Weapons Range	Federal and Provincial	Department of National Defence; Saskatchewan Environment, Fish and Wildlife Branch
AB	Waterton Lakes National Park	Federal-Canada	Parks Canada Agency
AK (Alaska)	Wrangell-St. Elias National Park and Preserve-Chitina RIver	State	Alaska Department of Fish and Game
AK	Wrangell-St. Elias National Park and Preserve-Copper River	State	Alaska Department of Fish and Game
AK	Delta Junction State Bison Range	State	Alaska Department of Fish and Game
AK	Farewell Lake	State	Alaska Department of Fish and Game
AK	Popof Island	State	Alaska Department of Fish and Game; Shumagin Corporation
AZ (Arizona)	House Rock State Wildlife Area	State	Arizona Fish and Game Department
AZ	Raymond State Wildlife Area	State	Arizona Fish and Game Department
BC (British Columbia)	Pink Mountain Provincial Park	Provincial	British Columbia Ministry of Water, Land and Air Protection
CA (California)	U.S. Marine Corps Base Camp Pendleton	U.S. Military	U.S. Marine Corps
CA	Santa Catalina Island	NGO	Catalina Island Conservancy
CI (Chihuahua)	Rancho El Uno Ecological Reserve	Federal-Mexico	Comisión Nacional de Áreas Naturales Protegidas
CO (Colorado)	Daniels Park	Municipal	Denver Parks and Recreation
CO	Genesee Park	Municipal	Denver Parks and Recreation
CO	Medano-Zapata Ranch	NGO	The Nature Conservancy
CO	Rocky Mountain Arsenal	Federal-US	U.S. Fish and Wildlife Service
IA (Iowa)	Broken Kettle Grasslands	NGO	The Nature Conservancy
IA	Neal Smith National Wildlife Refuge	Federal-US	U.S. Fish and Wildlife Service
IL (Illinois)	Fermi National Accelerator Laboratory	Federal-US	U.S. Department of Energy

Plains bison *(continued)*

State/Province	Site	Jurisdiction	Managing Authority
KS (Kansas)	Konza Prairie Biological Station	State/NGO	Kansas State University, Division of Biology; The Nature Conservancy
KS	Maxwell Wildlife Refuge	State	Kansas Department of Wildlife and Parks
KS	Sandsage Bison Range & Wildlife Area	State	Kansas Department of Wildlife and Parks
KS	Smoky Valley Ranch	NGO	The Nature Conservancy
KY (Kentucky)	Land Between the Lakes National Recreation Area	Federal-US	USDA Forest Service
MB (Manitoba)	Riding Mountain National Park	Federal-Canada	Parks Canada Agency
MN (Minnesota)	Blue Mounds State Park	State	Minnesota Department of Natural Resources, Division of Parks and Recreation
MO (Missouri)	Prairie State Park	State	Missouri Department of Natural Resources
MT (Montana)	American Prairie Reserve	NGO	American Prairie Foundation
MT	National Bison Range	Federal-US	U.S. Fish and Wildlife Service
ND (North Dakota)	Cross Ranch Nature Preserve	NGO	The Nature Conservancy
ND	Sully's Hill National Game Preserve (new herd)	Federal-US	U.S. Fish and Wildlife Service
ND	Theodore Roosevelt National Park	Federal-US	U.S. National Parks Service
NE (Nebraska)	Fort Niobrara National Wildlife Refuge	Federal-US	U.S. Fish and Wildlife Service
NE	Fort Robinson State Park	State	Nebraska Game and Parks
NE	Niobrara Valley Preserve	NGO	The Nature Conservancy
NE	Sully's Hill herd at Ft. Niobrara (original herd)	Federal-US	U.S. Fish and Wildlife Service
NE	Wildcat Hills State Recreation Area	State	Nebraska Game and Parks
OK (Oklahoma)	Tallgrass Prairie Preserve	NGO	The Nature Conservancy
OK	Wichita Mountains National Wildlife Refuge	Federal-US	U.S. Fish and Wildlife Service
SD (South Dakota)	Badlands National Park	Federal-US	U.S. National Park Service
SD	Bear Butte State Park	State	South Dakota Game Fish and Parks Dept.
SD	Custer State Park	State	South Dakota Game Fish and Parks Dept.
SD	Ordway Prairie Preserve	NGO	The Nature Conservancy
SD	Lame Johnny Creek Ranch	NGO	The Nature Conservancy
SD	Wind Cave National Park	Federal-US	U.S. National Park Service
SK (Saskatchewan)	Buffalo Pound Provincial Park	Provincial	Saskatchewan Environment, Parks Branch
SK	Grasslands National Park	Federal-Canada	Parks Canada Agency

Plains bison *(continued)*

State/Province	Site	Jurisdiction	Managing Authority
SK	Old Man on His Back Conservation Area	NGO	Nature Conservancy of Canada
SK	Prince Albert National Park	Federal-Canada	Parks Canada Agency
TX (Texas)	Caprock Canyons State Park/ Texas State Bison Herd	State	Texas Parks and Wildlife Department
TX	Clymer Meadow Preserve	NGO / Private	The Nature Conservancy; Private rancher
UT (Utah)	Antelope Island State Park	State	Utah Division of Wildlife Resources, Division of Parks and Recreation
UT	Book Cliffs Recreation Area	State	Utah Division of Wildlife Resources
UT	Henry Mountains	State	Utah Division of Wildlife Resources
WI (Wisconsin)	Sandhill Wildlife Area	State	Wisconsin Department of Natural Resources
WY (Wyoming)	Bear River State Park	State	Wyoming State Parks and Historic Sites
WY	Grand Teton National Park/Nat. Elk Refuge	Federal/State	U.S. National Park Service; U.S. Fish & Wildlife Service; Wyoming Fish and Game Department
WY	Hot Springs State Park	State	Wyoming State Parks and Historic Sites
WY/MT	Yellowstone National Park	Federal/State	U.S. National Park Service; U.S. Forest Service, Montana Fish, Wildlife and Parks; Montana Department of Livestock

Wood bison

State/Province	Site	Jurisdiction	Managing Authority
AB (Alberta)	Elk Island National Park	Federal-Canada	Parks Canada Agency
AB	Hay-Zama Lakes Complex	Provincial	Government of Alberta, Fish and Wildlife Division
AB/ NWT (Northwest Territories)	Wood Buffalo National Park	Federal-Canada	Parks Canada Agency
AK (Alaska)	Portage Glacier	ENGO1	Alaskan Wildlife Conservation Center
BC (British Columbia)	Etthithun Lake	Provincial	British Columbia Department of Water, Lands and Air Protection
BC	Nordquist Flats	Provincial	British Columbia Department of Water, Lands and Air Protection
MB (Manitoba)	Chitek Lake	Provincial	Government of Manitoba, Department of Natural Resources; Waterhen First Nation
NWT	Mackenzie Bison Sanctuary	Territorial	Government of NW Territories, Resources, Wildlife and Economic Development
NWT	Nahanni	Territorial	Government of NW Territories, Resources, Wildlife and Economic Development
NWT	Slave River Lowlands	Territorial	Government of NW Territories, Resources, Wildlife and Economic Development
YT(Yukon Territories)	Aishihik	Territorial	Government of Yukon

Herds in the progress of establishment:

State/Province	Site	Jurisdiction	Managing Authority
AK (Alaska)	Minto Flats	State	Alaska Department of Fish and Game- currently held at Alaska Wildlife Conservation Center

INTERNATIONAL UNION
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