SPECIES STATUS REPORT

Wood Bison

(Bison bison athabascae)

Sakāwmostos (Cree)
Dechįtah goegié (South Slavey)
Dechen yághe ejere, thachin ya n'jere (Dené sųłiné)
Dachan tat gwi'aak'ii (Teetł'it Gwich'in)
Aak'ii, Dachantat aak'ii (Gwichya Gwich'in)
Łek'aye, łuk'aye, kedä-cho', ejedi (Kaska Dene)
Ejuda (Slavey)
Tl'oo tat aak'ii, dachan tat aak'ii, akki chashuur,
nin shuurchoh, nin daa ha-an (Van Tat Gwich'in)

in the Northwest Territories

NORTHWEST TERRITORIES
SPECIES
AT RISK
COMMITTEE

Threatened

April 2016

Species at Risk Committee status reports are working documents used in assigning the status of species suspected of being at risk in the Northwest Territories (NWT).

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ABOUT THE SPECIES AT RISK COMMITTEE

The Species at Risk Committee was established under the *Species at Risk (NWT) Act*. It is an independent committee of experts responsible for assessing the biological status of species at risk in the NWT. The Committee uses the assessments to make recommendations on the listing of species at risk. The Committee uses objective biological criteria in its assessments and does not consider socio-economic factors. Assessments are based on species status reports that include the best available Aboriginal traditional knowledge, community knowledge and scientific knowledge of the species. The status report is approved by the Committee before a species is assessed.

ABOUT THIS REPORT

This species status report is a comprehensive report that compiles and analyzes the best available information on the biological status of wood bison in the NWT, as well as existing and potential threats and positive influences. Full guidelines for the preparation of species status reports, including a description of the review process, may be found at www.nwtspeciesatrisk.ca.

Northwest Territories Environment and Natural Resources

Environment and Natural Resources, Government of the Northwest Territories, provides full administrative and financial support to the Species at Risk Committee.

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Assessment of Wood Bison

The Northwest Territories Species at Risk Committee met in Yellowknife, Northwest Territories on April 7, 2016 and assessed the biological status of wood bison in the Northwest Territories. The assessment was based on this approved status report. The assessment process and objective biological criteria used by the Species at Risk Committee are available at: www.nwtspeciesatrisk.ca.

Assessment: Threatened in the Northwest Territories

Likely to become endangered in the Northwest Territories if nothing is done to reverse the factors leading to its extirpation or extinction.

Reasons for the assessment: Wood bison fit criterion (c) for Threatened.

(c) – There is evidence that the population size is small and there is a decline in population size such that it could disappear from the NWT in our children's lifetime.

Main Factors:

- The entire wood bison population in the Northwest Territories is estimated at about 2,500 animals in three disjunct populations (Greater Wood Buffalo Ecosystem, Mackenzie and Nahanni).
- An overall decline of at least 10 percent (%) was estimated over the past three bison generations. An overall decline of 50% was estimated over the most recent bison generation. In the most recent bison generation, only the small Nahanni population has shown an increase.
- The main threats are:
    - Three infectious bacterial diseases are currently of concern to the conservation of wood bison in the NWT (anthrax (*Bacillus anthracis*), bovine tuberculosis (*Mycobacterium bovis*), and bovine brucellosis (*Brucella abortus*)). The 2012 anthrax outbreak is of particular concern for the Mackenzie population.
    - Predation primarily by wolves and bears, especially on newborn calves.
    - Human-caused mortality, including bison-vehicle collisions, disease management actions and harvest contribute cumulative threats to wood bison.
    - Various factors may contribute to a loss of meadow habitat (e.g., changes in floods/drawdowns, fire regime, snow pack and water levels, and increased shrub encroachment).

Additional Factors:

- Future road encroachment in wood bison habitat may increase the zone of influence of human activity, especially for the Greater Wood Buffalo Ecosystem and Mackenzie populations.
- Anticipated future industrial development and corridors within certain segments of wood bison habitat may adversely impact wood bison populations in the NWT.
- The NWT is home to an estimated 32% of the global/continental population of wood bison.

Positive influences to wood bison and their habitat:

- Traditional management practices, land use planning initiatives, forestry remediation, fire management, co-management initiatives, and the bison-free buffer zone between Wood Buffalo National Park and the Mackenzie Wood Bison Sanctuary are all seen as positive influences on wood bison.

Recommendations:

- Increase the number of surveys to better track population numbers.
- Deploy radio collars to better track movements, distribution and adult survival.
- Predator management should be considered.
- Harvest management needs to continue.
- Local/community or Aboriginal involvement in any management planning needs to continue or be enhanced.
- Investigate ways to reduce bison-vehicle collisions.
- Continue with the careful management of disease and further investigation of options for preventing and mitigating disease outbreaks (e.g., anthrax).

Table of Contents

Executive Summary

Traditional and Community Knowledge	Scientific Knowledge
Description	
The appearance of wood bison in the Northwest Territories (NWT) was not well covered in the reviewed literature.	Wood bison are noted for their enormous size, high hump at the shoulders, long woolly pelage especially on the head and forequarters, wide muzzle, and short, round, curved horns extending upwards from the sides of the head. In mature animals, the coat is generally dark brown and black. As the largest native terrestrial mammal in North America, mature wood bison bulls measure over 1.8 meters at the shoulder and may exceed 1,000 kilograms (kg), whereas females average around 550 kg.

Traditional and Community Knowledge	Scientific Knowledge
Distribution	
Wood bison occur in various locations in the southern NWT, northern Alberta, northern British Columbia, and the Yukon. In the NWT, they are found in four populations: Mackenzie, Nahanni, Wood Buffalo National Park, and Slave River Lowlands.	Free-roaming populations of wood bison in the NWT presently occur south of Great Slave Lake in Wood Buffalo National Park and the Slave River Lowlands, north of the Mackenzie River, and in the Nahanni-Liard watershed, which is shared by the NWT, British Columbia and the Yukon. These bison form three populations in the NWT, known as the Greater Wood Buffalo Ecosystem population, the Mackenzie population, and the Nahanni population. The Greater Wood Buffalo Ecosystem population consists of six subpopulations; only three (Nyarling River, Hook Lake and Grand Detour) occur within the NWT.

Traditional and Community Knowledge	Scientific Knowledge
Biology and Behaviour	
Wood bison prefer grass and sedge meadows, which provide high-quality forage. Dry grasses and sedges are important winter forage. They also eat lichens. They avoid muskeg, steep terrain, and dense forest. Wood bison establish trails between favoured places, including along linear disturbances and crossing water bodies. Wood bison, especially the bulls, can travel long distances. Wood bison calve in late spring or early summer after an early fall rut, although young calves can occasionally be seen year-round. Herd size is variable and can change throughout the year. Wood bison are often seen in small groups. Caribou and wood bison tend to avoid each other and wood bison are sometimes seen as competitors to both boreal caribou and moose. Wolves are a major predator of wood bison. Diseases such as bovine brucellosis, tuberculosis, and anthrax, and the management of these diseases, are important topics in wood bison assessment.	As the largest land mammal in North America, wood bison require plenty of space. In the Mackenzie population, home ranges vary from 179 to 1,442 km^2, which is 4-100 times larger than those of other North American ungulates. Wood bison are generalist herbivores that specialize in grazing, meaning that they usually select sedge-grass food patches and then consume a variety of herbaceous plants according to their abundance. Although bison are primarily grazers, they will supplement their diet by browsing on woody vegetation. Wood bison habitat ideally consists of a mosaic of lowland meadow and upland meadow to ensure adequate forage resources and is typically interspersed with forest that is used for shelter, resting, ruminating and avoiding biting flies. Although wood bison often share the landscape with other animals, little dietary overlap exists between wood bison and these other species, except where the bison's diet has a high willow or lichen component. Willow is the most important food for northern moose, and woodland caribou depend on lichens. Female bison reach their maximum body weight at 10 years, while males reach theirs by 13 years. Males generally do not begin to breed until they are five or six years old. Average longevity of bison has never been determined but it is unlikely that many animals

	in the wild live past 20 years. Wood bison likely have only a single ovulation per year with a gestation period around 285 days or 9½ months. The majority of females produce calves every other year. Bison are gregarious animals and fusion and fission of herds is quite common. Cows and calves and young bulls may form large mixed herds. With the exception of the breeding season, bison bulls roam alone or in small temporary groups. When not being harassed, bison easily become habituated to human presence and infrastructure. Bison have displayed a tendency to congregate along roads and have become a traffic hazard in many areas. Bison also utilize cutblocks and linear features cut in forested areas. The only documented source of predation for bison is wolves. Wolves focus primarily on herds containing calves, rather than lone bison or bull groups. Defense strategies employed by calves include running to their mothers, a herd, the nearest bull, the front and center of a stampeding herd, and water bodies. When fleeing from wolves in open areas, cows with young calves take the lead, while bulls are seen at the rear of the herds.
Traditional and Community Knowledge	**Scientific Knowledge**
Population	
Recent wood bison population trends were not well documented in available traditional and community knowledge sources.	The most recent estimates indicate that the Nahanni population numbers 431 (2011) and the Mackenzie population numbers 714

	(2013). Within the NWT subpopulations of the Greater Wood Buffalo Ecosystem population, the Nyarling River subpopulation numbers 326 (2014), Grand Detour 368[1] (2014), and Hook Lake 715 (2014). The total population for the NWT is approximately 2,554. The proportion of the global and/or continental population occurring in the NWT is approximately 32 percent (%). Population estimates for the last three generations (approx. 1993-2014) of wood bison have shown growth in three of the five wood bison populations/subpopulations in the NWT (Nahanni population, Hook Lake subpopulation, and Nyarling River subpopulation), while two (Mackenzie population and Grand Detour subpopulation) are in decline (compared to approx. 1972-1993 estimates). Although the Mackenzie population decline can, in part, be attributed to the 2012 anthrax outbreak, it is important to note that the population was declining for approximately 12 years prior to this outbreak. Overall, the NWT population of wood bison has declined over the last three bison generations (1993-2014). The percent decline, estimated using two different methods, is 11% (International Union for the Conservation of Nature [IUCN] Criterion A exponential assumption, two data point calculator) or 23% (based on interpolated population numbers

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[1] Note that this number includes only the Government of the Northwest Territories' estimate of the Grand Detour subpopulation (Armstrong 2014) and not the results of Parks Canada's survey of Wood Buffalo National Park (Cortese and McKinnin 2015).

	using the linear annual growth rate between successive known population estimates). The decline in the last bison generation (2008-2014) has been 51%. There has been no evidence of immigration or emigration other than among the subpopulations of the Greater Wood Buffalo Ecosystem population. In the event that the Nyarling River, Grand Detour or Hook Lake subpopulations should disappear or experience a decline, the likelihood of rescue from Alberta is rather high because the Alberta bison are also subpopulations of the Greater Wood Buffalo Ecosystem population. There is virtually no probability that dispersal from elsewhere could repopulate the Mackenzie population. The Nahanni population is close to the Nordquist herd in northern British Columbia, but rescue, while possible, would be compromised until its numbers grow significantly. The Aishihik herd in southwestern Yukon offers virtually no potential for rescue to the Nahanni population.
Traditional and Community Knowledge	**Scientific Knowledge**
Habitat	
Wood bison are found in a relatively confined area around Wood Buffalo National Park, to the west of Great Slave Lake, around the Liard River, and across northern Alberta. Increasing willow and brush may be encroaching more on open meadows, which are considered to be good wood bison habitat. Wood bison have	The main landscape features providing the highest forage biomass for wood bison are marl lake basins, fens, floodplains, and salt plains. Wood bison habitat is constantly changing in area and quality in the NWT through vegetation succession and retrogression. Sedge meadows and grasslands

extended their range in recent decades, although there is likely good wood bison habitat in the NWT that is not currently supporting a wood bison population.	in wood bison range are inherently unstable. These early seral stages of vegetation succession must be revitalized and maintained by frequent flood/drawdowns and fires. Since the early 1970s there have been diminished flood/drawdown cycles in the range of the Greater Wood Buffalo Ecosystem population. In the range of the Mackenzie population there is currently less marl lake meadow habitat compared to the 1970s/80s because of higher water levels. The emergence of discontinuities in the preferred environment of bison results in habitat and population fragmentation. Whereas natural processes slowly alter the layout of the physical environment, land conversion by humans, including agriculture, rural development, urbanization, mining, fossil fuel exploration, timber harvesting, roads, and hydroelectric reservoirs, tends to have more immediate impacts on habitat fragmentation. However, wood bison often derive foraging opportunities from disturbances that revert mature forest to early successional vegetation, and these animals readily use road right-of-ways and seismic lines as travel routes.
Traditional and Community Knowledge	**Scientific Knowledge**
Threats and limiting factors	
The most important threats to wood bison include disease, disease eradication efforts, efforts to preserve genetic/subspecies purity, hunting, increased predation and lack of	Human-caused mortality, including harvesting and disease management actions like culls for disease control and vaccination round-ups, represents an important historical threat to

detailed studies. Hunting was considered to be the largest threat. Disease eradication efforts were considered to be a larger threat to wood bison than the diseases themselves. Other threats and limiting factors include Aboriginal exclusion from wood bison management processes in the late 1980s-1990, forestry in northern Alberta, pollutants, ranching, forest fires, predation, and the use of road salt (which attracts bison to roadways). Wood bison are also known to die off in large numbers in extreme events, such as anthrax outbreaks, winter starvation, and drowning due to both flooding and falling through the ice.	wood bison; one that populations have not yet recovered from. Currently, the Nahanni population and the Grand Detour and Hook Lake subpopulations (Greater Wood Buffalo Ecosystem population) are harvested. A relatively small number of bison are removed because of bison-human conflicts and to prevent the spread of diseases. There are four infectious bacterial diseases that are currently of concern to the conservation of wood bison. Anthrax (*Bacillus anthracis*) and bovine tuberculosis (*Mycobacterium bovis*) are considered to have the most serious disease implications for bison restoration. Bovine brucellosis (*Brucella abortus*) is also considered a significant impediment to recovery. Johne's disease (*Mycobacterium avium* subspecies *paratuberculosis*) is also considered a medium impediment by some expert groups. Vehicle collisions are an important cause of mortality for wood bison in the NWT, especially in the Mackenzie population (there have been at least 400 recorded mortalities on NWT highways since 1989). There has been concern about diminishing flood/drawdown cycles and detrimental effects on bison habitat downstream in Wood Buffalo National Park as a result of the W.A.C. Bennett Dam and the Williston Reservoir. In addition, declining snowpacks in the catchments of other main tributaries since the mid-1970s and a shorter ice season since the 1961-1990 period compound the problem. Frequent fire is a component of wood bison

	habitat maintenance. Forest expansion due to fire control after the mid-1900s likely contributed to a regional reduction in carrying capacity. Although the ecological role of fire is now better understood and its role in maintaining suitable wood bison habitat is acknowledged, the threat wildfires pose to other values at risk, including human lives, transportation, communities, infrastructure, and other species, will always need to be considered.
Traditional and Community Knowledge	**Scientific Knowledge**
Positive Influences	
Traditional management practices, land use planning initiatives, forestry remediation, fires, management, and the bison-free buffer zone between Wood Buffalo National Park and the Mackenzie Wood Bison Sanctuary are all seen as positive influences on wood bison.	Monitoring and removal of bison in the Bison Control Area between Wood Buffalo National Park and the Mackenzie River has continued since 1987 to reduce the risk of contact between infected and non-infected wild bison populations. The Greater Wood Buffalo Ecosystem population has essentially reached its limits of distribution, but the Nahanni and Mackenzie populations are still undergoing range expansion, and as this proceeds, the risk of a significant portion of the population falling victim to a local catastrophe or adverse climate diminishes. In the past, northern bison have been managed as isolated units, mainly because of conflicting federal, territorial and provincial government mandates. Now that the Greater Wood Buffalo Ecosystem population has been recognized as

	a distinct entity, subpopulations inside Wood Buffalo National Park are managed cooperatively with those subpopulations ranging outside of the Park. The Nahanni population extends across several jurisdictions and is managed in collaboration with the governments of Canada, the NWT, Yukon and British Columbia.

Technical Summary

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
Population trends		
Generation time (*average age of parents in the population*) (indicate years, months, days, etc.).	Information not available in sources.	7 years
Number of mature individuals in the NWT (or give a range of estimates).	Information not available in sources.	Approx. 1,966
Amount of change in numbers in the recent past; *Percent change in total number of mature individuals over the last 10 years or 3 generations, whichever is longer*.	Information not available in sources.	Population estimates for the last three generations (approx. 1993-2014) of wood bison have shown growth in three of the five wood bison populations/ subpopulations in the NWT (Nahanni population, Hook Lake subpopulation and Nyarling River subpopulation), while two (Mackenzie population and Grand Detour subpopulation) are in decline (compared to approx. 1972-1993 estimates). Overall, the NWT population of wood bison has declined over the last three bison generations (1993-2014). The percent decline, estimated using two

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
		different methods, is 11% (IUCN Criterion A exponential assumption, two data point calculator) or 23% (based on interpolated population numbers using the linear annual growth rate between successive known population estimates). The decline in the last bison generation (2008-2014) has been 51%.
Amount of change in numbers predicted in the near future; *Percent change in total number of mature individuals over the next 10 years or 3 generations, whichever is longer*.	Information not available in sources.	Predictive modeling was not undertaken; however, if the trends noted above continue, then we can expect a continuing population decline.
Amount of change happening now; *Percent change in total number of mature individuals over any 10 year or 3 generation period which includes both the past and the future*.	Information not available in sources.	Information not available in sources.
If there is a decline (*in the number of mature individuals*), is the decline likely to continue if nothing is done?	Information not available in sources.	Uncertain whether declines in Mackenzie population and Grand Detour subpopulation will continue.
If there is a decline, are the causes of the decline	Information not available in sources.	Not until the primary cause(s) of the decline have been

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
reversible?		determined.
If there is a decline, are the causes of the decline clearly understood?	Information not available in sources.	No.
If there is a decline, have the causes of the decline been removed?	Information not available in sources.	No.
If there are fluctuations or declines, are they within, or outside of, natural cycles?	Disease management and hunting pressures are considered outside of natural cycles.	Both.
Are there 'extreme fluctuation' (ups and downs) in the number of mature individuals?	No.	There are fluctuations but they are less than one order of magnitude.
Distribution Trends		
Where is the species found in the NWT? *Estimated extent of occurrence in the NWT (in km^2).*	Wood bison occur in populations in various locations in the southern NWT, northern Alberta, northern British Columbia, and the Yukon.	147,540 km^2
How much of its range is suitable habitat? *Index of area of occupancy (IAO) in the NWT (in km^2; based on 2 × 2 grid).*	Information not available in sources.	46,976 km^2
How many populations are	Information not available in	Three.

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
there? To what degree would the different populations be likely to be impacted by a single threat? *Number of extant locations in the NWT.*	sources. Different threats on populations in Alberta were noted in traditional knowledge sources.	
Is the distribution, habitat or habitat quality showing a decline that is likely to continue if nothing is done? *Is there a continuing decline in area, extent and/or quality of habitat?*	Wood bison habitat and habitat quality is declining with increasing forestry and development in northern Alberta, and encroaching willow/brush growth in open grassland meadows in the Slave River Lowlands and northern Alberta; however, wood bison distribution in the NWT has been observed to have increased in the last half-century.	Yes, declines have been documented in both area and quality of habitat.
Is the number of populations or amount of occupied area showing a decline that is likely to continue if nothing is done? *Is there a continuing decline in number of locations, number of populations, extent of occupancy and/or IAO?*	Information not available in sources.	No.
Are there extreme fluctuations in the range or the number of populations? *Are there extreme fluctuations (>1 order of magnitude) in number of locations, extent of occupancy*	Information not available in sources.	No.

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
and/or IAO?		
Are most individuals found within small and isolated populations? *Is the total population severely fragmented (most individuals found within small and isolated populations)?*	Information not available in sources.	No.
Immigration from populations elsewhere		
Does the species exist elsewhere?	Information not available in sources.	Yes.
Status of the outside population(s)?	Information not available in sources.	In Alberta, wood bison are Endangered (S1). In British Columbia, wood bison are S2, and in the Yukon they are S2S3.
Is immigration known or possible?	Information not available in sources. However, wood bison were noted to travel long distances, especially bulls.	No. Although bison in the Greater Wood Buffalo Ecosystem can move across the Alberta/NWT border, these bison are considered part of the same metapopulation. Immigration from other populations outside the NWT is unlikely because of large distances and bison exclusion measures.
Would immigrants be adapted to survive and reproduce in the	Information not available in	Yes.

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
NWT?	sources.	
Is there enough good habitat for immigrants in the NWT?	There is likely wood bison habitat in the NWT that is not currently populated with wood bison.	Yes.
Is the NWT population self-sustaining or does it depend on immigration for long-term survival?	Information not available in sources.	Self-sustaining.
Threats and limiting factors		
Briefly summarize negative influences and indicate the magnitude and imminence for each.	Hunting: Hunting was widely reported as affecting wood bison herds in the NWT. Disease eradication efforts: Disease eradication efforts such as herding animals to vaccinate, vaccinations or treatments, and allowing unmitigated hunting of diseased herds in the last half-century have threatened wood bison. It is unclear if disease eradication efforts will continue in the future. Efforts to preserve genetic/subspecies purity:	Human-caused mortality: Human-caused mortality (i.e., harvesting) and disease management actions (i.e., vaccination round-ups and culls for disease control) represent an important historical threat to wood bison. Harvesting and bison removal for disease management are still occurring but at a lower level than in the past. Infectious disease: Four infectious diseases of concern: anthrax (*Bacillus anthracis*), bovine tuberculosis (*Mycobacterium bovis*), bovine

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
	Efforts to preserve the genetic distinctiveness of wood bison from plains bison imported to the Wood Buffalo National Park area during the 20th century was considered a threat, such as the exclusion of wood bison from hunting laws (as 'hybrids') by the government of Alberta. <u>Disease</u>: Diseases such as bovine brucellosis, tuberculosis, and anthrax are important threats for wood bison. Imminence and degree are not discussed in traditional and community knowledge sources.	brucellosis (*Brucella abortis*), and Johne's disease (*Mycobacterium avium* subspecies *paratuberculosis*). The first two are considered to have the most serious implications for bison restoration. <u>Vehicle collisions:</u> Vehicle collisions are an important cause of mortality for wood bison in the NWT, especially in the Mackenzie population. <u>Habitat loss</u>: Downstream effects of diminishing flood/drawdown cycles, declining snowpacks, a shorter ice season, and fire control are all of concern. <u>Low genetic diversity</u>: Most wood bison herds originate from just a few individuals. This lack of genetic variation can make herds vulnerable to disease outbreaks and the adverse effects of inbreeding.

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
		Predation: Historical population decline in the Greater Wood Buffalo Ecosystem population has been attributed, at least in part, to the cessation of wolf control in the NWT. Age structure of bison herds (with older animals boosting the wolf population) and alternate prey (e.g., muskrat) has possibly also contributed to heavy wolf predation. Episodic catastrophes: Drowning events are well-documented among wood bison populations. Climatic anomalies, such as harsh winters and heavy precipitation, can also impact sedge growth and habitat availability.
Positive influences		
Briefly summarize positive influences and indicate the magnitude and imminence for each.	Traditional management: Traditional management practices ('only taking what you need') are considered a positive influence.	Controlling human-caused mortality: Introduction of hunting restrictions reduced the most significant source of mortality.

Question TK/CK; *Science*	Traditional & Community Knowledge	Scientific Knowledge
	Land use planning: Land use planning initiatives, such as protection of wood bison habitat near Wood Buffalo National Park will be a positive influence if passed. Forestry remediation: Forestry remediation, including tree planting of forestry cutblocks, is a positive influence. Forest fires: Forest fires of moderate intensity can be a positive influence by creating bison habitat and encouraging forage. However, the impacts from the severe 2014 and 2015 fire seasons have yet to be assessed. Wildlife management: Good wildlife management was seen by some traditional knowledge holders as a positive influence. Buffer-zone: The bison-free buffer zone between Wood Buffalo National Park and the Mackenzie Wood Bison	Managing disease: Monitoring and removal of bison in the Bison Control Area reduces risk of contact between infected and non-infected bison. Range expansion: Range expansion in the Nahanni and Mackenzie populations reduces risks associated with local catastrophes or adverse climate. Interagency cooperation: Inter-jurisdictional cooperation in the management of the transboundary Greater Wood Buffalo Ecosystem and Nahanni populations. These populations were previously subject to conflicting federal, territorial and provincial government mandates.

Question TK/CK; *Science*	**Traditional & Community Knowledge**	**Scientific Knowledge**
	Sanctuary is a positive influence on wood bison in preventing disease transmission. Imminence and degree are not discussed in traditional knowledge sources.	

Traditional and Community Knowledge Component

PREAMBLE

Wood bison historically roamed across a large area, including much of the Northwest Territories (NWT). They were hunted to near-extinction in the late 1800s. Wood bison have been present in Wood Buffalo National Park and adjacent areas throughout the decline and recovery, and re-introduced herds in the NWT now exist around the Liard and South Nahanni rivers (Nahanni population) and west of Great Slave Lake (Mackenzie population). There is a greater amount of recorded traditional and community knowledge of wood bison in areas where the herds have had an uninterrupted presence – in particular in the South Slave area and into northern Alberta. For this reason, some of the information included in this report about wood bison biology and behaviour, state and trends, and threats, was collected from sources referring to wood bison in northern Alberta, including a portion of the information in Gates *et al*. (2001a) and Mitchell (2002), and all the information in Schramm (2005) and Schramm *et al*. (2002). Additionally, many of the available traditional knowledge sources relate to disease eradication. The Nahanni and Mackenzie populations are considered disease-free and for these and other reasons, there are few sources with recorded traditional or community knowledge about these populations.

SPECIES OVERVIEW

Names and classification

Common Name (English):	Wood bison
	Buffalo (note – commonly used term, but a misnomer)
Common Name – French:	Bison des bois
Scientific Name:	*Bison bison athabascae*
Cree:	Sakāwmostos (bush bison) (Napier pers. comm. 2015)
Dené sųłiné/Athabasca Chipewyan First Nation:	Dechen yághe ejere or thachin ya n’jere (Marcel *et al*. 2012)

Teetł'it Gwich'in:	Dachan tat gwi'aak'ii (Gwich'in Language Centre 2006)
Gwichya Gwich'in dialect:	Aak'ii, Dachantat aak'ii (Andre and Kritsch 1992; Andre pers. comm. 2012)
Kaska Dene:	Łek'aye, łuk'aye, kedä-cho', ejedi (Lotenberg 1996)
Slavey:	Ejuda (Lotenberg 1996)
South Slavey:	Dechįtah goegié (Constant pers. comm. 2013)
Van Tat Gwich'in dialect:	Tl'oo tat aak'ii, dachan tat aak'ii, akki chashuur, nin shuurchoh, nin daa ha-an (Lotenberg 1996)

Kaska interviewees in the Yukon also used the moniker 'shaggy' to refer to wood bison (Lotenberg 1996). Alaskan Gwich'in communities use the names aak'ìi for both muskoxen and bison. They also use ch'itthay dighan, ch'atthaii daghan choo, nan'aak'ii choo, dachantèe aak'ìi. Traditionally, a hand signal accompanied the name to distinguish wood bison from muskoxen. This hand signal was known across the Gwich'in territory into the NWT (Stephenson *et al.* 2001).

Life form: large land mammal.

Description

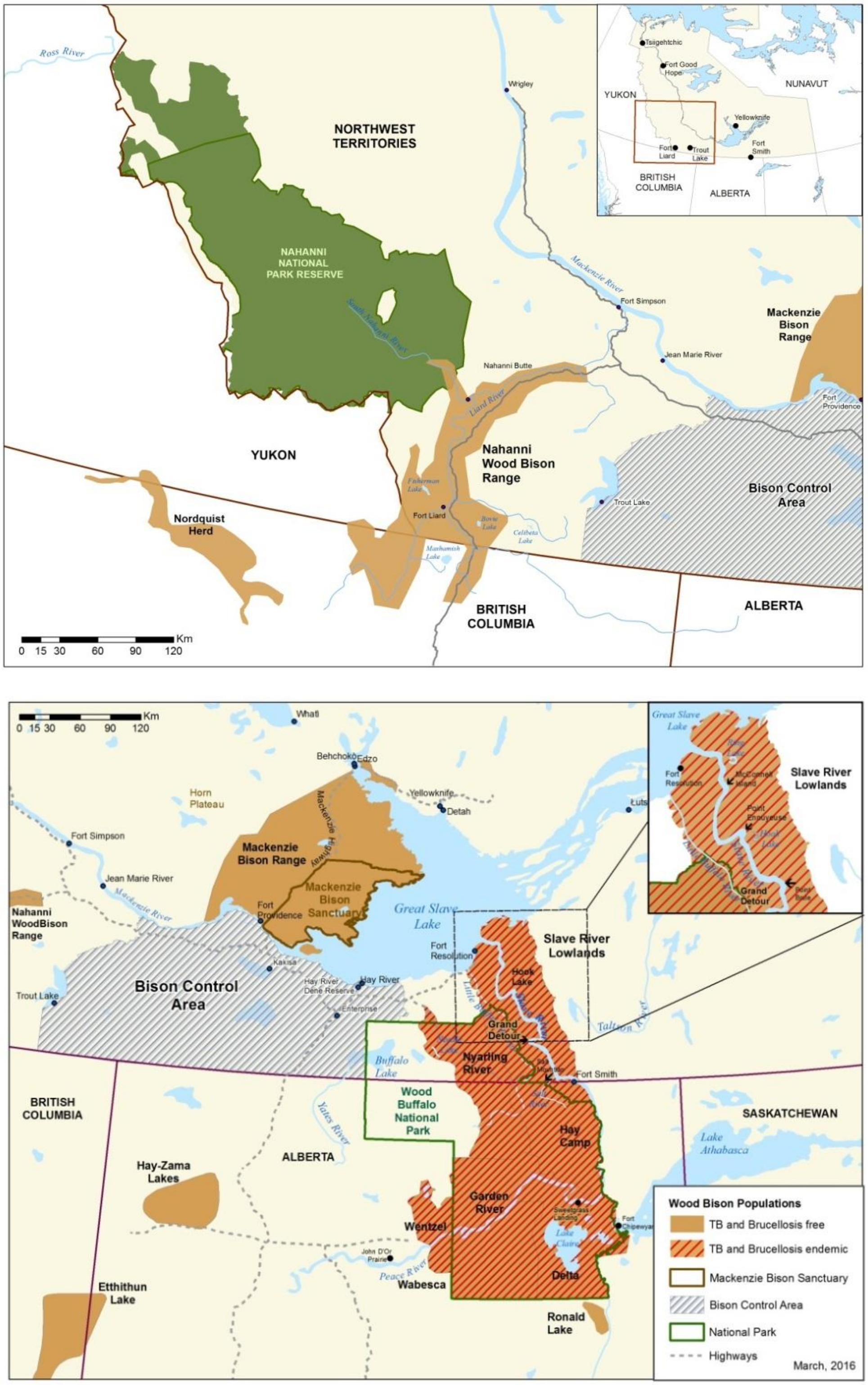
The appearance of wood bison in the NWT was not well covered in the reviewed literature (see Figure 1, p. 30). Information about differences between two northern Alberta herds is included under *Physiology and Adaptability*, p. 43.

Figure 1. Wood bison. Photo credit: J. Winbourne (used with permission).

Distribution

NWT Distribution

Wood bison can be found in the southern NWT (South Slave and Dehcho regions as well as portions of the North Slave region). Traditional and community knowledge sources use the terms ‘herd’ and ‘population’ interchangeably. For the purposes of this report however, ‘population’ is used to describe the four main groups of wood bison in the NWT (Mackenzie, Nahanni, Slave River Lowlands and Wood Buffalo National Park) as well as the Alberta bison (Wentzel, Wabasca, Hay-Zama Lakes, and Ronald Lake populations), while ‘herd’ is used to describe the subpopulations of the Slave River Lowlands and Wood Buffalo National Park (Figs. 2a and 2b, p. 31).



Figures 2a and b. Distribution maps for wood bison populations and subpopulations noted in this report based on data from Environment and Natural Resources (ENR) (split into two maps to permit better viewing of place names). Maps prepared by B. Fournier (ENR). Wood bison sightings do occur outside of core herd ranges.

Status of Wood Bison in the NWT – Traditional and Community Knowledge

Slave River Lowlands population

The Slave River Lowlands population is situated just outside of Wood Buffalo National Park in the NWT portion of the Slave River valley (Figure 2b, p.31). For the purposes of this report, the Slave River Lowlands population is considered to consist of two herds: Grand Detour (sometimes referred to as Little Buffalo) and Hook Lake. The range of the Hook Lake herd is from just inside Wood Buffalo National Park and in the western portion of the Slave River Lowlands to the east of the Slave River. The range of the Grand Detour herd is around the Little Buffalo River with calving taking place between the Little Buffalo River and the large meadows to the east (Gates *et al*. 2001a; Mitchell 2002). Information from interviews conducted by Gates *et al*. (2001a) indicates that some of the Grand Detour herd was originally from Sweetgrass, north of Lake Claire in Alberta (Gates *et al*. 2001a; Mitchell 2002). Wood bison from the Slave River Lowlands population have been observed near the Taltson River north of Taltson Prairie in the winter. The eastern extent of their range is the Taltson River. They do not use the rocky Canadian Shield country to the east of the river on a regular basis, although they are known to cross the river occasionally and return (Gates *et al*. 2001a; Mitchell 2002). One year in the late 1990s, a group of wood bison crossed the Slave River at McConnell Island, where they stayed in the meadows around Rat Slough and Ring Lake (Gates *et al*. 2001a; Mitchell 2002).

Wood Buffalo National Park population

The Wood Buffalo National Park population straddles the NWT and Alberta. Traditional and community knowledge sources describe four herds within this population; of these, only the Nyarling River herd occurs within the NWT (the other three herds, while occurring within Wood Buffalo National Park, are present only in Alberta). The Nyarling River herd's range is south of Great Slave Lake in the NWT. The Nyarling River herd is located in Wood Buffalo National Park, east of Buffalo Lake and straddling the NWT/Alberta border (Gates *et al*. 2001a; Mitchell 2002) (Figure 2b, p.31). Kátł'odeeche First Nation members have harvested wood bison along the Yates River, which flows into Buffalo Lake outside of Wood Buffalo National Park (Crosscurrents Associates Ltd. and Maskwa Environmental Services Ltd. 2007). Gates *et al.* (2001a) also reported a second-hand account of a sighting south of Buffalo Lake near Yates River, and wood bison sightings along the Yates River west of Wood Buffalo National Park and north of the Caribou Mountains, and along the shore of Buffalo Lake (Gates *et al*. 2001a; Mitchell 2002).

Mackenzie population

The Mackenzie population is nestled to the west of Great Slave Lake, including the eastern portion of the Horn Plateau (Figure 2b, p.31). Community knowledge reported during a workshop in Fort Providence in October 2000 indicates that late in the summer, wood bison from the Mackenzie population move further west, into the eastern portion of the Horn Plateau and along the Horn River drainage (EBA Engineering Consultants Ltd. and Canadian Wildlife

Service [CWS] 2006). The Mackenzie population has demonstrated a northward expansion in recent years (Mitchell 2002) (Fig. 2b, p. 31). In the late 1990s or early 2000s, there were sightings of wood bison about 30km south of Behchokǫ̀ along the Mackenzie Highway (Mitchell 2002; EBA Engineering Consultants Ltd. and CWS 2006). More recently, bison have been observed as far north as Whatì (Richardson pers. comm. 2015) (Figure 2b, p. 31), although these are considered extra-limital movements and not representative of a true expansion of range (Armstrong pers. comm. 2015).

Nahanni population

The Nahanni population range includes the southwestern NWT, southeastern Yukon and northeastern British Columbia. It occurs within the traditional territory of the Acho Dene Koe First Nation (ADKFN) and the Nahanni Butte Dene Band (Armstrong pers. comm. 2015), largely in the Fort Liard area and along the Liard River and Highway #7 corridor. The majority of available traditional knowledge of the Nahanni population is derived from ADKFN compilation efforts (Fanni 2014); however, it should be noted that Fanni (2014) may not have interviewed enough Elders to provide a clear representation of the knowledge in the community as a whole.

Groups of wood bison occurring in this area consist of both males and females of all ages (Fanni 2014). Although wood bison were historically present in the area, ADKFN members interviewed by Fanni (2014) were confident that prior to the reintroduction effort started in 1980, wood bison hadn’t occurred in their traditional territory for at least four human generations. More recently, ADKFN members confirmed the general distribution of the Nahanni population developed by ENR (Figure 2a, p.31, shows the most current distribution developed by ENR, but it differs slightly from the distribution map used by Fanni (2014) for his study, which was based off of Larter and Allaire (2007)) (Fanni 2014).

Other herds and areas

Wood bison sightings do occur outside of known herd ranges. Wood bison are seen along the south shore of Great Slave Lake, and although they do not leave the shore area to venture inland (Gates *et al*. 2001a; Mitchell 2002), they have been known to cross the Mackenzie River at Wrigley Harbour (Environment Canada 2015d). Wood bison are also seen north of Wood Buffalo National Park along the road to Hay River, particularly in burned-out areas (Gates *et al.* 2001a; Mitchell 2002), and near Buffalo Lake, Copp River, and Buffalo River on the western limit of Wood Buffalo National Park (Environment Canada 2015d). In 2011, a wood bison carcass was reported on the Mackenzie River ice between Fort Good Hope and Tsiigehtchic. A Renewable Resource Officer reported that a grizzly bear was feeding on it (Andre pers. comm. 2012). Hunters from Trout Lake saw tracks from what may have been a wood bison, possibly from the Nahanni population, at kilometre 45 of the Trout Lake winter road in 1985 (Larter and Allaire 2007).

Historically, wood bison ranged over a much larger area in the NWT, Yukon, and Alaska (Lotenberg 1996; Stephenson *et al*. 2001). According to oral history accounts, wood bison became scarce or extirpated in Alaska earlier than in the lower Mackenzie River area (i.e., the current Gwich'in Settlement Area). This was likely prior to European contact. However, there may have been a very small number of wood bison in Gwich'in territory in Alaska and the adjacent Yukon (around Old Crow, Yukon) as late as the early 19th century (Stephenson *et al*. 2001).

> *"Charlie Peter Charlie, Sr. of Vuntut Gwich'in First Nation corroborated information about bison occurring around North Mackenzie. He claimed that according to his grandfather, 'the people of Fort McPherson [were] killing bison across the river from the community of Fort McPherson in the 1820s." (Lotenberg 1996: 13)*

Tsiigehtchic Elders indicate that wood bison likely disappeared from the area north and south of the Mackenzie River around 200 years ago.

> *"Hyacinthe Andre [a Tsiigehtchic Elder] said he had heard "old stories" referring specifically to the Travaillant Lake area… as having once supported bison, that bison were once hunted to the north near the arctic coast, and that bison once occurred on the "barren-grounds" adjacent to the Anderson River, mentioning that bison skulls had been found there. He does not recall the Gwich'in name for bison, but notes they disappeared a long time ago and that it has been at least 200… years since bison were hunted in the region… Mr. Andre clearly differentiates bison from muskoxen, and that these animals "were powerful and could run through four feet of snow with no problem." (Stephenson et al. 2001: 134)*

When wood bison were living in the area, they were hunted by the Gwich'in (Stephenson *et al*. 2001). In the Yukon, wood bison historically occurred around Ross River and may have dispersed into adjacent regions throughout central and western Yukon, possibly into northern British Columbia, and rarely, perhaps even as far north as Vuntut Gwitchin (Van Tat Gwich'in) territory. Lotenberg (1996) suggests that these sightings were dispersing animals passing through, rather than residents.

Search effort

Wood bison distribution around Wood Buffalo National Park is considered to be well-known by NWT hunters (Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b). Traditional knowledge of the Nahanni population was compiled recently by Fanni (2014) in a limited study that collected geospatial information, ADKFN traditional knowledge of bison, and ADKFN attitudes towards bison. As noted earlier, constraints associated with sample size and verification limit the ability to draw broad conclusions from this study. There are no available traditional knowledge sources with information about search effort for the Mackenzie population.

BIOLOGY AND BEHAVIOUR

Habitat requirements

Little Red River Cree and Salt River First Nation hunters and Elders indicate that habitat preference cannot be generalized across populations/herds, and is instead herd-specific and implicated in the appearance and size of individual herds (Schramm 2005; Environment Canada 2015e).

Bison occurring within Little Red River Cree traditional territory are from three populations/herds: Wentzel Lake, Wabasca (Mikkwa) and Garden River (referred to as south-western Parks herd in Schramm *et al.* (2002)) (Figure 2b, p. 31). All three are located within Alberta, with the Wentzel Lake and Wabasca populations occurring immediately south-west of Wood Buffalo National Park, and the Garden River (south-western Parks) herd occurring in the south-west corner of Wood Buffalo National Park (Schramm *et al.* 2002). Bison from all three herds are wood bison.

> *"In this study, the most interesting research result on bison habitat is that habitat preferences seem to be different for all three herds and cannot be generalized. Also, there is no common pattern in the formation of winter and summer herd sizes. Combined with the observed morphological differences between animals of the three herds, the results of this study can inspire a large variety of future research topics. The Little Red River Cree TEK experts link morphological differences to habitat preferences. According to their observations, the Wentzel Lake herd (bison with wood bison morphology in boreal habitat) is at one end of the scale and the Mikkwa herd (bison with plains bison morphology in prairie habitat) is at the other end. The south-western Parks herd is somewhere in the middle, displaying more of a wood bison morphology but also interacting with the Mikkwa herd." (Schramm 2005: 178)*

Generalized information about wood bison habitat requirements was also gathered during a traditional knowledge study in northern Alberta and the southern NWT (Gates *et al.* 2001a; Mitchell 2002) as well as by Environment Canada in recent consultation meetings (Environment Canada 2015e). Overall, and recognizing different regional habitat preferences (Environment Canada 2015e), wood bison tend to prefer grass and sedge meadows, such as those associated with dry lakebeds and oxbows, sloughs near rivers, and old beaver meadows. Meandering rivers with multiple oxbows provide good habitat (Gates *et al.* 2001a; Mitchell 2002). In the early spring, south-facing slopes are snow-free earlier and are attractive to wood bison. Where a deep and crusted snow remains later into the spring, such as in the Caribou Mountains, forage is less available (Schramm *et al.* 2002).

In the spring, wood bison seek the new growth of grasses and sedges, which they will select over broad-leaf plants. This becomes their dominant food source for the season. New grass is particularly favoured by wood bison. They may feed on the small new leaves of willows and small willow-like plants (Schramm 2005) although this is disputed by members of the Salt River First Nation (Environment Canada 2015e), and are known to consume horsetails (Schramm 2005). Some grasses can make them sick and are avoided (Environment Canada 2015e).

Wood bison use the drier edges of wet meadows in the summer where forage is plentiful as well as forestry cut blocks and open prairie. Wood bison are known to prefer areas where the ground is solid to make walking easier. The high-quality forage, including buffalo grass (Environment Canada 2015e), allows wood bison to gain weight in the summers to prepare them for the August rutting season (Schramm 2005; Gates *et al*. 2001a; Mitchell 2002).

Dry grasses and sedges are the most important winter feed for wood bison. Wood bison may use river banks where dried grass hanging over the edge of the bank is not covered by snow, and frequent the edges of frozen beaver ponds where grasses and sedges are available (Schramm 2005; Environment Canada 2015e). Wood bison also rely on caribou lichen, and possibly arboreal lichen, in the winter if dried grasses and sedges are inaccessible due to large amounts of snow in January-March. Also, while this vegetation may lodge and freeze in the wet meadows, lichens found in spruce stands will 'stand up' and be available under the lighter snow cover (Schramm and Krogman 2001; Schramm *et al*. 2002; Schramm 2005). The centres of meadows that were too wet to use in the summers have high-quality forage that is used in the winter when the ground is frozen and can support the wood bison. The shifting use of different portions of the meadows helps to maintain the meadows (Gates *et al*. 2001a; Mitchell 2002).

When wood bison were present in the Yukon in the past, they were known to use wind-blown areas in the winter. These snow-free areas were important to the bison as their short legs make travelling through deep snow difficult. Deep snow will cause wood bison to leave an area. It was noted in one study however, that wood bison could dig through snow to obtain food (Lotenberg 1996). Bison were also known to consume muskrat push-ups in the winter (Schramm *et al*. 2002).

> *"Wood Bison need free-ranging access to their habitat in order to get certain required plants. These plants may assist in healing the Wood Bison from certain diseases: "Same thing with humans, [if we are] fed food we don't want to eat, we'll get sick too. Same as buffalo. ... they eat lots of things [in the wild]...they eat spruce bough for their digestion, willows, everything."" (Interviewee in van Kessel 2002: 91)*

Wood bison may also seek out burned areas soon after a fire, which provide good habitat and include several types of plants that are attractive to them, although Salt River First Nation members indicate that large fires may ultimately be detrimental to wood bison (Environment Canada 2015e) (discussed in further detail in *Threats and Limiting Factors*, p. 52). Gates *et al*. (2001a) and Mitchell (2002) indicate that older burned out areas may also provide predator relief from both wolves and humans, who may find the deadfall difficult to move through; although, in contrast, members of the Salt River First Nation indicate that the deadfall in burn areas may impede wood bison movement as well as increase their vulnerability to predation (Environment Canada 2015e). Although wood bison do graze in cut blocks, forest fires are considered to be more important in opening up habitat (Gates *et al*. 2001a; Mitchell 2002).

Prescribed burns such as those undertaken during the Hook Lake Wood Bison Recovery Project were also considered to be valuable for the local ecosystem. The burns maintained high-quality grassland areas open for use by wood bison and other wildlife (Gates *et al*. 2001a; Mitchell 2002). One Fort Resolution resident indicated that prescribed burning in the area was required as there were not enough wood bison to prevent shrub encroachment through grazing. Respondents were divided on the issue of when the prescribed burns should happen – either spring, or late summer (van Kessel 2002). The decrease and disappearance of wood bison in the Yukon is blamed on increasing forest cover replacing open areas, which brought moose and displaced the bison.

In 2014 and 2015, the NWT experienced particularly severe fire seasons, with 385 fires impacting about 3.4 million hectares in 2014 (ENR 2014) and 245 fires impacting 646,954 hectares in 2015 (ENR 2015a). Short and long-term impacts from these fires have yet to be determined, although Fort Providence harvesters have observed bison moving into these recent burn areas to consume the fresh grasses (Environment Canada 2015b).

Wood bison avoid muskeg, dense forest, and regions of steep terrain (Gates *et al*. 2001a; Mitchell 2002). “A buffalo wouldn’t go in the muskeg. A muskeg is too soft for a buffalo” (John James Antoine *in* Gunn 2009: 91). Bedding areas are generally along trails and are at the edges of open grassy areas (Gates *et al*. 2001a; Mitchell 2002).

Salt licks are used by bison. Along the Garden River road in northern Alberta, salt licks were used by wood bison in the Wentzel herd before hunting pressure caused the wood bison to retreat (Schramm 2005).

Movements

Wood bison are known to establish trails or corridors between favoured habitat patches. When colonizing an area, the trails are quickly formed. Trails may develop along human-made linear disturbances such as seismic lines and roads. Once a route is established, it is used continuously over long time periods (ENR 2010a). Wood bison tend to use the most direct route, which may include water crossings. Water crossings are usually at river bends and shallow areas with low banks (Gates *et al*. 2001a; Mitchell 2002). Wood bison mobility increases in the winters when the frozen soil and ice supports their weight (Gates *et al*. 2001a; Mitchell 2002).

Rivers can impede wood bison movement if the banks are steep or the river is too wide – wood bison are not typically known to cross wide expanses of water. The Little Buffalo River in the Slave River Lowlands area is not a barrier to wood bison movement; the river is regularly crossed at numerous locations, allowing the wood bison to move in and out of Wood Buffalo

National Park (Figure 3, p.39). Likewise, wood bison groups have been seen swimming across the Liard River (Larter and Allaire 2007). In contrast, the wide Mackenzie River is considered a significant barrier (Figure 4, p. 40).

The Hay River, upstream of Alexandra Falls, is not a barrier to wood bison movement, but is not crossable immediately downstream (north) of Alexandra Falls due to steep banks. Wood bison can only cross downstream once the river nears the community of Hay River. They will cross the Salt River and the road exiting Wood Buffalo National Park around Salt Mountain to access the Mission Farm and Foxhole meadows to the north, and some will travel to Needle Lake and head up and down through the ridges and meadows that run between the Slave River on the east and the Little Buffalo River on the west (Larter and Allaire 2007), as well as travel in the small meadows between Hook Lake and Needle Lake (Gates *et al*. 2001a; Mitchell 2002). These wood bison travel to Grand Detour and then travel north along the sloughs adjacent to the Slave River to Hook Lake. A crossing point for wood bison exists at Point Brule on the Slave River (Gates *et al*. 2001a; Mitchell 2002) (Figure 3, p.39). The Slave River is only rarely crossed by wood bison, in locations where the banks are low (Figure 3, p.39) (Gates *et al*. 2001a; Mitchell 2002). The crossing locations of wood bison in the Slave River Lowlands are known to local hunters (Nishi *et al*. 2000).

Wood bison have also been seen on the Slave River both near Point Ennuyeuse and north of Long Island (Gates *et al*. 2001a; Mitchell 2002). To get to preferred meadows, wood bison will travel through brushy areas, but this poor habitat is considered a partial barrier to their movement, so they tend to move through it quickly (Gates *et al*. 2001a; Mitchell 2002). In the northern portions of Wood Buffalo National Park, good habitat is widely dispersed (Figure 3, p.39) (Gates *et al*. 2001a; Mitchell 2002).

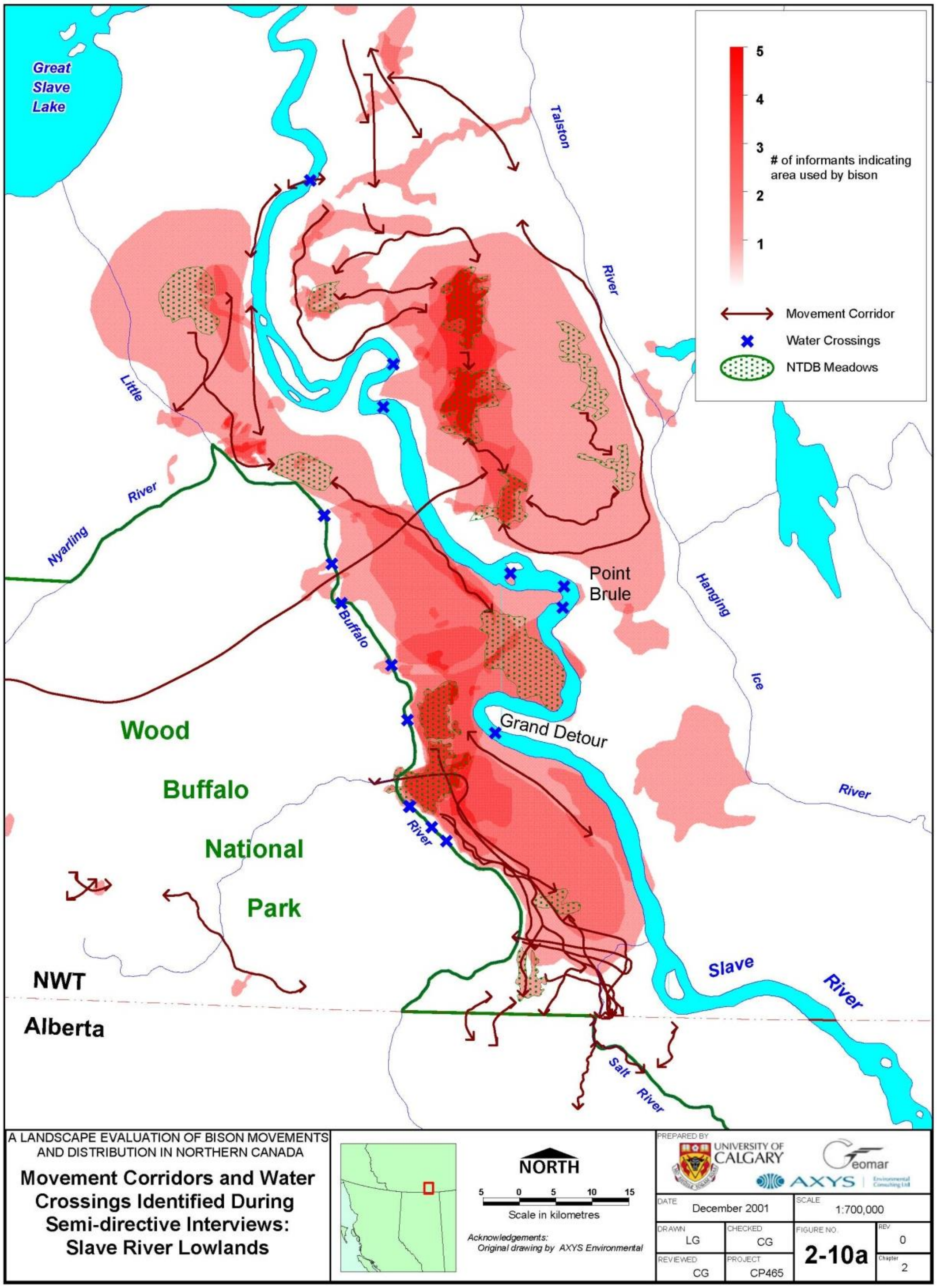


Figure 3. Movement corridors and water crossings identified during semi-directed interviews: Slave River Lowlands [study area] (Hook Lake and Grand Detour subpopulations) (Gates *et al*. 2001).

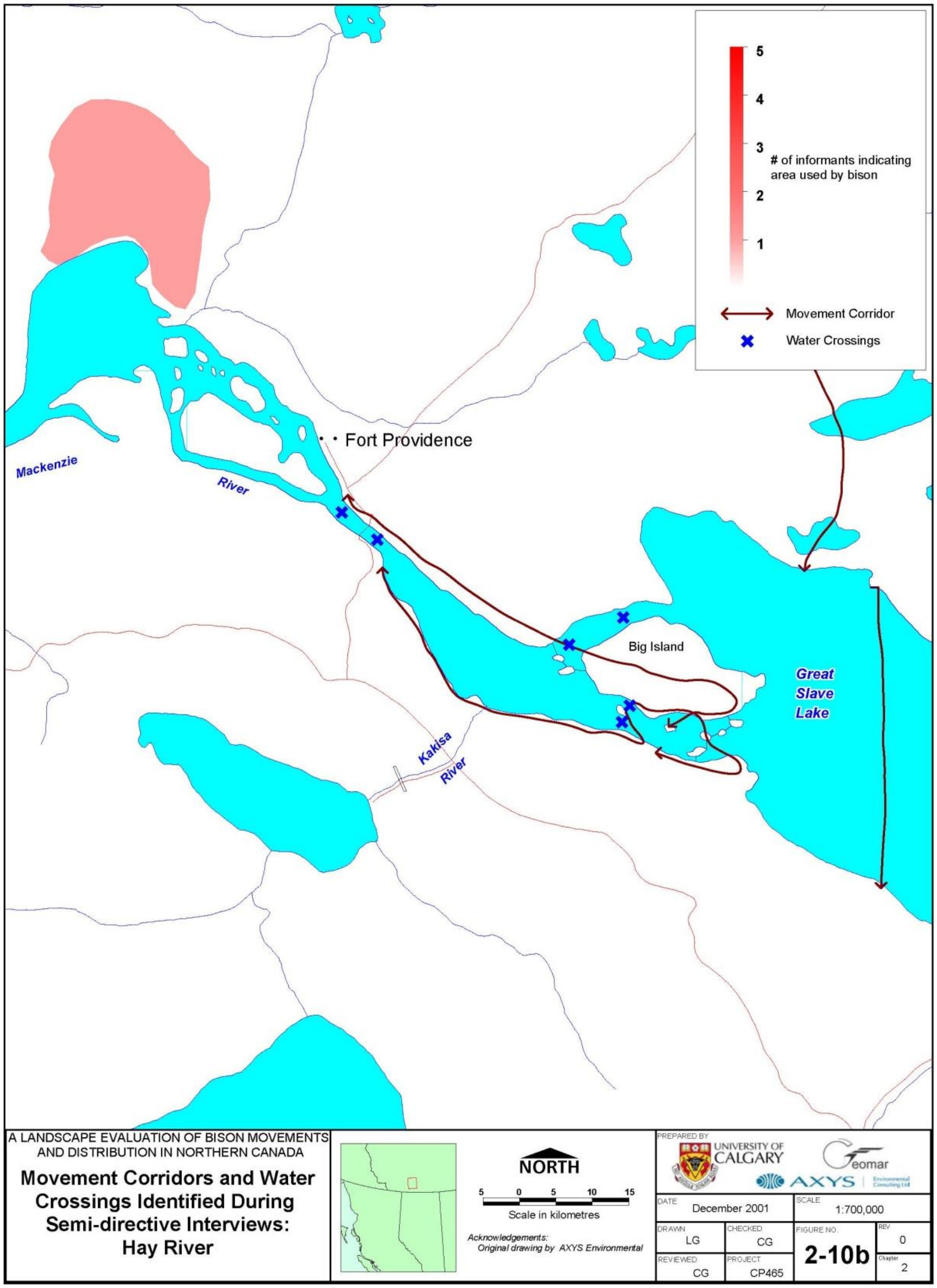


Figure 4. Movement corridors and water crossings identified during semi-directed interviews: Hay River [study area] (Gates *et al*. 2001a).

Interviews conducted by Gates *et al*. (2001a) indicate that cows and calves in the Slave River area disperse in the summer into smaller groups and congregate again in wintering areas (Gates *et al*. 2001a; Mitchell 2002). Little Red River Cree traditional knowledge experts note a difference in the dispersal and congregation behaviour between wood bison occurring within Wood Buffalo National Park and those located outside the Park. These experts note that while the Wentzel herd (occurring outside Wood Buffalo National Park) lives in small groups in the summer and slightly larger groups in the winter, the Wood Buffalo National Park herds stay in large herds in the summer and smaller herds in the winter (Schramm 2005).

Wood bison that are observed at the edge of established ranges, outside of the main herds, tend to be bulls. Bulls are more likely to travel alone, disperse great distances from their herd, and/or stay in small bull-only groups (Gates *et al*. 2001a; Mitchell 2002). One bull was known to leave the Wabasca herd occasionally, cross into Wood Buffalo National Park, and return with a number of cows (Schramm 2005).

Information collected by ENR (2010a) indicates that collared bison in the Nahanni population use roads and seismic lines a lot and move extensively in the summer, including into British Columbia and back. This is supported by limited interviews conducted by Fanni (2014), in which ADKFN members noted that bison movements occur principally along the Liard River and the Highway #7 corridor. These movement routes consist of hard ground, which is seen to facilitate movement more than in areas with muskeg or swamp. Animals in the Nahanni population also use ATV trails and old seismic cut-lines to access Maxhamish Lake, Fisherman Lake and Bovie Lake (Fanni 2014). While animals can be seen year-round at Fisherman Lake, they only access Maxhamish Lake and Bovie Lake rarely, in small numbers and when the ground is frozen. The area is generally considered to be too swampy to constitute ideal habitat for wood bison. Wood bison may also use the Celibeta Lake area, but only tracks (no direct sightings) have been observed (Fanni 2014).

Little Red River Cree Nation and Tallcree First Nation participants in a traditional knowledge study indicated that hunting pressure was a major barrier to wood bison movement and range expansion in northern Alberta (Schramm *et al*. 2002). In addition, when pieces of river ice pile and jumble together, the resulting ice jams also obstruct bison movement (Gates *et al*. 2001a; Mitchell 2002). Steep and high elevation areas limit bison dispersal as well; for example, the Caribou Mountains in northern Alberta just south of the NWT border (Gates *et al*. 2001a; Mitchell 2002).

Table 1 (p. 42) summarizes biophysical factors influencing bison movements and distribution, interpreted from traditional knowledge interviews conducted by Mitchell (2002).

Table 1. Biophysical factors influencing bison movements and distribution, from Mitchell (2002).

Factor	Nature of effects
Slope	• Bison are associated with riparian meadows and avoid steep slopes. • Water crossings occur in areas with shallow banks.
Lake size	• Bison do not cross wide expanses of water unless adequate ice has formed. • Bison do not swim in waves (i.e., high wind, wide rivers and lakes).
River width	• Bison rarely cross wide rivers; however, small rivers are readily crossed.
Habitat as a barrier	• Large expanses of muskeg are barriers. • Shield country is a barrier.
Ice conditions	• Ice cover provides opportunity for crossing water bodies. • Spongy or weak ice is avoided and, if used, may be a hazard. Drownings. • Rough ice on lakes or rivers is a barrier.
Habitat affinity	• Graminoid meadows (i.e., grasses and/or sedges) are preferred habitat. • Meadows are typically riparian (i.e., associated with water bodies and drainages), for example, inundated areas along lakes and rivers.
Cut blocks and disturbed habitat	• Bison use early seral stage (regrowth after disturbance). • Linear disturbances (seismic lines and road edges) may provide grazing habitat.
Fire	• Bison move into recently burned areas in response to availability of grasses, sedges and forbs. • Bison move into burned forests in which downed trees (deadfall) provide escape cover from hunters and wolves.
Hunting	• Pressure from hunters increases in winter because hunters can track bison and can move more freely on frozen ground (increased access). • Seismic lines and roads increase hunting pressure (improved access). • Bison avoid areas with high hunting pressure. • Hunting can eliminate local populations.
Roads and seismic lines	• Bison do not avoid roads and seismic lines unless hunting pressure is heavy. • Use of roads and seismic lines by bison depends on forage plant abundance (grasses and sedges).
Natural corridors	• Corridors are associated with watercourses. • Corridors follow and link graminoid habitat patches.
Cattle	• Cattle do not generally influence bison movements.
Fences	• Serve as a barrier to movements.

Population density	• Area occupied is positively related to density.
Human disturbance	• Growth of human population and infrastructure displace bison.

Life cycle and reproduction

Life cycle and reproduction was not well-covered in available traditional or community knowledge sources. Breeding is known to take place in August (Gates *et al*. 2001a; Mitchell 2002; Schramm 2005; Environment Canada 2015e). The Grand Detour herd (part of the Slave River Lowlands population) is known to seek high areas between the Little Buffalo River and adjacent large wet meadows to calve (Gates *et al*. 2001a; Mitchell 2002). The Wentzel herd in northern Alberta is known to seek out spruce bluffs for calving. The trees offer shade and cover (Schramm 2005).

The Wentzel herd and bison in southern Wood Buffalo National Park are known to calve between May and early-June, although young calves have been seen year-round. One Garden River resident saw calves born in the fall during the anthrax vaccinations; many others saw calves being aborted during vaccination round-ups that were carried out by Wood Buffalo National Park between 1965-1977 (Northern Diseased Bison Environmental Assessment Panel 1990a; Schramm and Krogman 2001; Schramm 2005).

Physiology and adaptability

Bison use their heads to dig through the snow to reach their food, or they may blow snow away (van Kessel 2002; Schramm 2005); however, according to Yukon oral history, the wood bison's short legs make it difficult for them to move in deep snow, and as such they seek out snow-free areas in the winter (see *Habitat Requirements*, p.35; Lotenberg 1996). However, a Tsiigehtchic Elder indicated that wood bison were large and capable of running through even very deep snow (Stephenson *et al*. 2001).

In the past, wood bison in the Yukon were considered difficult to kill with arrows, as they are 'fast runners'. Although some groups did harvest them with arrows, others relied upon a snare system. They were considered a dangerous animal to hunt, as they are aggressive or 'put up a fight' (Lotenberg 1996; Stephenson *et al*. 2001).

Bison in the Wentzel herd stay in small family groups of 6-15 individuals. They are not known to coalesce into a large herd or large groups, although the small groups may come together to form slightly larger groups. The formation of these slightly larger groups is based on seasonal conditions. Heavy snow cover encourages the formation of larger groups as it is easier on individuals, in particular calves, when the work required to break through the snow crust is shared more widely. Wentzel herd bison are known to stay in smaller groups if the snow cover is light, as well as in the summer (Schramm 2005).

Wood bison in southwest Wood Buffalo National Park are generally encountered in smaller groups as well, although they have occasionally been seen in groups as large as 100 during the trapping season (winter) (Schramm 2005). As noted in *Movements*, p.37, some traditional knowledge sources suggest cows and calves will separate into smaller groups in the summer and coalesce in the winter at feeding areas (Gates *et al*. 2001a; Mitchell 2002). However, some traditional knowledge holders indicate that Wood Buffalo National Park herds stay in larger herds in the summer and smaller herds in the winter (Schramm 2005).

Wood bison in the Wentzel herd shed in spring, and use tree trunks, uprooted trees, and wallows during that time. They have a preference for the rough bark of spruce trees to rub on (Schramm 2005). The smell of the spruce trees helps to mask the bison's odour and protect it from wolves. Wallowing and rubbing continue throughout the insect season in the summer (Schramm 2005). Oral history from Alaska indicates that wood bison are not bothered by mosquitoes like other ungulates, due to their hair coat. However, they do harbour parasites in their coats (Stephenson *et al*. 2001).

Interactions

Interactions with harvesters

Gates *et al*. (2001a) and van Kessel (2002) note that wood bison are hunted throughout their range in the NWT, except where prohibited; however, this may differ based on regional attitudes towards wood bison.

The Salt River First Nation considers wood bison to be sacred and an essential component of their livelihood (Environment Canada 2015e). In contrast, members of the Kátł'odeeche First Nation have indicated that they do not have a strong relationship with bison, although this is perhaps because they have been barred from hunting them in Wood Buffalo National Park since the early 1920s. A lot of the traditional knowledge about this species has therefore been lost over time (Environment Canada 2015d). Similarly, in a limited study (Fanni 2014), some members of the ADKFN indicated that wood bison are never harvested by their members because they are thought to feed on garbage along Highway #77 and because their hides are too tough to be useful for traditional materials. However, this attitude may not be prevalent as some members, both young and old, have actively hunted bison (Larter pers. comm. 2016a). Younger members of the ADKFN indicated less opposition to harvesting and eating bison (Fanni 2014). Reynolds *et al*. (1980), who, in studying the suitability of the Liard-South Nahanni rivers region for the establishment of a herd of reintroduced wood bison, indicated that the transfer of wood bison to this region ought to be carried out, in part because the local people supported the re-establishment of wood bison as an alternate meat source. Hunting is discussed in more detail in

Threats and Limiting Factors, p.52.

More generally, wood bison are often felt to be a nuisance in Dehcho and Tłı̨chǫ communities, having lost their fear of humans (ENR 2008, 2010a, 2012; Environment Canada 2015a). It is felt that wood bison adversely impact traditional pursuits by competing with boreal caribou and moose (Dehcho First Nation [DFN] and Resources, Wildlife and Economic Development [RWED] 2002, 2004; Cluff *et al*. 2006; ENR 2006, 2008, 2012; Fanni 2014; Environment Canada 2015a), by making it difficult to set small mammal snares, and by trampling or eating plants and berries that would normally be harvested by communities (Fanni 2014). However, it has also been noted that bison may be getting blamed for unsuccessful harvests simply because they are visibly present, rather than due to any actual measurable adverse effect they may have on other harvestable species (Allaire pers. comm. 2015). Further, although wood bison were present in the NWT historically (early 1900s) (ENR 2012), there is the feeling that wood bison are a 'novel' wildlife species; likely the result of wood bison being absent from the landscape for a number of generations (ENR 2008, 2012; Environment Canada 2015a). Dehcho First Nations delegates at the 6th Biennial Regional Wildlife Workshop (ENR 2012) noted that more education for communities regarding the use of bison as a meat resource was needed. "If we were culturally connected to bison we wouldn't have a problem" (Priscilla Canadian *in* ENR 2012: 2).

Fanni (2014) raises another point:

> *"Unfortunately, the negative effects of the presence of bison disproportionately affect ADK Elders, a fact which, because of the high social standing of the latter, magnifies the already hostile attitudes of ADK members towards the animals." (Fanni 2014: 15)*

There is however, some indication that attitudes, at least in Fort Liard and Fort Providence, are changing. Danny Allaire (pers. comm. 2015) has observed increasing harvest and consumption of bison meat by locals following efforts by territorial government representatives to distribute meat harvested from problem bison kills. Stories about bison also certainly still exist. ADKFN members have discussed how they used to travel from communities to their traditional camps using old bison trails, before the reintroduction of bison. Members of the Jean Marie River First Nation used to travel to the Slave River in the summer to trade for bison hides because there were no more bison in their region. Hunters that lived on the Liard River historically hunted bison by scaring them into the river, drowning them by paddling up to them and splashing water into their noses, and then dragging them to shore to be butchered (Allaire pers. comm. 2015).

Interactions with predators

Predators of wood bison include black bears, wolves, and cougars. Black bears and other predators will kill calves in the spring. In response, wood bison move to locations where predation is less likely. Wolves are known to follow wood bison herds around. Wolf population numbers may be linked with wood bison and moose population numbers – wolf numbers may decrease as ungulate numbers decrease (Schramm 2005). Wolf predation may also impact wood bison in other ways; the Northern Diseased Bison Environmental Assessment Panel noted that wolf predation may be causing wood bison to be smaller in size physically (1990b).

Wolves are known to take mainly calves, although they will occasionally take an old or diseased animal, or target a healthy 'fat' animal (Schramm 2005). Wolves are known to not 'touch the boss' of the herd. Hunters have seen small herds with very few calves remaining (Schramm 2005).

> *"I see their tracks, wolf tracks... following the buffalo. But they kept their distance; they don't want to go right up. Unless there's a few calves in a small herd, that's easy prey for them. Well, a big herd, maybe ten, twelve, they won't go. They'll stay away. But they will just circle a few times and then leave… But if there's about maybe five and there's a couple of calves, oh yeah, they go after them, right now." (Malcolm Auger in Schramm 2005: 133)*

One hunter has seen three adult cows taken by wolves at around the same time. They could not escape the wolves due to snow conditions (Evans pers. comm. 2012).

Wood bison face wolves head on and chase them away. When approached by wolves, wood bison stay together as a group, circling the calves, making them very hard to kill. Wolves have the best chance to kill a wood bison if they can cause the group to 'open up.' If they decide to flee, the animals will go single file, led by a bull or bulls and with several large cows in the back, with the calves in the centre. In this formation, a bull at the rear is particularly vulnerable to attack, as wolves attack the genital region and will bite their testicles and rip them open (Schramm 2005).

Wood bison use seismic lines and open meadows for their improved ability to see approaching wolves. Seismic lines were not used by wood bison as much after trophy hunting became common in northern Alberta though (Schramm 2005). Wood bison are particularly vulnerable to predation by wolves during the summer when the soft, moist ground forces the heavy bison to sink, making it difficult for them to manoeuver (Schramm 2005).

The communities of Fort Chipewyan and Fort Smith have urged government to control wolf predation on wood bison through predator control programs since the 1930s. Wolf populations were controlled in the 1940s and 1950s and wolf numbers did decrease, although they increased again in the 1960s. A change in policy at Wood Buffalo National Park precluded further predator control programs (Carbyn and Trottier 1988). Hunters felt that any of the various proposed eradication plans suggested over the years to completely remove diseased wood bison from the Wood Buffalo National Park area would cause large changes to the relationships between wood bison predators and other prey animals (see *Threats and Limiting Factors - Disease eradication efforts*, p.54) (Ferguson 1989).

An increase in wood bison range and population is seen as causing an increase in wolf numbers in the North Slave region. This is considered a threat to other ungulates, in particular boreal woodland caribou (Cluff *et al.* 2006). Likewise, in the Dehcho region, it has been noted that there are too many wolves around the Mackenzie Bison Sanctuary and that predator management could be incorporated into management plans for wood bison and caribou (ENR 2008).

> *"Wood Bison have been seen with injuries from other predators as well. One hunter noted that he has seen Wood Bison that had been 'raked' (clawed) by either cougars or Black Bears." (Evans pers. comm. 2012 in Fanni 2014: 15)*

Interactions with competitors

Boreal woodland caribou are known to avoid areas adjacent to wood bison range despite the presence of good caribou forage (Schramm and Krogman 2001). Wood bison are seen as competitors for slow-growing lichens consumed by boreal woodland caribou in the Caribou Mountains, although the bison tend to stay in the western portion and the caribou in the east. This point was also made by some ADKFN members, who noted that competition for resources was particularly concerning during harsh winters or dry summers (Fanni 2014). Interviewees in this limited study (Fanni 2014) explain the mutual avoidance (caribou avoiding wood bison and wood bison avoiding caribou) in several ways, including the caribou avoiding the wolves near the bison, but also that the bison forage heavily on the caribou's preferred food. Wood bison and boreal woodland caribou are said to 'dislike' one another (Chocolate 2011). Aboriginal hunters also suggest they mutually agree or cooperate to remain apart (Schramm 2005).

An explanation for the avoidance of the caribou range by bison, however, is still lacking.

> *"When I discussed the issue with Malcolm Auger he replied, "They don't bother each other". I asked Mr. Auger if the two species communicate, and he replied that they did. This is an aboriginal explanation of the phenomenon where an agreement exists between both ungulate species to stay out of each other's ranges." (Schramm 2005: 176)*

Increasing wood bison range and populations are seen as a threat to boreal woodland caribou and moose by NWT communities (DFN and RWED 2002; RWED 2004; Cluff *et al*. 2006; ENR 2006; Larter and Allaire 2007; ENR 2008, 2012; Fanni 2014; Environment Canada 2015a, b, and d). Residents of Nahanni Butte and Fort Liard have expressed concern that the increasing population of the Nahanni herd of wood bison may compete with moose – a preferred country food source (Larter and Allaire 2007). ADKFN members noted that moose will not graze near wood bison as a result of the distinct smell of their urine and feces and have almost disappeared from the Fort Liard area. One ADKFN harvester also described wood bison as "bullies in a playground", having observed them urinating on salt licks (Fanni 2014: 15). However, concerns have been raised with this study and the perspectives it presents. In addition to the study limitations noted earlier (e.g., few interviewees), the effects of the construction of the Liard Highway may have been understated or overlooked (e.g., increased access, traffic, etc.) and little recognition is given to changes in harvesting practices over time (e.g., over-harvesting moose, relying only on big game rather than harvesting chickens (grouse), rabbits, fish, beavers, etc. to supplement the diet). Directly tying wood bison to a decline in moose may therefore be difficult (Allaire pers. comm. 2015).

According to Yukon Elders, wood bison lived in the eastern Yukon in the past. During that time, there were few moose in the area. There may also have been fewer caribou in some areas. Elders indicated that when moose populations in the Yukon increased, the wood bison left the area. Moose moved into the area as forests increased and open areas decreased, perhaps as late as 1900 (Lotenberg 1996). Alaskan Gwich'in agree that moose entered their territory historically (around 400 years ago), around the same time as wood bison became scarce or extirpated (Stephenson *et al*. 2001).

Parasites and diseases

Tuberculosis, brucellosis (Ferguson 1989) and anthrax (Schramm *et al*. 2002) are known diseases of wood bison. These diseases and their impacts are discussed in more detail in *Threats and Limiting Factors*, p.52.

Oral history suggests that some wood bison diseases may have been present in the mid- to late-1800s in the NWT. According to information gathered and presented in a paper by Ferguson and Laviolette (1992):

> *"Oral tradition from the Fort Smith area also provides an example of sudden mortality among the wood bison of the area. Laviolette recalls the story passed on by the late Germaine Tourangeau and others, a story told to them when they were young men by the late Chief Pierre Squirrel, who was then an elder himself. Chief Squirrel said that when he was a young hunter, there were many wood buffalo. 'Then one summer season the wood bison died off so quickly at Foxhole prairie that the bones were almost side by side' (Laviolette 1989). 'That big Salt Plain was just black with dead wood buffaloes'." (Louis Brown pers. comm. 1985 in Ferguson and Laviolette 1992: 48)*

Ferguson and Laviolette (1992) also noted fur trade references of Aboriginal hunters describing disease outbreaks in wood bison as well as other ungulates in proximity to Fort Chipewyan in 1821, 1823 and 1831. Unfortunately, these sources only note mortality; they do not provide the details necessary to determine cause of death.

STATE AND TRENDS

Population

Abundance

Information on abundance in the NWT was not included in sources reviewed.

Trends and fluctuations

Trends and fluctuations in the numbers of wood bison in the NWT were not well covered in the available literature. One Fort Resolution resident did note that the population there had not yet returned to the peak levels observed in the 1970s (Environment Canada 2015c), while members of the Kátł'odeeche First Nation indicated that the bison population in their region has been fairly stable over time (Environment Canada 2015d).

For residents of Fort Resolution, there were differing views on the effect of the three key diseases (brucellosis, tuberculosis, and anthrax) on wood bison. Some felt that the effect of the diseases on bison population trends was overstated by government officials and a few respondents even suggested that the diseases were an invention of, or at least very exaggerated by, government officials. Diseases were described as a natural part of life for wildlife. Some felt that only older animals became ill with disease; however, some participants did feel that disease was a factor in bison population trends, and was a threat – even if government interventions caused the disease (van Kessel 2002).

Population dynamics

Population dynamics were not covered in traditional and community knowledge sources reviewed.

Possibility of rescue

The possibility of rescue was not covered specifically in sources reviewed; however, traditional and community knowledge sources confirm that wood bison occur in Alberta and that long distance movements are possible (see *Movements*, p.37, for more information). This implies that rescue of NWT populations/herds is possible.

Likelihood of immigration

Wood bison, in particular bulls, are known to travel long distances (Gates *et al*. 2001a; Mitchell 2002). Barriers to wood bison movements include large areas of poor habitat such as muskeg, some wide rivers, ice jams, steep terrain, and areas with increased hunting pressure. Barriers are discussed in *Movements*, p.37.

Status of populations elsewhere

Little Red River Cree counts of the Wentzel herd in northern Alberta were always less than 26 individuals, with 60-100 wood bison in the Wabasca herd and the adjacent Wood Buffalo National Park (Schramm and Krogman 2001).

The population of the Wentzel herd in northern Alberta was declining in the late 1990s/early 2000s, and the main cause of the decline was an increase in hunting pressure related to easy access from a road built to John D'Or Prairie and Garden River. A lack of hunting regulations compounded the issue (Schramm *et al*. 2002). The population in southern Wood Buffalo National Park is decreasing as well (Schramm 2005).

The Ronald Lake herd (between Fort McMurray and Fort Chipewyan) is seen to be declining by interviewees of the Athabaska Chipewyan First Nation (Candler and Firelight Group Research Cooperative 2011).

Possibility of captive breeding

Some Fort Resolution residents felt that the innate 'wildness' of captured wood bison used in the unsuccessful attempt at creating a new disease-free herd through the Hook Lake Wood Bison Recovery Project would allow them to re-adapt to wild conditions if released. Others felt that captive bison would need to be weaned slowly from their human-supplied feed and fenced from wolves for a time, for the wood bison to learn how to survive (van Kessel 2002).

Habitat

Habitat availability

As described in *NWT Distribution* (p.30), good wood bison habitat can be found to the east of the Slave River, in meadows around the Little Buffalo River, along the Yates River outside of Wood Buffalo National Park, between the Nyarling River and Grand Detour on the Slave River, in patches along the south shore of Great Slave Lake, and around Hook Lake. The higher ground in the northern portions of Wood Buffalo National Park provide widely dispersed but good wood bison habitat (Northern Diseased Bison Environmental Assessment Panel 1990a; Gates *et al*. 2001a; Mitchell 2002). Wood bison calve in the high ground areas between the Little Buffalo River and the large wet meadows to the east (Gates *et al*. 2001a; Mitchell 2002). Wood bison are known to use burned-out areas (Gates *et al*. 2001a; Mitchell 2002).

Based on oral history of wood bison range extending to the Beaufort Sea (Lotenberg 1996; Stephenson *et al*. 2001), much of the NWT may have, or may have been, suitable wood bison habitat that is currently not used by wood bison. Cut blocks may be appealing for wood bison, indicating that logging may open areas of preferred habitat (Schramm 2005).

Habitat fragmentation

Habitat fragmentation was not covered in the reviewed traditional and community knowledge sources.

Habitat trends

The encroachment of willows into meadows, which are important wood bison habitat, has been noted in the Slave River Lowlands (Gates *et al*. 2001a; Mitchell 2002; Schramm 2005; Environment Canada 2015c). Meadows could be restored with a burn (Gates *et al*. 2001a; Mitchell 2002; Schramm 2005).

Changes in habitat mentioned by Cree Elders and hunters in northern Alberta include an increase in willows and brush-dominated areas where more open grasslands used to exist. The brush is considered to be poorer bison habitat than the previous open grassland. The encroachment of willows may also relate to water table changes brought on by the construction of the Bennett Dam (Schramm 2005; Environment Canada 2015c) and the cessation of over-bank flooding in some springs due to ice-jams forming on the Peace and Slave rivers (Armstrong pers. comm. 2015). This same pattern of brush incursion into open grasslands having a negative impact on wood bison is also reflected in oral history accounts from Alaska. When wood bison were extirpated from Alaska, oral history indicates that some open grassy areas were replaced with brushier vegetation (Stephenson *et al*. 2001; Schramm 2005). In the Yukon, open areas suitable for wood bison have also been overgrown with willows and forests over the last four hundred years (Lotenberg 1996).

Prime wood bison habitat in northern Alberta around Wood Buffalo National Park was considered to be 'drying up' in the late 1980s, but in the NWT, the habitat was considered prime (Northern Diseased Bison Environmental Assessment Panel 1990b).

Distribution trends

The distribution of wood bison in the NWT has increased in the last half-century (Cluff *et al*. 2006), although little further detail was provided in the available sources. Environment Canada (2015a) noted that expansion of the Mackenzie population in particular has been noted, with the range expanding north towards Whatì in recent years, perhaps as the result of newly constructed roads and trails providing increased access to the area. This expansion is not supported by Tłı̨chǫ communities, which are concerned about potential impacts to communities as well as habitat overlap with boreal and barren-ground caribou. Community members have suggested the creation of a bison control area to prevent further northward expansion of the Mackenzie population.

THREATS AND LIMITING FACTORS

Traditional knowledge holders in available sources described various threats to wood bison populations, including hunting, disease/disease eradication efforts, efforts to preserve genetic/subspecies purity, and lack of detailed studies. Hunting was considered to be the largest threat by some knowledge holders, while others felt that vehicle collisions and anthrax were the threats of greatest concern. Disease eradication efforts were considered by some to be a larger threat to wood bison than the diseases themselves.

Wood bison are also known to die off in large numbers in extreme events, due to a variety of reasons: anthrax, winter starvation, and in particular, drowning due to both flooding and falling through the ice (Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b).

Hunting

Hunting was widely reported as affecting wood bison herds in the NWT. In 2002, members of the Deh Gah Gotie First Nation (Fort Providence, NWT) were concerned about over-harvest by their own people; the species of concern was not specified but may have included the Mackenzie bison population. They noted that the attitude of shooting an animal just for the sake of shooting it is something that needed to change (DFN and RWED 2002). With the exception of 4-5 males harvested annually by the Deh Gah Gotie First Nation under a Wildlife Permit (Armstrong pers. comm. 2016a), hunting of the Mackenzie population was halted in response to declines after a major anthrax outbreak in 2012.

Herd animals such as wood bison are relatively easy for hunters to find and can provide more targets than a solitary animal (Schramm 2005). Oral history from Alaska indicates that wood bison may have been hunted to extirpation there during times of high human population and game scarcity. Hunting was implicated in the historic extirpation of wood bison from Alaska (Stephenson *et al*. 2001).

A big game outfitter harvested bison in the Hook Lake Lowlands during the late-1960s/early 1970s, but this harvest was closed as a result of community concerns that too many large breeding males were being harvested, which affected the breeding stock (Beck pers. comm. 2016).

Outfitting and trophy hunting of the unprotected Wentzel herd in Alberta has put severe hunting pressure on that herd. Subsistence hunters were also using this herd until a voluntary ban was put into place. The ban is not observed by outfitters (Schramm 2005). The Little Red River Cree identified trophy hunting of wood bison as a threat in 2001. The Government of Alberta does not regulate hunting of the Wentzel herd as they have not designated the herd as ‘wildlife’.

Therefore, hunting can occur year-round and is considered an important threat (Stephenson *et al.* 2001).

In contrast, members of the Kátł’odeeche First Nation question whether the earlier extirpation of wood bison from their region was the result of overharvest or whether it was simply a reflection of the land being unable to support wood bison (Environment Canada 2015d).

When hunting pressure increases, wood bison are known to move into the bush (poorer habitat) and away from access routes (Gates *et al.* 2001a; Mitchell 2002; Schramm 2005). Hunting pressure tends to increase in conjunction with increased access to wood bison habitat. Seismic lines and other linear disturbance, while creating forage for wood bison, also increase hunting pressure through increased access (Schramm 2005). Road construction around John D’Or Prairie in northern Alberta changed wood bison behaviour due to increased access; the hunting pressure drove the wood bison to remain in the Caribou Mountains rather than travelling to the prairie to access salt licks and food, never or rarely coming closer than seven kilometres from a road. This change was particularly hard on the wood bison in the late winter and early spring (Schramm and Krogman 2001; Schramm *et al.* 2002). An increase in linear disturbances relating to development has served to greatly increase the ease of access to hunting areas that were previously remote and inaccessible in northern Alberta. This has increased hunting pressure on wood bison in the area, in particular in the late winter and early spring (Gates *et al.* 2001a; Mitchell 2002). Industrial development may also bring more non-Aboriginal hunters (i.e., employees) to an area, which can increase hunting pressure:

> *“I do a lot of flying from here to Fort Smith. The first year I was here I remember flying and coming on three herds of buffalo, and the herds of buffalo, I would estimate altogether would be about 300 buffalo. This was two years ago [1973]. Since that time I have never seen a herd over 25 buffalo. We at council and myself do not blame all of this on the development of Pine Point, but we do know that there has been hunting and over-hunting in that area by whites who do not need that meat for food because they are paid well at their jobs. ... So when I've been flying around the area I have seen an abundance of skidoo trails, far too many to be made by just the people from Fort Resolution. We know that the buffalo have been chased by planes and skidoos, and in one instance we know, because it was reported, that buffalo were at least, if not shot from a helicopter, were picked up by helicopter.” (Larry McConnell in Berger 1975: 3066)*

Predation

Predators such as cougars, wolves, and black bears are negatively impacting the wood bison population in the NWT (Northern Diseased Bison Environmental Assessment Panel 1990b; Environment Canada 2015a, c and e). Wolves are seen as killing more than they can eat. Members of the Salt River First Nation have reported wolf packs of 100 individuals attacking smaller groups of 30 wood bison around Lake Claire in Wood Buffalo National Park (Environment Canada 2015e). Trapping, which controlled wolf populations somewhat, has declined in recent decades. As wolf predation causes a decline in wood bison population numbers, the end of the bounty on wolves for trappers was considered to be harmful for wood bison populations (Northern Diseased Bison Environmental Assessment Panel 1990b).

Disease eradication efforts

In the late 1980s, northern Aboriginal hunters indicated that scientific assessments of disease prevalence were inflated because of the small sample size of biological specimens and other problems with the data:

> *"Overwhelmingly, Native groups and individuals challenge the [Diseased Wood Bison] Task Force's statement that the wood bison of the WBNP area currently suffer such a high rate [>35%] of disease." (Ferguson 1989: 4)*

In their experience of hunting wood bison in the 1970s and 1980s, wood bison were not diseased at the high level suggested by scientists at that time (Ferguson 1989). Aboriginal hunters in the South Slave area of the NWT and northern Alberta suggested that only about ten percent of wood bison in and around Wood Buffalo National Park were diseased. Some hunters indicated that the Hook Lake herd was disease-free at the time. Aboriginal hunters indicated that a declining population of wood bison is likely due to many factors, rather than just disease, which is naturally present in wood bison. Additionally, they recommended that the issue of disease eradication must be based on a whole ecosystem approach, and management plans must deal with all diseased herds together, rather than piecemeal (Northern Diseased Bison Environmental Assessment Panel 1990a).

Aboriginal hunters indicated that some presence of disease in herds is natural. Eradicating diseased animals and herds is indicated as a threat to wood bison generally (Ferguson 1989). In 1990, disease eradication efforts were seen by northern communities as a way to bring northern forests into agricultural or logging productivity, rather than to deal with the issue of wood bison disease (Northern Diseased Bison Environmental Assessment Panel 1990a; Environment Canada 2015e).

Another aspect of disease eradication efforts that was noted in the late 1980s as a threat to wood bison was the way disease monitoring and prevention were carried out, including driving the animals by helicopter flights, herding, corralling, and other techniques (Ferguson 1989). Forcing wood bison to run using herding practices can also have disastrous consequences. Many animals, perhaps several thousand, drowned during misguided herding attempts (Northern Diseased Bison Environmental Assessment Panel 1990a).

> *"Respondents described seeing healthy animals chased by helicopters and people during the winter months. They reported that the animals would foam or froth at the mouth, appear to*

> *have severely laboured breathing, and that as a result, many bison collapsed, were trampled, aborted calves, or died from other injuries." (van Kessel 2002: 81)*

Aboriginal hunters noted that diseased animals often showed signs of handling (for example, ear tags), indicating that they were possibly vaccinated or otherwise corralled. The vaccine itself and the stress of corralling were noted as possibly increasing the likelihood of disease (Ferguson 1989; van Kessel 2002). Some Aboriginal hunters link the start of the anthrax vaccination program with the decline of the herds. The effects of the vaccine may also be lingering, as some hunters indicated that the flavour of the non-vaccinated herds outside the park is superior. The non-vaccinated animals are leaner and better-tasting than those that were vaccinated (Schramm *et al*. 2002). A hunter in the Taltson River area indicated that the only two diseased wood bison he had killed out of twenty had ear tags (Northern Diseased Bison Environmental Assessment Panel 1990a). More recently, a tuberculosis testing project proposed by the University of Saskatchewan and Parks Canada is opposed by the Salt River First Nation (Environment Canada 2015e).

The anthrax vaccination program itself was considered to have been very damaging to the wood bison populations. Community members recall many wood bison dying while being rounded up in inappropriate ways, breaking legs, splitting hooves, or becoming too tired to continue running.

> *"Many people in Fort Smith saw buffalo staggering along with blood pouring out of their frozen mouths to fall along the way… buffalo lying all along the road, dead, some with calves sticking halfway out of them." (Northern Diseased Bison Environmental Assessment Panel 1990a: 150)*

Additionally, community members have heard that anthrax was injected into wood bison, which were then allowed to die from it as a scientific experiment, along with other practices considered extremely inhumane, such as allowing crippled wood bison to die over a period of months rather than euthanizing them (Northern Diseased Bison Environmental Assessment Panel 1990b). Game wardens killed wood bison during anthrax outbreaks, and continued to kill them even after the community noted that the outbreak was already subsiding (Northern Diseased Bison Environmental Assessment Panel 1990a).

Bison recovery activities conducted under the Hook Lake Wood Bison Recovery Project, such as corralling wood bison, in particular in small pens during calving, and feeding the wood bison and allowing them to become dependent or 'lazy' was seen as inappropriate to some Elders. The feed was noted to be dry, and not containing the plants required for the wood bison to remain healthy and heal from disease. The removed bison calves were also at risk of not learning the proper skills they would need to survive in their own habitat, generally taught to them by their mothers. Subsequently, released captive wood bison may shape or use the environment differently from the existing wild herds. Some respondents would have preferred minimal handling and contact between wood bison and people during the program (van Kessel 2002; Schramm 2005). Replacement wood bison, which might be captured or raised in captivity prior to being released after an extermination, might also be less healthy and capable or ‘weak and tame’ (Northern Diseased Bison Environmental Assessment Panel 1990b).

In the 1990s, government policy relating to the re-establishment of disease-free wood bison after eradication of diseased herds was considered a threat by Aboriginal communities: considering the long-term nature of the disease eradication process (over a decade or more), changes in government policy could endanger the wood bison herds if the government changed their policy direction during the time when there were no bison in the area – in other words, decided to not proceed with re-introduction (Northern Diseased Bison Environmental Assessment Panel 1990a). If the diseased wood bison herds are destroyed and replaced, a lack of genetic variability within the replacements is considered a threat to the future of wood bison (Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b).

Efforts to preserve genetic/subspecies purity

Efforts to preserve the genetic distinctiveness of wood bison from plains bison imported to the Wood Buffalo National Park area during the 20th century was considered a threat at worst, or unnecessary at best. There is a suggestion that it is considered more acceptable or justifiable to government policy makers and conservationists to slaughter the ‘impure’ and diseased bison and to replace them with rescued wood bison, rather than commit to other forms of management. The categorization of the wood bison as hybrids has also denied the Wentzel herd protection from hunting in Alberta (Schramm 2005).

> *“Subspecies purity is not a valued concept to local Native peoples. The establishment of a wood bison population in itself is seen as a worthwhile endeavour but the slaughter of another wood bison population to make way for wood bison is seen as irrational. Why place a higher value on an animal which is, let's say, 90% wood bison, 10% plains bison than on an animal which is 90% plains bison, 10% wood bison?” (Ferguson 1989: 5)*

> *“From the harvester's point of view, the value of the two subspecies is seen as the same: ‘they both taste the same’. Over and above this, Native people commented that this EuroCanadian cultural value on subspecies purity is actually a dangerous philosophy.” (Ferguson 1989: 5)*

Additionally, local views of whether or not the bison are ‘hybrids’ question if an animal can be considered a hybrid after more than half a century. The concern was expressed that ‘purebred’ wood bison are more under the control of the federal and territorial governments, suggesting a political reason for the eradication of hybrid bison (Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b). However, it should be noted that this is not a universally held belief, with knowledge holders in the Tłı̨chǫ indicating that hybridization with domestic or plains bison, or cattle, was a threat that should be mitigated by preventing contact among these animals (Environment Canada 2015a).

Disease

Bison diseases such as brucellosis and tuberculosis are considered by some Fort Resolution residents and Cree hunters to be a normal aspect of the natural life cycle of wood bison (van Kessel 2002; Schramm 2005). Alternatively, some Cree hunters and Elders felt that disease in wood bison related to a longer population cycle, perhaps on the order of 150 years. Disease will not infect every animal of a population (Schramm 2005). In order to heal from diseases, certain plants and herbs must be consumed (Northern Diseased Bison Environmental Assessment Panel 1990a; van Kessel 2002). Therefore, wood bison need free access to their habitat to have free choice of these plants (van Kessel 2002).

Diseased wood bison carcasses are identified by hunters through an examination for lumps, discolouration, pus-filled sacs, and other abnormalities. They also look for fluid or whiteness in the animals' lungs, and for a healthy liver. Hunters may leave the carcass for scavengers, bury/burn it, or feed the meat to their dogs if the animals are considered to be diseased (van Kessel 2002; Schramm 2005). Although some hunters from Fort Smith and Fort Resolution indicated that diseased wood bison meat is not consumed (Gates *et al*. 2001b), other hunters indicated that thoroughly cooked or dried wood bison meat was consumed (Beck pers. comm. 2016).

Tuberculosis and brucellosis are known to exist in wood bison in the Wood Buffalo National Park area. As noted earlier in *Threats and Limiting Factors - Disease eradication efforts* (p.54), in the late 1980s, Aboriginal hunters felt that the disease occurrence was over-estimated by scientists. However, they also indicated that disease may be harboured outside of the diseased animal within the wood bison's habitat or perhaps by other animals such as predators, scavengers, or other ungulates, and felt that eradicating diseased individuals and herds may not be effective in eliminating the presence of disease from wood bison altogether (Ferguson 1989; Environment Canada 2015e).

Fort Resolution participants in van Kessel's (2002) study had various understandings of how disease spreads, for example, by mosquito, or through over-exertion relating to government management techniques (i.e., from intense sweating from being herded).

The effects of anthrax are of concern to northern Alberta Cree (Schramm *et al*. 2002), Tłı̨chǫ and Dehcho (Environment Canada 2015a and b) hunters; more so than brucellosis or tuberculosis. The anthrax vaccine given to animals in the 1970s is also considered to be a lingering threat, passed from cow to calf. The actual vaccination program is known to have been deadly to wood bison. Cree hunters also indicate that the time it takes for anthrax to kill a wood bison is longer than several days, as wood bison were observed dying from anthrax on high ground, more than two days travel from the infection site (Schramm *et al*. 2002).

Lack of detailed studies

In the late 1980s, Aboriginal hunters indicated that there was a lack of clear information about wood bison diseases; how they spread and how or if they can or should be managed (Ferguson 1989). Mismanagement of diseased wood bison herds, without better information, threatened the herds. The transportation of diseased plains bison to the Wood Buffalo National Park area was used as an example of how management intervention had threatened wood bison. Additionally, Aboriginal hunters felt that perhaps domestic animals should be tested upon entering the NWT, for the protection of the disease-free status of the Mackenzie population (Ferguson 1989). A decade later, in the 1990s, some Fort Resolution residents maintained an uncertainty about how wood bison diseases are spread and prevented (van Kessel 2002).

In the 1990s, during the Northern Diseased Bison Environmental Assessment Panel (1990a, 1990b), numerous representatives from communities around Wood Buffalo National Park indicated that further studies on wood bison, wood bison disease, changes to the water system, wolf predation, and many other topics were needed in order to make informed decisions about disease management in particular.

Other threats

In the late 1980s-1990, Aboriginal exclusion from wood bison management processes and bison-free zone monitoring was considered a threat (Ferguson 1989; Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b; Environment Canada 2015d). In particular, there existed a fear that the management of wood bison was to allow for increased agriculture at the expense of the wildlife-based economies of the north (Ferguson 1989; Northern Diseased Bison Environmental Assessment Panel 1990a, 1990b; Environment Canada 2015e).

Forestry in northern Alberta is considered a threat in several ways. Active logging causes wood bison to leave an area, and regions with a greater amount of logging are less attractive to wood bison. Wood bison tend to stay in areas with less logging (Schramm and Krogman 2001; Schramm 2005). Forest Management Agreements were recently signed in the Fort Providence and Fort Resolution areas (ENR 2015 b, c and d) and land use permits have been issued for timber harvesting in both areas (Mackenzie Valley Land and Water Board 2015a and b). At a meeting with Deninu Ku'e First Nation members, concerns were raised about potential effects on wood bison in the Fort Resolution area (Environment Canada 2015c). Environmental pollutants, for example the pollution of the Peace River, are considered a threat and are linked by Cree hunters to disease in wood bison (Schramm 2005).

Captive wood bison herds are considered to be less healthy than free-ranging wood bison, even if the captive herds are disease-free. An excess of human handling and the use of fenced-in areas is considered a threat to the health of those wood bison being contained (Schramm 2005). The introduction of ranching in wood bison habitat in the NWT was considered a future threat (Northern Diseased Bison Environmental Assessment Panel 1990a).

Although fire is recognized as a natural component of the landscape, and small-scale fires as being beneficial to wood bison, the large fires seen in recent years are seen by some as a potential threat to wood bison. These fires can destroy animals and habitat, resulting in immediate mortality and longer term decline owing to a lack of food resources, increased vulnerability to predation (Environment Canada 2015e), and reduced capacity for movement as a result of deadfall within burn areas. These large fires are blamed on a combination of climate change and fire management decisions, and it has been recommended that the focus should be on keeping fires small (Environment Canada 2015e). In areas where lichen provides emergency food for wood bison during extreme weather (i.e., in the Caribou Mountains in northern Alberta), forest fires can damage the soil (Environment Canada 2015a) and lichen supplies. Lichens do not regenerate quickly after a forest fire (Schramm 2005). In contrast, harvesters from Fort Providence, an area that experienced a number of fires in recent years, have noticed that bison seem attracted to the fresh plant growth in burn areas (Environment Canada 2015a). As noted in *Habitat Requirements* (p. 35), impacts from the severe 2014 and 2015 fire seasons (Fig. 5, below) (ENR 2014, 2015a) have yet to be assessed.

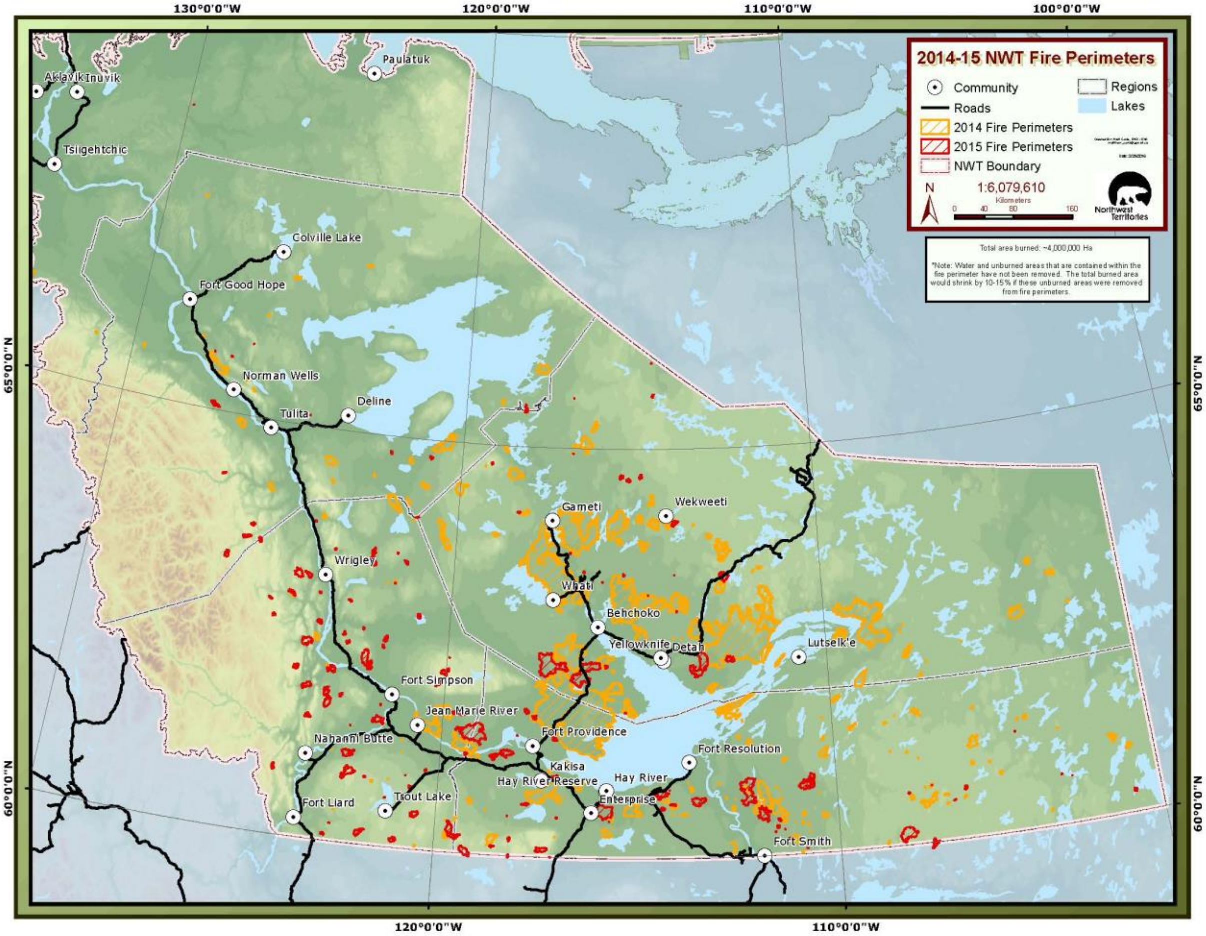


Figure 5. 2014/15 fire season in the NWT. Map prepared by M. Coyle, Forest Management Division, ENR.

Members of the Dehcho First Nation and the Tłı̨chǫ noted concern with the number of wood bison being killed on highways, with some knowledge holders in these regions indicating that they considered this the most important threat facing wood bison (Environment Canada 2015a and b). They noted that this appeared to be related, in part, to the use of road salt on highways, which attracts bison (ENR 2012; Environment Canada 2015a).

Drowning events can also adversely impact bison populations. A number of instances of bison falling through thin ice and drowning have been documented (Allaire pers. comm. 2015; Environment Canada 2015a). Boat and barge traffic have also been noted as a potential threat to wood bison in the NWT, given the waves and wakes this type of traffic can create. Wood bison sit quite low in the water while swimming, with their noses just a few centimeters above the water, which makes them vulnerable to drowning from any increase in wave action (Larter *et al.* 2003; Allaire pers. comm. 2015; Environment Canada 2015c).

POSITIVE INFLUENCES

Aboriginal traditional management techniques of only hunting what is needed for comfortable existence and following traditional 'rules' are a positive influence on wood bison by promoting reasonable hunting levels (Ferguson 1989; van Kessel 2002).

As noted earlier (*Interactions*, p.44), Fanni (2014), in a limited study, observed that negative attitudes towards wood bison among ADKFN members were most often present among men and Elders. With youth having more open attitudes towards wood bison (having spent their lives around them), Fanni (2014) noted that working with youth presents an opportunity to improve community attitudes towards wood bison.

Land-use planning initiatives, if passed, could have a positive influence on wood bison. For example, the Athabasca Chipewyan First Nation's proposed 'thunzea, dechen yághe ejere and et'thén protection zone' would protect the land to the east of Wood Buffalo National Park in Alberta and manage the area to protect and increase wood bison, barren-ground caribou, and boreal woodland caribou (Marcel *et al.* 2012). Likewise, the possible future approval of the Dehcho Land Use Plan has the potential to complement wood bison management in the Dehcho region (Armer pers. comm. 2015). Management planning processes are also underway for the Nahanni population, Mackenzie population, and herds of the Slave River Lowlands (ENR 2010b; Armstrong pers. comm. 2014). A draft plan has been prepared for the Mackenzie population to date, with completion anticipated by spring 2016 (Armstrong pers. comm. 2015).

Tree planting or remediation of forestry cut blocks was considered a good way to mitigate some, but not all, of the damage to the ecosystem that happens during logging (Schramm 2005).

Forest fires of moderate intensity can increase bison habitat by encouraging forage such as grasses and sedges (Schramm 2005) and although the impacts from the severe 2014 and 2015 fire seasons (ENR 2014, 2015a) have yet to be assessed, Fort Providence harvesters have observed bison moving into these burn areas to consume the fresh plant growth (Environment Canada 2015b). Prescribed burns associated with the Hook Lake Wood Bison Recovery Project were seen by some Elders as being vital and important to wood bison.

> *"So right now it's [Hook Lake area] at a stage where it's going to evolve into a big willow community. One of the ways to stop that encroachment was to prescribe burning ... The old timers used to do that [prescribed burning] all the time. This time of year springtime. They knew, eh- like they knew that the land is dependent on fire." (Interviewee in van Kessel 2002: 83)*

Similarly, several recent dry years and the absence of natural flooding and spring freshet may improve wood bison habitat by promoting the growth of grassy meadows (Environment Canada 2015a).

The intensive management of wood bison in the Hook Lake Bison Recovery Project was seen by some respondents in van Kessel's (2002) study as a positive influence - that people were 'taking care' of the diseased bison even if it was not traditional – it was recognized to be a required step to control disease.

The wood bison-free buffer zone between diseased and hybrid wood bison in Wood Buffalo National Park and the Mackenzie Bison Sanctuary was seen as effective (i.e., wood bison-free), in the late 1980s (Ferguson 1989).

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The preparer would like to thank all the Elders, hunters, and other participants in meetings and traditional knowledge studies who generously provided their knowledge over the years. Their names are included, when possible, in the *Traditional and Community Knowledge contributors section*, p.151.

The preparer would like to thank Tom Chowns and John Nishi, who were particularly helpful in identifying sources or providing further information and assistance.

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Status of Wood Bison in the NWT – Traditional and Community Knowledge

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Biography of Preparer

Kristi Benson, B.A., M.A. Heritage Specialist Ms. Benson has 13 years of experience in conducting anthropological, oral history, traditional knowledge, archaeological, heritage policy, GIS, and other heritage projects. Her experience in the heritage field has taken place primarily with NWT communities. Ms. Benson co-prepared the species status reports (traditional and community knowledge component) for boreal woodland caribou and Dolphin and Union caribou for the NWT Species at Risk Committee. Ms. Benson has also acted as research manager for three TK projects specifically relating to species at risk. She conducted research, prepared relevant reports, and managed the review process (including verification sessions) for the Gwich'in Traditional Knowledge of the Rat River Char study. She also supervised several other Gwich'in traditional knowledge studies relating to species at risk: boreal woodland caribou, grizzly bears, and wolverine. During these projects she conducted interviews, managed information and files, trained and supervised local interviewers, and prepared final reports. Ms. Benson has also provided traditional knowledge about barren-ground caribou for the designatable units assessment in 2011, and has compiled traditional knowledge for other species at risk assessments (pika, polar bear, and others). Ms. Benson also has experience as the project director for a multi-year Gwich'in traditional knowledge study relating to the Mackenzie Gas Project, where she managed the budget, participated in the hiring committee for assistants, conducted community consultation, conducted interviews, handled contracts for transcribing, wrote reports, and many other tasks. Ms. Benson has conducted numerous studies with the Gwich'in Social and Cultural Institute since her first association with them in 2004, and has worked with harvest study data and traditional trails data in the Sahtú Settlement Region as well. She has also worked with Inuvialuit communities conducting heritage research and worked with the International Polar Year with scientists and communities across the NWT.

Scientific Knowledge Component

SPECIES OVERVIEW

Names and classification

Scientific Name:	*Bison bison athabascae* Rhoads (1897)
Common Name (English):	Wood bison
Common Name (French):	bison des bois
Populations:	Greater Wood Buffalo Ecosystem, Mackenzie, and Nahanni
Synonyms:	*Bos bison* Linnaeus (1758)
Class:	Mammalia
Order:	Artiodactyla
Family:	Bovidae (cattle, buffalo, bison, yak, antelopes, sheep, goats)
Subfamily:	Bovinae (large antelope, cattle, buffalo, bison, yak)
Tribe:	Bovini (cattle, buffalo, bison, yak)
Subtribe:	Bovina (cattle, bison, yak)
Species:	American bison
Life Form:	Animal, vertebrate, mammal, ungulate (hoofed)

The American bison (*Bison bison*) and the European bison (*B. bonasus*) are recognized as the two extant species of bison. The American bison is represented by the subspecies known as wood bison (*B. b. athabascae*) and plains bison (*B. b. bison*). Wood bison in the Northwest Territories (NWT) fall within the following three populations: Greater Wood Buffalo Ecosystem, Mackenzie and Nahanni. The Greater Wood Buffalo Ecosystem consists of six distinct subpopulations: Nyarling River, Grand Detour, Hook Lake, Hay Camp, Delta, and Garden River. Some authors have referred to the Grand Detour subpopulation as the Little Buffalo subpopulation. Only the Nyarling River, Grand Detour and Hook Lake subpopulations occur primarily within the NWT, while the other three are centred in Alberta. Because of the different approaches various studies have taken, this report refers to the subpopulations of the Greater Wood Buffalo Ecosystem, as well as its two geographic ranges, which are Wood Buffalo National Park and the Slave River Lowlands. The Park contains the Nyarling River, Hay Camp, Delta, Garden River and part of the Grand Detour subpopulations, whereas the Slave River Lowlands is home to the Hook Lake and most of the Grand Detour subpopulations. For the purposes of this report, the term "herd" may be used interchangeably with "population" and "subpopulation".

Systematic/taxonomic clarifications

There have been a series of taxonomic revisions of North American bison. Allen (1876) carried out the first study that included both living and extinct species. After a proliferation of new fossil discoveries led to descriptions of several genera and dozens of species and subspecies, Lucas (1899) attempted to disentangle the complicated synonymy in bison taxonomy by recognizing seven species. However, a confusing array of new genera, species and subspecies continued until Skinner and Kaisen (1947) carried out a very comprehensive revision of bison systematics. For all living and extinct North American bison, they attempted to stabilize the levels of genus to one, subgenus to five, species to 10, and subspecies to four, but because of dating limitations, their morphotype groupings were prone to error (Schultz and Hillerud 1977). With improved dating methodology and rejection of unusual fossil characteristics that were fragmentary, insignificant, or unlikely to have adaptive value, the detailed revision by McDonald (1981) reduced the classification of North American bison to five species and four subspecies, including the one living species (*B. bison*) and its two subspecies. The most recent systematic study was conducted by Van Zyll de Jong (1986) who analysed the morphometrics of extinct, historical, and remnant populations, particularly as they relate to wood bison.

Since the 1980s, there have been major advances in genetics that are providing taxonomic clarifications and identifying classification errors, such as similar morphology being incorrectly deemed the result of common ancestry. Nomenclature is unsettled and another taxonomic revision that synthesizes current information may be due.

As research into taxonomic issues continues, precise genetic distances and degree of relatedness among all bovines could eventually be determined, but the ranking of genus, species and subspecies may not be resolved without universally accepted criteria. The American bison is a relatively young species and plains-wood bison divergence is recent. Plains bison genetic introgression in the 1920s did not alter the unique evolutionary pathway of wood bison. The prevailing position of the International Union for the Conservation of Nature (IUCN) Bison Specialist Group (Gogan *et al*. 2010) and the Government of the Northwest Territories (Environment and Natural Resources (ENR) 2010a) concurs with Van Zyll de Jong *et al*. (1995) that all bison in the NWT are wood bison. Whether wood bison is a *bona fide* subspecies, or a lower taxonomic variant of the American bison (*B. bison*) does not diminish the validity of its conservation as a morphologically and genetically distinct entity (*Species at Risk Act* 2002; *Species at Risk (NWT) Act* 2009).

For more information on systematic and taxonomic clarifications, refer to *Appendix A1* (p. 209).

Description

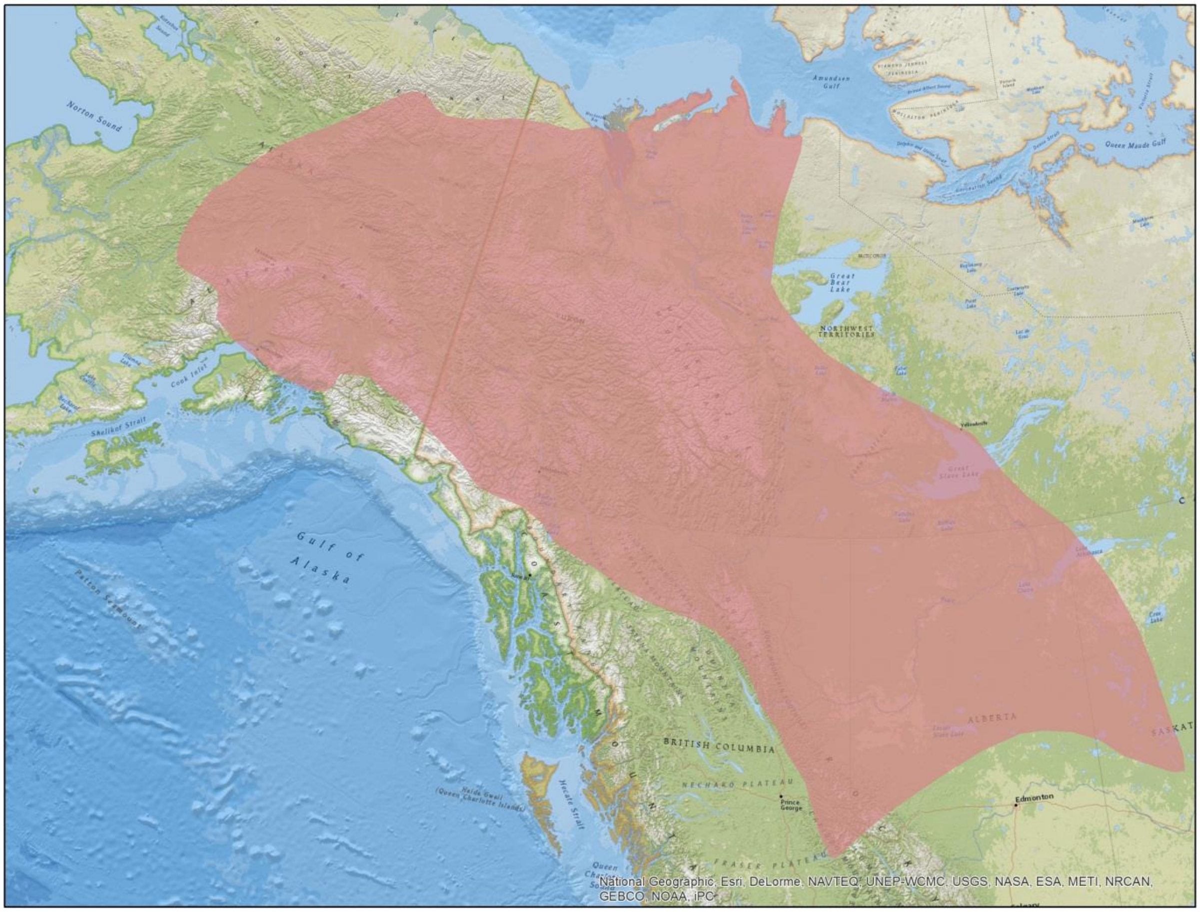
Wood bison are noted for their enormous size, high hump at the shoulders, long woolly pelage especially on the head and forequarters, wide muzzle, and short, round, curved horns extending upwards from the sides of the head (Figure 6, below). In mature animals, the coat is generally dark brown and black. Calves are born with a ruddy, coppery yellow appearance, which becomes darker after a few months when they start to form their hump. As the largest native terrestrial mammal in North America, mature wood bison bulls measure over 1.8 meters (m) at the shoulder and may exceed 1,000 kilograms (kg), whereas females average around 550 kg (Reynolds *et al*. 2003). Olson (2006) found that wood bison in the Elk Island National Park Isolation Area average 17 percent (%) heavier than plains bison of Elk Island National Park. Wood bison are also darker than plains bison, have a more pronounced forwardly placed hump, less slope along the back to the rump, and a lighter line extending from the crest of the hump to the hindquarters. Also, plains bison have a very distinctive golden-coloured cape on the forequarters, and more hair on the front legs and throat. Detailed descriptions of the differences between wood and plains bison are found in Geist and Karsten (1977), Van Zyll de Jong (1986), Van Zyll de Jong *et al*. (1995) and Olson (2006).

Figure 6. Wood bison (photo credit Terry Armstrong, ENR).

Distribution

Continental distribution

According to archaeological discoveries, historical records and traditional knowledge of aboriginal peoples, the original range of wood bison included the interior sedimentary plain north of the Aspen Parkland in British Columbia, Alberta, and Saskatchewan, as well as large areas of the northern cordillera in British Columbia, the Yukon and Alaska (Van Zyll de Jong 1986; Gates *et al*. 1992a; Lotenberg 1996; Stephenson *et al*. 2001), as well as the majority of the western NWT, as shown in Figure 7, below.



National Geographic, Esri, DeLorme, NAVTEQ, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC

Figure 7. Approximate historical continental distribution (map by B. Fournier, ENR, based on Stephenson *et al*. 2001).

Most wood bison habitat in the NWT has a very strong association with the dense lacustrine soils exposed by the recession of Glacial Lake McConnell (Raup 1933; Thieret 1959; Gates *et al*. 1992a; Carbyn *et al*. 1998). Lake McConnell, the second largest Pleistocene lake in North America, covered an area of 240,000 km^2 and contained Great Bear Lake, Great Slave Lake, and

Lake Athabasca within its former basin (Cameron 1922; Smith 1994). Wave action in the ancient lake drew fine clay and silt particles deep into the basin, and deposited coarser sand and gravel as beach ridges (Day 1968). Fluvial processes in floodplains of the large river courses sorted soil particles in a similar manner (Day 1966; Day 1972). Dense, moderately impermeable soils flood easily and produce a high biomass of fine fuel loads that are able to burn frequently, two processes that allow sedges and grasses to have a competitive advantage over woody plants (Raup 1933; Moss 1953).

Free-roaming populations of wood bison presently occur in the Greater Wood Buffalo Ecosystem of the NWT and Alberta; north of the Mackenzie River in the NWT; in the Nahanni – Liard watershed shared by the NWT, British Columbia and Yukon; near Hay-Zama Lakes in Alberta; and in the area of the Yukon's Nisling River. In Alaska, where native wood bison herds were declared extinct in 1941, the Wood Bison Reintroduction Project finally saw the release of 130 wood bison into the wild near Shageluk in 2015. Wood bison had been brought to the Alaska Wildlife Conservation Center awaiting reintroduction (Michaelis 2015). This release is an important milestone in wood bison recovery.

NWT Distribution

As late as 420 years before present, wood bison occurred as far north as the Arctic coast (Harington 1990). Currently, there are three populations of wood bison in the NWT, known as the Greater Wood Buffalo Ecosystem, Mackenzie, and Nahanni populations (Figure 8, p.71). The Greater Wood Buffalo Ecosystem centres of abundance are largely contained within Wood Buffalo National Park, except for the Grand Detour subpopulation (mostly outside of the Park) and the Hook Lake subpopulation (completely outside of the park). These two subpopulations occupy the Slave River Lowlands, with the Grand Detour subpopulation being west of the Slave River and the Hook Lake subpopulation being east of the Slave River, both entirely within the NWT. Most of the Nyarling River subpopulation may be found in the NWT, although its southern extremities extend into Alberta. Except for a minor extension into the NWT, the Hay Camp subpopulation occurs mostly within Alberta. The Garden River and Delta subpopulations occur entirely within Alberta. As shown by Figure 8, p.71, the complete range of the Mackenzie population lies within the NWT, while the Nahanni population has extended part of its range into northern British Columbia and the southern Yukon.

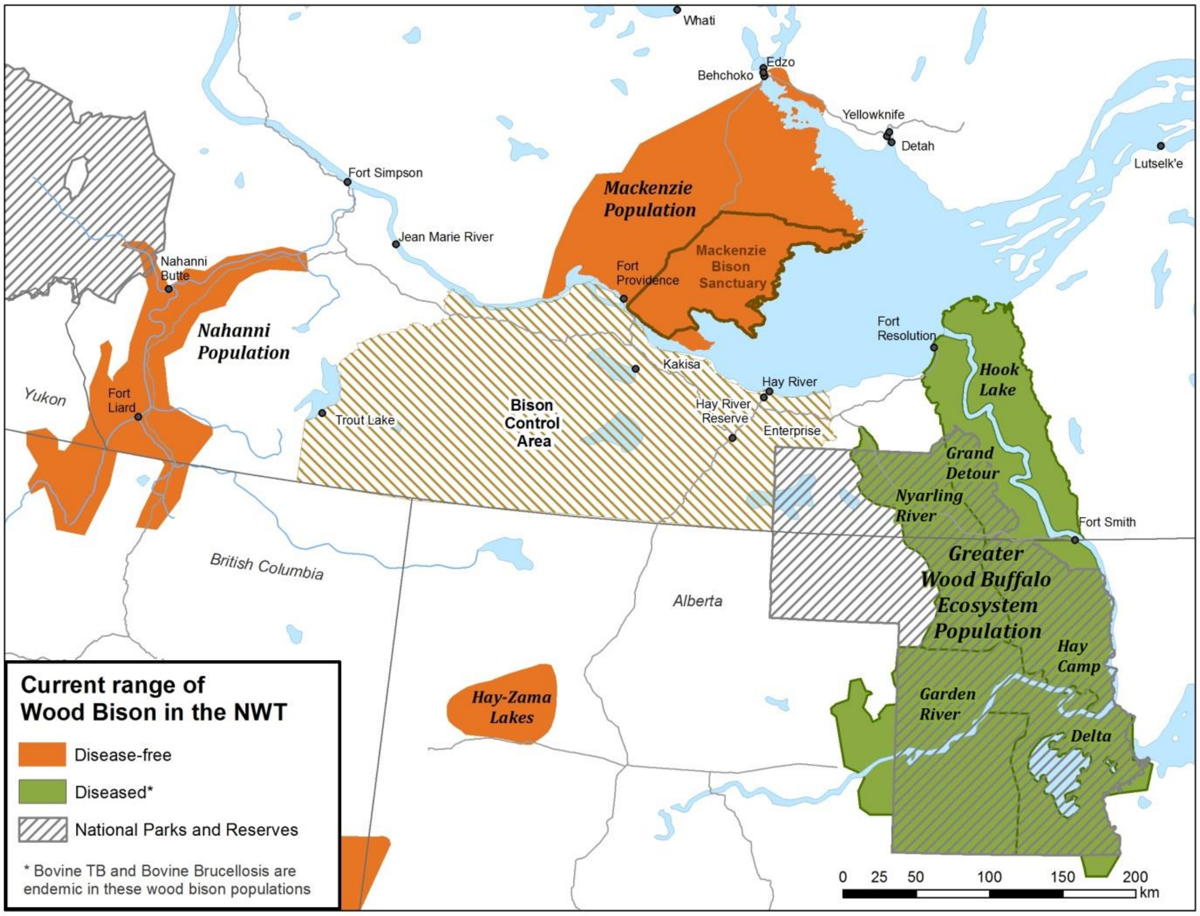


Figure 8. NWT wood bison distribution (map by B. Fournier and K. McGreish, ENR). Wood bison have also been observed outside core ranges.

The term ‘location’, as defined by the Species at Risk Committee (SARC) (2012), is a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the species present. For the Greater Wood Buffalo Ecosystem and Mackenzie populations, the most important threatening event is disease, whereas a mass drowning event is the most important threatening event for the Nahanni population. Because these populations are geographically isolated from one another and because the subpopulations within the Greater Wood Buffalo Ecosystem are interconnected to varying degrees, there can be considered to be three locations in the NWT.

SARC defines extent of occurrence as “the area included in a polygon without concave angles that encompasses the geographic distribution of all known populations of a species” (2012:22). Using this measure, the extent of occurrence for wood bison in the NWT (encompassing the Greater Wood Buffalo Ecosystem, Mackenzie and Nahanni populations) is approximately 147,540 km^2, calculated using a single minimum convex polygon around all three populations and subtracting the area of the polygon that occurs outside the borders of the NWT.

Area of occupancy is defined by SARC as, "the area within 'extent of occurrence' that is occupied by a species, excluding cases of vagrancy. The measure reflects the fact that the extent of occurrence may contain unsuitable or unoccupied habitats" (2012:22). The area of occupancy for wood bison in the NWT is approximately 43,237 km^2. This was calculated by summing the area totals of polygons drawn around each of the three NWT wood bison populations, and subtracting the areas of the polygons that occur outside the borders of the NWT.

The index of area of occupancy (IAO) is a measure that aims to provide an estimate of area of occupancy that is not dependent on scale. The IAO is measured as the surface area of 2 km x 2 km grid cells that intersect the actual area occupied by the wildlife species (i.e., the biological area of occupancy). The IAO for wood bison in the NWT is 46,976 km^2, calculated as the surface area of 2km x 2km grid cells overlaying the NWT range of wood bison (see Fig. 8, p. 71 for range map).

Search effort

After wood bison had reached the brink of extinction and the *Unorganized Territories Game Preservation Act* was passed in 1894 to protect them, officers of the North West Mounted Police were appointed as ex-officio game guardians. These guardians conducted patrols throughout the present and former range of wood bison in the NWT (Herschmer 1898; Jarvis 1907; Preble 1908; Routledge 1908; McLeod 1909; Mellor 1910; Seton 1911; McLeod 2011), focusing on locating the remaining wood bison, determining exact numbers, and evaluating whether the 1894 game act was effective.

When the Royal North West Mounted Police were relieved of their special supervision of wood bison in 1911, the responsibility was transferred to Game Guardians, under the direction of the Forestry Branch. All searches for wood bison were carried out on the ground with dog teams in the winter and by canoe and horseback during the rest of the year.

As a prelude to a Dominion reserve for wood bison, Seibert (1923) and Kitto (1924) carried out comprehensive surveys of bison distribution from 1920 to 1922. Their work determined the boundaries for the creation of Wood Buffalo Dominion Park in 1922 (or Wood Buffalo National Park as it was later renamed in 1930). Seibert's investigations were mainly focused in the NWT portion of the range as he mapped distribution and habitat. After the *National Parks Act* was passed in 1930, a warden service replaced the Game Guardians with cabins, roads, trails and telephone lines constructed throughout the park for improved bison monitoring efforts (Kitto 1930).

In an attempt to overcome difficulties of estimating the bison population from the ground, the first aerial bison survey in Wood Buffalo National Park was in 1931, with the cooperation of the Royal Canadian Air Force. All bison were to be photographed from orderly flight lines over the winter range, and a Park Warden was present for a direct visual count. Reports from the wardens described the outcome as unsatisfactory, mainly because of the problem with forest cover (Soper 1941). Despite these limitations (Soper 1941), aerial surveys were restarted by Oldham (1947) and have been used exclusively for population estimates ever since. In 1949, Fuller (1950) improved upon Oldham's strip transect techniques by surveying later in the winter, employing two observers, covering a narrower strip, and maintaining unidirectional flight lines.

Until 1974, surveys in Wood Buffalo National Park were limited to the high bison concentrations of the Hay Camp and Delta subpopulations, mainly to assist with the placement of vaccination corrals (Tempany and Cooper 1975). In 1975, coverage was extended to the Nyarling River and Grand Detour ranges, but survey effort in those areas varied among years (Bradley and Wilmshurst 2005). Surveys in the Slave River Lowlands followed the same flight lines as established by Rippin in 1971 for the next several years (Van Camp and Calef 1987), which would have limited search effort in peripheral areas. Minimum population estimates for the Hook Lake subpopulation in 1987, 1994, 1996 and 2000 were based solely on total counts because the herd had declined to such low numbers.

In 2002, permanent transects were established in the lower density areas of Wood Buffalo National Park, resulting in an annual effort exceeding 100 hours. Prior to the establishment of permanent transects in the high-density areas of Wood Buffalo National Park in 1991, search effort changed almost every year (Bradley and Wilmshurst 2005). Lower density areas that were covered by reconnaissance flights depended on available funding. Fifty survey hours were flown annually. To enable comparisons with 1990s level of effort, the increase in survey effort was compensated by buffering the flight lines (Bradley and Wilmshurst 2005). The 2009 bison survey was classified into four strata consisting of total count, strip transect, combined total count/strip transect, and reconnaissance of areas that were expected to contain few or no bison (Vassal and Kindopp 2010).

The 2009 Slave River Lowlands survey of the Hook Lake and Grand Detour subpopulations used over 23 hours of flying time, and was coordinated with Wood Buffalo National Park's bison survey. The ranges of the Hook Lake and Grand Detour subpopulations are fairly well defined within the Slave River Lowlands. Searches rarely cross the Taltson River. Although bison have occasionally been reported on the Precambrian Shield, east of the Taltson (Ogilvie 1979), it contains little potential habitat (Armstrong pers. comm. 2012).

Growth of the Mackenzie population was documented by total count surveys carried out every year. The procedure was to search 100% of the marl lake beds occupied by bison and the major trails connecting them. Initially, less than three hours of flight time were sufficient to account for virtually the entire population. However, after bison started invading the Mink Lake area in 1980, the survey flight time doubled and the number of bison observed became the minimum estimate for the population, with no accompanying estimate of precision. In addition to systematic surveys in 1989, 1992, 1996, 1998, and 2000, targeted searches to monitor movements were documented by field officers in the wildlife sightings appendices of their monthly reports (Chowns pers. comm. 2012).

As the Mackenzie population became too large and dispersed to rely solely on total counts, the study area was stratified into high, medium and low density units (Gates *et al*. 1991). The high density stratum consisted of the main meadows where bison concentrated, and which were also still covered by total counts. Systematic parallel transects covered medium and low density strata between areas of high density. Since the first Mackenzie bison anthrax outbreak in 1993 (Gates *et al*. 1995), regular, widespread searches have been carried out in the summer season for carcass detection and disposal (Dragon and Elkin 2001; ENR 2010). The 2013 re-survey of the Mackenzie population following an anthrax outbreak in the summer of 2012 utilized distance sampling, a survey technique particularly useful for estimating wildlife abundance in forested areas (Armstrong 2013b). Distance sampling collects data on the distances of the animals from randomly placed lines (Buckland *et al*. 2001).

In 1987, a bison-free management zone (Bison Control Area) was established south of the Mackenzie River and north of the Mackenzie Highway, between Mills Lake and Hay River, to prevent movement of brucellosis- and tuberculosis-infected bison from the Greater Wood Buffalo Ecosystem population into the ranges of the Mackenzie and Nahanni populations. In 1990, the control area was greatly expanded to the Alberta border, between Trout River and Wood Buffalo National Park (Gates and Gray 1992). Since then, the control area has been searched several times per year, by ground and by air, for the purpose of removing bison (Greig and Cox 2012).

The Nahanni population was established in 1980 when 28 wood bison from Elk Island National Park were released (Reynolds 1982). The population was monitored by surveys that tracked the total count and expanding distribution (Larter and Allaire 2007). Aerial surveys of the primary bison range in the Nahanni Butte and Netla and Kotaneelee rivers areas, the Liard River Valley and its islands from Flett River to Fort Liard, and the cutblocks in the La Biche River area of northeastern British Columbia were carried out in 1995, 1996, and 1997 to generate a minimum population estimate (Larter and Allaire 2007). However, these were not systematic aerial surveys of the population that could be replicated.

A biological program for the Dehcho Region was established in 2002, which included more regular monitoring of the growing Nahanni bison population (Larter and Allaire 2007). In 2003, information from local residents and the governments of British Columbia and the Yukon on bison distribution was added to the knowledge base for compilation of a map of the winter range of the Nahanni bison population. For the 2004 aerial survey, 1,288 km of parallel strip-transect lines were flown at 4 km intervals over the Nahanni population's winter range in the NWT, British Columbia and the Yukon (Larter *et al*. 2007). A similar survey of nearly 20 hours was carried out in 2011, except that the transect lines were increased to 2,155 km at 3.5 km apart (Larter and Allaire 2013). Because most of the Nahanni population's winter range is forested, with major river drainages, mountains and deep valleys bisecting it, seven bison were equipped with satellite collars to determine a sightability correction factor, and improve the delineation of the search area.

For more information on historical search effort, refer to *Appendix A3* (p. 221).

BIOLOGY AND BEHAVIOUR

Habitat requirements

Food

Meadow vegetation is essential for wood bison to meet their food requirements. Looman (1979) concluded that ‘meadow’ communities in boreal regions occur on soils with a high water table that are dominated by coarse sedges (*Carex* spp.) and reedgrasses (*Calamagrostis* spp.). Reynolds *et al*. (1978) differentiated dry meadows from wet meadows. However, the boundary between these two meadow types shifts according to precipitation. If lowland meadows become inundated in wet years, higher soil moisture compensates somewhat by boosting sedge-grass production in meadows at slightly higher elevations. A mosaic of lowland meadow and upland meadow is necessary to ensure adequate forage resources during changing climatic conditions.

Solonetzic soils, having chemical and physical properties conducive to the development of a form of true grassland, occur in the southern margins of wood bison range, but almost this entire habitat has been replaced by agriculture (Wilkinson and Johnson 1983). Although small remnants occur in the Alberta portion of Wood Buffalo National Park, none likely exists in the NWT (Schwarz and Wein 1997).

Coarse sedges have unique characteristics beneficial for satisfying the energy demands of wood bison through the long winters. A portion of the next spring’s shoots are formed the previous autumn and the biomass of this green standing crop available in winter may be quite high (Bernard and Bernard 1977). Reynolds *et al*. (1978) observed that when sedges freeze in the autumn, they retain digestible nutrients. During winter, these levels may actually be twice as high as in summer (Bernard and Hankinson 1979). After the long winters, bison capitalize on sedges’ ability to undergo high nutrient uptake at the beginning of the next growing season, and these plants do this most effectively when the supply of nutrients is low (Bernard *et al*.1988). In the Nahanni area (Larter and Allaire 2007), Slave River Lowlands (Reynolds *et al*. 1978), and Wood Buffalo National Park (Fuller 1966), sedges were found to be the main source of food. In the Mackenzie Bison Sanctuary, the proportion of sedges in the diet was highest in winter and midsummer, while intake of grasses and shrubs increased dramatically during spring green-up (Larter and Gates 1991).

Awned sedge (*Carex atherodes*) is the forage species most preferred by wood bison. The other species of coarse sedge (*C. rostrata*, *C. aquatilis*, *C. retrorsa*, and *C. bubulosa*) appear to be less palatable. Consumption of *C. aquatilis* seems to be more apparent in spring, possibly because it greens-up earlier than other forages, and in more nutrient-rich environments. Moss (1953) remarked about the wide ecological amplitude of *C. atherodes* as a leading dominant throughout the reed swamp – marsh – wet meadow – low grassland plant communities of northwestern Alberta. It thrives best in areas that are seasonally flooded with shallow water, and neutral to slightly alkaline pH (Jeglum 1971). Of all forage species tested in the Slave River Lowlands, Hawley *et al*. (1981b) found *C. atherodes* to have the greatest digestibility for bison. It is also highly profitable in digestible energy relative to the time required for cropping, chewing and swallowing (Fortin *et al*. 2002). In the Mackenzie Bison Sanctuary, Larter (1988) found *C. atherodes* generally had higher percent nitrogen content than *C. aquatilis* throughout the year, whether in wet or drier meadows.

Reedgrasses, especially bluejoint (*Calamagrostis canadensis*) and willows (*Salix* spp.), are highly preferred at certain times of the year and they are also associated with moist, fertile conditions. Reedgrasses have very low winter digestibility, whereas willows are most digestible in winter and show the least amount of change through the seasons (Hawley *et al*. 1981b).

Jensen *et al*. (2003) estimated that the area of suitable and critical habitat in the Mackenzie and Greater Wood Buffalo Ecosystem bison ranges actually contains more than 60% forest, and when bison used treed habitats, they tended to select aspen and jackpine stands. In their study of bison foraging in aspen habitats, Hudson and Frank (1987) found that the critical amount of forage biomass in summer and autumn to support these animals was 779 kg/hectare (ha), and autumn aspen leaves were a readily available bulking agent. According to Strong and Gates (2009), treed habitats in northern Alberta generally produced less than the amount of biomass needed for wood bison to maintain an efficient foraging rate, and did not provide adequate nutrition in winter. In the Mackenzie Bison Sanctuary, Larter and Gates (1991) observed forage quantity and quality becoming more homogeneous during autumn when bison dispersed amongst all habitats. Coniferous forests, which supplied the greatest biomass of lichen, were heavily used in this brief period. Because grass and other herbaceous forage is dependent on the amount of solar radiation that reaches the forest floor, a greater biomass of summer food is produced in recent burns, open woodlands and clearcuts (Raup 1933; Chowns 1986; Carbyn *et al*. 1993; Redburn *et al*. 2008). The availability of these drier habitats is most important when deep water and soft ground in wet meadows preclude bison use in summer and reduce year round grazing pressure on sedge meadows that are vital in winter.

Water

The range of plains bison may be restricted by the availability of water (e.g., Truett 1996). In summer, plains bison historically moved to water on an almost daily basis, and on occasion, thirst motivated long distance movements over several days (Hornaday 1889; Dary 1989). The selection of habitat patches by plains bison at Prince Albert National Park was influenced by distance to water (Fortin *et al*. 2003). Similar small scale movements of wood bison may be expected during periods of drought. Although these animals' requirement for forage plants growing in moist conditions usually predisposes them to close proximity to water, the Salt Plains of the Greater Wood Buffalo Ecosystem are left with large areas of brackish water in late summer that bison avoid.

Cover

This term has generally been defined as vegetation or topography that veils, conceals, shelters, or protects an organism from predators, unfavourable climate, or other adverse conditions. Wood bison habitat is typically interspersed with forest that is used for shelter, resting, ruminating and avoiding biting flies (Reynolds *et al*. 1978). The main anti-predator strategy for bison is to run for dense timber to rid themselves of their pursuers. Fuller (1960) believed that bison have much less chance of success against a wolf (*Canis lupus*) attack in the open. Dense coniferous forest canopies intercept snow and reduce wind velocities, resulting in lower accumulation and lighter falling snow that is not as susceptible to crust formation (Moen 1973). These conditions provide less of a mechanical barrier to bison movements.

Sheltered micro-climates appear to be an important factor in selection of winter feeding sites. During cold temperatures and high windchill, Fuller (1966) observed that bison split into smaller groups and moved into forested cover. Raup (1933) observed a March thaw followed by hard crusting that resulted in bison retreating to sheltered feeding areas where the thawing had less effect. Foraging often occurs in protected meadows where snow depth, density, and hardness are less than in windswept open sites (Reynolds *et al*. 1978).

Soper (1941) described parturient cows (cows about to give birth) as secretive and speculated that calving sites were in thick woodland retreats, where they remained until the new calf was mobile enough to join the post-calving aggregations. Calef and Van Camp (1987) postulated that the abundance of interspersed woodlands providing cover for parturition may be a mitigating factor for the lack of synchrony in wood bison calving, compared to bison of the open plains. The scarcity of information regarding the birth of calves probably attests to the level of seclusion that the maternal cows seek.

Space

As the largest land mammal in North America, wood bison require plenty of space. In their study of Mackenzie bison, Larter and Gates (1990) found home ranges to vary from 179 to 1,442 km^2, which is 4 to 100 times larger than those of other North American ungulates. The ranges of females were the most extensive, probably because female-dominated mixed herds required larger grazing areas, and these are separated by tens of kilometers of forest. Bull groups were observed using smaller habitat patches ignored by the mixed herds. According to Guthrie (1980), the high shoulder hump of bison permits a cantering gait that is not particularly rapid, but powerful and energy efficient for long distance movements between habitat patches.

Allometry is the study of how characteristics of living creatures change with body size. If there is a strong allometric relationship between body mass and home range of bison, then an allometric calculation can be used to anticipate the expected or ideal amount of space required by individuals in a population. Larter and Gates (1990) tested several interspecific regressions of body mass (M) and home range size (A) for females using the relationship $A = 4.9(M^{1.56})$ (Swihart *et al*. 1988) and determined a range size of 1,030 km^2.

Because of their large sizes and long life spans, ungulates tend to exist in populations at or near the environmental carrying capacity (McCullough 1999). This is particularly apparent if the ungulate has enough space to move away from its predators at the critical calving period (Fryxell *et al*. 1988; Fryxell and Sinclair 1988), or if it is too large and dangerous to be easily killed (Sinclair 2003). Relatively sedentary ungulate populations tend to be more regulated by predation, especially if alternate prey is part of the system. McDonald (1981) suggested that human predation may have been sufficient to keep wood bison populations below carrying capacity.

Movements

Wood bison have rarely been known to carry out regular seasonal migrations and their movements may best be described as nomadic within their home ranges. An exception is the spring movement into the Salt Plains, and subsequent abandonment in late summer when the availability of fresh drinking water diminishes. In historic times, large scale movements of bison herds could be controlled by native people by alternately greening and burning traditional hunting grounds (Pyne 1997). Bison are often faithful to core areas and at a finer scale they have seasonal preferences. For feeding, wet meadows are more accessible in winter when the substrate is frozen. Drier sites contain green forage that is most digestible in spring and summer. In late summer and autumn, smaller groups disperse through the forest.

Some movements may be stimulated by predation, adverse snow conditions or flooding. Carbyn *et al*. (1993) tracked a bison herd in Wood Buffalo National Park for 86 km after a wolf attack. Calef and Van Camp (1987) observed a southward movement from normal winter range in the Slave River Lowlands after a snowstorm was followed by freezing rain. In Prince Albert National Park, bison avoided areas of high snow-water equivalent in winter (Fortin *et al*. 2009). After flooding of the most important sedge meadows in the Mackenzie Bison Sanctuary reached its height in spring 1992, many hundreds of bison moved to the drier Great Slave Lake shoreline meadows, and at least 44 animals travelled south into the Bison Control Area (Gates *et al*. 1992b). After high water levels in the Peace – Athabasca Delta during the spring of 1997, Joly (2001) documented 22% of his collared bison crossing the Peace River northward from the delta, then a return of 14% of them by summer.

Although bison are good swimmers, they are reluctant to enter the Mackenzie River and generally avoid the rough ice in winter. In the Slave River Lowlands, bison rarely cross the

Slave River, yet some notable traverses have probably occurred (Calef 1976; Calef and Van Camp 1987; Gates *et al*. 2001b). In contrast, the Nahanni bison regularly cross the narrower Liard and South Nahanni rivers year round (Larter *et al*. 2003; Larter and Allaire 2007).

Bison rarely embark upon long distance journeys through inhospitable terrain, unless they are aware of favourable habitat at their destination. They also concentrate their movements along cutlines and highway corridors (ENR 2010). Joly (2001) tracked one radio-collared animal from Hay Camp to the Grand Detour area of the Slave River Lowlands west of the Slave River, and another from Hay Camp to the Nyarling River area. Range expansion usually begins with pioneering bulls (Larter *et al*. 2000).

Life cycle and reproduction

Age groups

Bison are usually classified into seven different sex and age classes based upon body size, pelage, horn shape and horn wear (Fuller 1959; Gates *et al*. 1991; Komers *et al*. 1993):

- Calves – Young of the year of both sexes, typically being born in April-May with calving largely completed by July. Their reddish-tan coats turn dark chocolate brown at about three months of age and by four to six months horn nubs may be visible.
- Yearlings – Animals one to two years old of both sexes with spike-shaped horns of 10-30 centimetres (cm) in length. Body size is smaller than adult females.
- Cows or adult females – Animals of two years and older in breeding condition. No ‘spike-horn’ stage. Their horns are more slender than those of all males and have a pronounced recurve toward the middle line of the skull resulting in a distinct S-shape in older cows. The front of the skull is narrower than that of adult males.
- B1 males or juvenile bulls – Two, three and some four year olds. ‘Spike-horns’ point upward or outwards and always point away from each other. Body size is similar to or slightly smaller than cows; however, the horn base is wider than cows.
- B2 males or sub-adult bulls – Animals four to six years of age. Starting to become successful breeders. Horn base is wider than cows and the horns point straight up or towards the middle line of the skull. The hair on the head and shoulders is shorter than in adult bulls. Body size ranges between that of cows and adult bulls.
- B3 males or younger mature adult bulls – Animals of seven to 12 years of age. Horns are curved toward the middle line of the skull and may show the start of wear on the tips. Hair on the chest and head is fully developed leaving no open space between the horns. Body size is much larger than cows.

- B4 males or older mature adult bulls – Animals of at least ten years of age. The distinction between B3 males and B4 males is the noticeable wear on the horns in B4 males, often resulting in wide blunt ends.

Age at maturity

At the Elk Island National Park Isolation Area, weights of female bison begin to level off (asymptotic body weight) by six years of age, and females achieved their maximum body weight at 10 years. Male bison reached an asymptotic body weight at eight to nine years and maximum body weight by 13 years (Olson 2002; Reynolds *et al*. 2003).

The breeding success of sub-adult males is suppressed when there is competition with older bulls; therefore, males generally do not begin to breed until they are five or six years old (Komers *et al*. 1994a, 1994b). The age of highest breeding success for males was seven to nine years.

Average longevity of bison has never been determined. McHugh (1958) documented females in captivity living into their fourth decade. Fuller (1966) identified the oldest age class from the reduction slaughters of the 1950s as up to 30 years, but it is unlikely that many animals in the wild live past 20 years (Meagher 1973). Meeting nutritional requirements is hampered when teeth wear to the gumline. Haynes (1984) found tooth wear in Wood Buffalo National Park bison to be much lower than in plains bison, and he attributed this to dietary differences. Grasses, the main food of plains bison, contain more abrasive silica than the sedges that wood bison largely depend upon, and more gritty material is ingested when grasses are grazed from drier substrates. Horsetails (*Equisetum* spp.) contain high levels of silica. Nahanni bison are particularly susceptible to tooth wear (and likely shorter lifespans), compared to other wood bison because of the unusually high amount of these plants in their diet (Larter and Allaire 2007).

Sex ratio

Upon examination of 840 mature females at the annual bison reduction slaughters in Wood Buffalo National Park from 1952-1956, Fuller (1960, 1961, 1966) found the primary sex ratio (in utero) to be 112 males: 100 females, or 53% males. Palmer (1916) calculated a similar ratio of 54% males from a sample of 460 bison from United States (U.S.) national herds. The adult sex ratio is difficult to determine as accurately because composition surveys usually target herds of mixed sex and age in open habitats, while bull groups that spend more time in forest cover are more likely to escape detection. The males of many ungulate species often have higher rates of early mortality than females. This appears to be true for wood bison and the sex ratio would be expected to skew more towards females as the average age of the population becomes older.

Calef and Van Camp (1987), in a study of population dynamics between 1974 and 1983, suggested that hunting may favour higher survival of females if bulls are selected for their size and trophy value, as in the Hook Lake subpopulation where the ratio was 32 males: 100 females (24% males).

From a sample size of 1,156 in the entire Mackenzie bison range, Gates *et al*. (1991) determined the June 1989 adult sex ratio to be 94 males: 100 females (48% males). However, the sample subset of 895 from the Mackenzie Bison Sanctuary showed a ratio of 83 males: 100 females (45% males). Where range expansion was being led by pioneering bulls in the Mink Lake area of the Mackenzie population, they found the proportions to be significantly different ($\chi^2 = 16.18$, df = 1, $P > 0.05$) at 150 males: 100 females (60% males). Gates *et al*. (1995) determined the July 1993 adult sex ratio to be 78 males: 100 females (44% males) from a sample size of 473 in the Mackenzie Bison Sanctuary. With a ratio already tipped in favour of females, the anthrax outbreak that began three weeks later removed 119 more males than females from the population.

In 2013, the Mackenzie ratio was 87 males: 100 females (47% males), from a sample size of 169. Since 1999, the sex ratio has averaged 86 males: 100 females, and ranged between 66 and 105 males: 100 females (40-51% males) (Armstrong 2013a).

From 1999 to 2006, the sex ratio in the Nahanni population averaged 92 males: 100 females, and ranged between 65 and 121 males: 100 females (39-55% males) (Larter and Allaire 2007).

Generation time

Gross *et al*. (2006) used the Carey (1993) formula to calculate generation times for U.S. National Park Service bison herds. Experimental removal of old animals resulted in populations that consisted almost entirely of animals less than eight years old (which may be somewhat comparable to a sudden, sharp increase in population numbers). Removal of younger animals resulted in populations with an unusually high proportion of older animals, which may be analogous to a declining population with low recruitment (Gross *et al*. 2006). Variation in age structure changes generation time. A shift to a greater proportion of older cows in a population causes generation time to lengthen. Generation time of females ranged from less than five years when animals eight years of age and older were removed from reproduction, to a maximum of 12.7 years when virtually all breeding cows were very mature. Gross *et al*. (2006) also simulated the effects of varying cow-calf removals, random removals and the target proportion of males, on average generation time of cow and bull bison. For a scenario with adult sex ratios near parity and random removals of animals, the average generation time was approximately seven years. Hedrick (2009), using the average of highest reproductive success, also estimated generation length for plains bison at seven years.

An average generation time of seven years is probably an equally valid estimate for wood bison. Theoretically, during the lifespan of an animal, there could be at least six overlapping generations.

Fecundity

Most of the knowledge about bison productivity has been derived from studies of plains bison. Wild plains bison have only a single ovulation per year and the gestation period has been estimated at 285 days or nine months (Haugen 1974). Ovulation and gestation time in wood bison is likely similar; Armstrong pers. comm. (2015) has noted a gestation period of 270-300 days (9-10 months) in wood bison in the NWT. Evidently, nutritional condition has a direct effect on the fecundity of bison. For example, McHugh (1958) reported an average pregnancy rate for mature cows at 90% on the National Bison Range in Montana, as opposed to 35% observed by Lott and Galland (1987) for undernourished bison on Santa Catalina Island, California.

Although mature females in some other plains bison herds bear calves every year (Rutberg 1984; Shaw and Carter 1989; Wolff 1998), this has not been apparent in Yellowstone National Park. Meagher (1973) found that approximately 50% of sexually mature cows produced calves, and suggested that the majority of females produced calves every other year.

Similarly, a 1990 to 1993 study in Yellowstone National Park by Kirkpatrick *et al*. (1996) showed a 48.2% annual pregnancy rate with 85% of all mature cows becoming pregnant on alternate years, and only 15% of lactating cows being fertile. They also found that more than 80% of all pregnancies (in either lactating or non-lactating cows) occurred in cows older than three years, and that 100% of all pregnancies among lactating cows occurred in cows older than four years. These results were consistent with bison herds subjected to harsh environments or poor nutrition. Adverse environmental conditions seemed to contribute to prolonged lactation and delayed ovulation the following season, and these effects were more pronounced for younger cows. Of the three variables Kirkpatrick *et al*. (1996) found to be influencing the reproductive success of Yellowstone National Park bison, environmental conditions such as winter severity appeared to have more profound impacts than either age or lactational status.

Mature wood bison females usually do not breed every year (Fuller 1966; Soper 1941). For Wood Buffalo National Park, Fuller (1961, 1966) estimated the average conception rate of an adult female to be 67% during her lifetime. This was at a time in the 1950s when there were no reports of harsh environmental conditions for the bison population. Calef (1984) suggested that in some years all cows in the Mackenzie population would have been bearing calves in order to achieve the high rate of increase reported for this population in the first two decades following re-introduction (26%). Reynolds *et al*. (2003) reported a relationship between density and fecundity in bison at the Elk Island National Park Isolation Area.

Embryos from cows that were lactating tended to be smaller than those from cows not lactating (Fuller 1961, 1966) and Green and Rothstein (1991) found the young born to females following a year of not breeding were larger and more fecund than the young of females that reproduced the previous year. The highest reproductive success for females is between 3 and 12 years of age. Wilson *et al*. (2002) and McHugh (1958) reported a significant decrease in pregnancy after age

12, although females may continue to breed until more than 16 years of age (Green 1990).

Fuller (1961, 1966) investigated the sexual maturity of bison during the annual reduction slaughters in Wood Buffalo National Park. He found some pregnant yearling females that had conceived when they were about 15 months of age. This ranged between 4% at Hay Camp and 12% in the Peace – Athabasca Delta. Among females, 40% of two year-olds and 52% of three year-olds had bred for the first time. Of the few male bison studied, 1 of 6 yearlings, 3 of 8 two-year-olds and all six three-year-olds had attained sexual maturity. The age of first successful reproduction is expected to be delayed by brucellosis in bison of the Greater Wood Buffalo Ecosystem. Most animals abort the first pregnancy following infection but will usually carry subsequent pregnancies to term (Canadian Food Inspection Agency [CFIA] 2012).

Physiology and adaptability

Physiological requirements

The voluntary feed intake for bison has been calculated to be 0.009 kg/kg body mass/day for sedge, and 0.011 kg/kg body mass/day for grass (Richmond *et al*. 1977). On a sedge diet, Hawley *et al*. (1981a) measured an average weight gain of 0.42 kg/day in summer and 0.04 kg/day in winter. Bison probably need to consume water every day (McHugh 1958).

Neither the upper physiological limit of heat tolerance in summer, nor the lower limit of cold tolerance in winter has ever been determined. Beringian bison were able to thrive in periglacial environments where the winters were colder than where wood bison live today (Guthrie 2001). Heat tolerance is likely to be high if plains bison inhabiting the American southwest are any indication.

Foraging habits

In their analysis of tooth microwear, Rivals and Semprebon (2011) found the wood bison sampled to be grazers to the same extent as plains bison, despite what had been reported about their feeding ecology. Although Beringian bison were grazers, other Pleistocene bison sampled were graze-dominated mixed feeders, or browse-dominated mixed feeders. Wood bison are generalist herbivores that specialize at grazing, meaning that they usually select sedge-grass food patches and then consume a variety of herbaceous plants according to their abundance (Reynolds *et al*. 1978). For example, in the Mackenzie Bison Sanctuary and the Yukon, lichens constitute a significant part of the bison diet in the autumn (Larter and Gates 1991; Fischer and Gates 2005), whereas this type of plant material is less important in Wood Buffalo National Park (Raup 1933). Horsetails are a major dietary component for Nahanni bison (Larter and Allaire 2007), but not so much in Wood Buffalo National Park (Raup 1933), and have not been identified in the diets of other populations.

Although bison are primarily grazers, they will supplement their diet by browsing on woody vegetation. Introduced plains bison near Farewell, Alaska, feed on willows (*Salix* spp.) almost exclusively in summer and a mixture of willows and shrubs in the autumn because of their availability. The animals do not return to sedge-grass meadows until winter (Waggoner and Hinkes 1986). Hawley *et al*. (1981b) determined that willows in the Slave River Lowlands had high digestibility in winter and suggested if snow depth or ice conditions forced the bison to browse extensively, willow may be an important source of energy. In 1987, decreased precipitation in the Mackenzie Bison Sanctuary reduced the standing crop of all forages, especially sedges in the preferred summer foraging habitat (Smith 1990). This was offset by higher consumption of grass and willow, indicating the capability of wood bison to broaden their diet when sedge biomass declines (Larter and Gates 1991).

The quantitative model of the ‘forage maturation hypothesis’ (Fryxell 1991) predicts that the food intake of ruminant ungulates is constrained by availability at low forage biomass, and by digestibility at high forage biomass. Bergman *et al*. (2001) observed that *C. atherodes* digestibility declined with increasing biomass, while short-term sedge intake rates by wood bison increased with decreasing biomass. This indicates that bison behave as time minimizers rather than energy maximizers. The adaptive value of this trait is that bison can spend minimal time grazing in the open, and more time digesting a large volume of low quality food in cover where they can be less exposed and more alert to predation. Hudson and Frank (1987) found that bison compensated for low biomass in boreal aspen habitats by foraging more efficiently, and suggested that efficient foraging on grassy swards at low biomass density is a competitive advantage where forage is limited and there are few opportunities to forage selectively.

Preferred forage is sensitive to overgrazing and may be replaced by less palatable species such as common spike-rush (*Eleocharis palustris*) if grazing is excessive (Millar 1973). Bison have lesser tendencies than cattle to overgraze their range, and they generally only bite off the top third of the plant (Reynolds *et al*. 1978). Bison show strongest selectivity for leaf tissue and strongest avoidance of stem tissue when grazing tall swards of sedge (Bergman *et al*. 2000). In the Mackenzie Bison Sanctuary, Smith (1990) found that moderate grazing increased productivity in many forage species mainly by reducing the accumulation of dead plant material.

Susceptibility to environmental changes

Compared to most other North American ungulates such as deer (*Odocoileus* sp.), moose (*Alces alces*) and caribou, bison are slow to colonize new range if the current range deteriorates, perhaps because high quality wood bison habitat tends to be patchier and more insular on the landscape than for other species. Where and when to settle is weighed between the benefit of searching for high quality habitat, and the cost of mortality due to increased searching time (Shachak and Brand 1988).

Bison are particularly susceptible to agricultural development because both bison and farmers share a penchant for extensive level tracts of fertile soils.

Susceptibility to extreme conditions

There are many adversities faced by bison that are compounded by more than one factor. Bison can tolerate shallow, soft snow, but deeper, longer lasting snow tips the energetic balance against them. Bison have a lower morphological index for snow-coping ability than wolves, making them easy prey in winter (Telfer and Kelsall 1984). In the late 1800s, there was an apparent mass mortality of bison near the Peace River after heavy snowfall was followed by rain and refreezing (Ogilvie 1893; Whitney 1898). The ensuing thick crust impaired foraging and mobility of bison and allowed hunters easy access to the herds. MacFarlane (1908) mentioned testimony about wood bison herds perishing in the Peace River region because of excessively deep snow, and how vulnerable they were to wolves and hunters under these conditions.

Calef and Van Camp (1987) suggested that the severe snow conditions of 1974-75 in the Hook Lake range may have caused bison there to become nutritionally stressed and more vulnerable to wolf predation. After taking advantage of the weakened bison, the wolves may have increased in numbers and exerted additional predation pressure on the surviving bison.

Van Camp (1975) concluded that undisturbed snow deeper than 50-60 cm in the Elk Island National Park Isolation Area hindered the movements of calves and undisturbed snow deeper than 65-70 cm impeded adults. In the Slave River Lowlands, Reynolds and Peden (1987) observed that 53-60 cm of snow curtailed extensive movements by calves, and high snow density and hardness related to spring thaw hindered foraging (Reynolds and Peden 1987). In Prince Albert National Park, Fortin *et al.* (2003) observed that bison were less likely to visit meadows when snow depth was 38 cm deep, but during a winter with less snow (27 cm), meadow use was unaffected by snow depth.

In Yellowstone National Park, bison shifted feeding sites when snow depth exceeded 127 cm (Meagher 1971). Fuller *et al.* (2007) found spring calf to adult ratios in Yellowstone National Park bison to be negatively correlated with the winter snow pack, and Delgiudice *et al.* (1994) documented physiological stresses that bison suffered during winter nutritional deprivation.

Adaptations to adverse conditions

Bison have a dense, woolly undercoat overlain by longer guard hairs, which makes them resistant to cold temperatures (Peters and Slen 1964; Meagher 1973). Bison feeding activities are not nearly as limited by wind or cold as in cattle (Hawley 1987). Normally, the physiological response of an animal to cold is an elevated metabolic rate. For bison calves, Christopherson *et al.* (1978) found that metabolic rate decreased from 0^0 C to minus 30^0 C, most probably as an adaptation to conserve energy. However, a slight windchill coupled with minus 30^0 C increased the metabolic rate. Compared to cattle, bison are more efficient at digesting forage low in crude protein and high in fibre (Peden *et al.* 1974; Richmond *et al.* 1977; Hawley 1987). Maximum digestion of a limited, low quality food supply allowed metabolism to shift from growth to maintenance during winter as a survival mechanism.

Wood bison have longer limbs than plains bison (McDonald 1981), providing an advantage in deep snow. Of all North American ungulates, bison have the greatest sexual dimorphism in foot loadings, with females much lighter than males (Telfer and Kelsall 1984). Relatively low foot loading gives females an energetic advantage over males in movement over wind-packed snow. Separate winter ranges allow wider use of habitat and less grazing pressure on forage resources. Bison forage in winter by swinging their heads to 'crater' through the snow. When snow is deep, bison save energy by making trails, switching to higher biomass sedge meadows and coordinating cratering activities (Van Camp 1975). They also have the ability to browse tall shrubs and saplings above the snow line.

Although the winter tick (*Dermacentor albipictus*) is a serious ectoparasite of moose, Mooring and Samuel (1998) found that plains bison in Elk Island National Park harboured lower tick densities than sympatric moose, elk (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*). Grooming behaviour and dense pelage are adaptations of bison that reduce ectoparasite infestations. McMillan *et al*. (2000) suggested that among the plausible explanations for wallowing behaviour in bison, only seeking relief from biting insects was consistent with both the annual and daily patterns associated with this activity.

Interactions

Conspecifics

Bison are gregarious animals and fusion and fission of herds is quite common (Fuller 1960). Cows with calves and young bulls may form large mixed herds. With the exception of the breeding season, bison bulls roam alone or in small temporary groups. Unfortunately, the bison's gregarious behaviour facilitates greater opportunities for disease transmission (diseases are discussed in more detail in *Threats and Limiting Factors*, p. 119). In their analysis of radio tracking data, Chen and Morley (2005) found Wood Buffalo National Park bison to have a pronounced fidelity to subpopulations and strongest cohesion and coordinated movements during summer.

Komers *et al*. (1993) observed that males were often more solitary with advancing age. During the rut, dominant bulls often tolerated younger males. Males seemed to leave female groups to recover from battles, but not to search for estrus cows. As female groups frequently merge and split, males are able to encounter many potential mates by remaining with a group. Cows with calves tended to aggregate, possibly because of similar high nutritional demands, and as a defense against wolves.

In winter, foraging with an increasing number of conspecifics was advantageous for Prince

Albert National Park bison because it strengthened their selection for the highly nutritious *C. atherodes* (Fortin and Fortin 2009). The behaviour of other herd members may reveal the location of suitable food patches hidden beneath the snow.

In the Konza Prairie in Kansas, Post *et al*. (2001) found that bison calves had the highest quality diets of all groups in the population, and mature bulls had the poorest diets. Bulls could compensate for the low energy food by consuming greater amounts, and this would reduce competition for higher quality forage that was more vital to the calves and lactating females.

Within polygynous mating systems, selection for body size and aggressive behaviour in males restricts access to females to certain age classes of males (Jarman 1983). If the number of bulls mating is small, genetic diversity will potentially be lower. Compared to the large breeding aggregations of plains bison where access to females is controlled by a dominance hierarchy (Lott 1979), the mating behaviour of wood bison may more closely resemble a harem system (Wilson *et al*. 2002). As they break up into smaller groups in the forest, wood bison increase the number of breeding clusters available. This could allow subordinate bulls greater opportunity to contribute to the gene pool (Komers 1992), or, alternatively, less opportunity if the harems are well defended (Wilson 2001; Wilson *et al*. 2002). Although the age at which male bison may breed is a selective factor, Bork *et al*. (1991) found that most Elk Island National Park Isolation Area bulls will eventually mate through the course of their lifetimes. They also suggested that increased random mating within a bison population is facilitated by extensive movements through home ranges and thorough population mixing.

Descriptions of the social organization of wood bison may be found in Soper (1941), Fuller (1960), Calef and Van Camp (1987), Chowns (1987), Larter and Gates (1990), Carbyn *et al*. (1993), and Komers *et al*. (1993). Wood bison form post-calving aggregations in June and July with the largest groups occupying the most open habitats. With the onset of rut in mid-July, the herds fragment into smaller groups and larger herds do not begin to reform until early winter.

Humans

Detection of human scent is one of the greatest stimuli to cause the flight reaction in bison (Fuller 1960). Despite this, when not being harassed, bison easily become habituated to human presence and infrastructure. For example, from the time they were first constructed throughout bison range, bison have displayed a tendency to congregate along roads (Fuller 1960), and have become a traffic hazard in many areas (ENR 2010). Bison also utilize cutblocks and linear roadways cut in forested areas in the Liard Valley of the NWT and British Columbia (Larter pers. comm. 2012).

Calef (1976) reported that bison reaction to aircraft was highly variable. At normal survey altitudes, some groups began to run away when aircraft were as much as two miles (3.2 km) away. Others did not move until circled or approached at low altitude. Some groups ran for long distances and others stopped after the aircraft headed away. Calef (1976) also observed that bison reaction to land vehicles was variable and the animals quickly settle down when not being pursued. Humans walking or on horseback could usually approach to within 400 m using tall grass and willows as a screen.

Predators

The only scientifically documented source of predation for bison is wolves. However, Chowns (1987), Van Camp (1987) and Carbyn *et al.* (1993) speculated that black bears (*Ursus americanus*) may also be minor predators. They are very common in meadow habitats during the calving season, presumably because of the availability of fresh green forage. After hibernation, bears need to restore their protein requirements (Schwartz and Franzmann 1991) and these activities overlap with calving bison. Likewise, calving Nahanni bison may be exposed to grizzly bear (*Ursus arctos*) predation. Reports of grizzly bear attacks on bison in other parts of North America are rare (Roe 1970; MacNulty *et al*. 2001; Wyman 2002). Wolverines (*Gulo gulo*) have never been implicated as a predator, but they occur in bison habitat and are capable of killing other young ungulates.

When predator-prey relationships are near equilibrium, prey has a higher probability of escaping than being killed, unless a vulnerability factor appears that tips the advantage to the predator. Fuller (1966) considered the three classes of bison most vulnerable to predation to be calves, the aged, and the injured. In Yellowstone National Park, Smith *et al*. (2000) observed that wolves killed primarily calves and debilitated older adult bison. A study by Husseman *et al*. (2003), which compared wolf and cougar hunting strategies, found that the longer chases and lower capture success of wolf packs had a stronger culling effect on disadvantaged prey than did ambush hunting by cougars. Selectivity for weakened prey may be due to the victim's slower avoidance behaviour, decreased awareness, reduced stamina, and possibly visual, scent, or behavioural cues (Wild *et al*. 2011). For example, bison suffering from disease-induced lameness should be more vulnerable to wolves (Tessaro 1989; Tessaro *et al*. 1992).

In their Wood Buffalo National Park study from 1979 to 1981, Carbyn *et al*. (1993) observed that wolves focused primarily on herds containing calves, rather than lone bison or bull groups. Carbyn and Trottier (1987) found that anti-predator strategies were highest in maternal bison when the calves were young. Defense strategies employed by calves included running to their mothers, a herd, the nearest bull, the front and center of a stampeding herd, and water bodies (Carbyn and Trottier 1988). When fleeing from wolves in open areas, cows with young calves took the lead, while bulls often were seen at the rear of the herds. Cows and particularly bulls were sometimes seen defending calves. Carbyn *et al*. (1993) and Larter *et al*. (1994) observed that after high early mortality rates, vulnerability of calves gradually decreased through their first year of life.

Because group size varies according to bison abundance, Carbyn *et al*. (1993) found that wolves could be encountering a stable number of bison groups, but smaller groups as bison numbers decline. If the functional response of wolves is related to the number of bison groups and not the number of individual bison (Huggard 1993), the killing rate would be expected to stay high until bison reach very low numbers.

Wolf packs in bison range often have overlapping territories and some packs seem to be tolerant of others (Van Camp 1987; Carbyn *et al*. 1993). These may be adaptive mechanisms to deal with the spatial behaviour of bison, as a wolf-bison predator-prey relationship may be less constrained by territorial behaviour.

In his review of wolf populations in the NWT, Mair (1954) suggested that in a stable population, one quarter of the adults would be lost each year, but there are a number of factors that periodically increase the loss. Wolves are susceptible to outbreaks of rabies, distemper, mange, and parvovirus, but the effects of these diseases on northern wolf populations is poorly known (Brand *et al*. 1995). During wolf studies in Wood Buffalo National Park from 1951 to 1952, Fuller and Novakowski (1955) discovered the pup to adult ratio to be 1 to 4 instead of 3 to 1 as would be expected. They suggested this to be indicative of a depressed wolf population suffering significant losses of young in the first six months, probably due to disease. Recent growth of the Park's bison population may be indicating that the wolf population has declined because of disease or reduced prey availability (Joly and Messier 2004b).

While studies of predator-prey interactions have focused on the demographic effects of wolves killing bison, 'risk effects' on bison have never been examined. Risk effects may become apparent when prey alter their behaviour in response to predators. Although anti-predator strategies counter direct mortality, they may also carry costs that have adverse impacts on prey demography. Preisser *et al*. (2005) listed some of these costs as reduced energy income, energetic investment in defensive structures, lower mating success, increased vulnerability to other predators, and emigration. Wolf predation risk in the Greater Yellowstone Ecosystem appears to negatively affect progesterone levels in female elk, leading to reduced calf production (Creel *et al*. 2007). Also, lower forage intake of elk in the presence of wolves resulted in nutritional deficits that threatened reproduction and winter survival (Christianson and Creel 2010). Risk effects can be large and if their influence on population dynamics is ignored, reduced reproduction is easily mistaken for limitation by food supply (Creel and Christianson 2008).

Competitors

Although wood bison often share the landscape with moose, elk, woodland caribou (northern mountain and boreal ecotypes), white-tailed deer, mule deer (*Odocoileus hemionus*) and possibly the stone subspecies of mountain sheep (*Ovis dalli stonei*), there is less congruency at finer habitat scales. Little dietary overlap exists between wood bison and these other species (Gogan *et al*. 2010), except where the bison's diet has a high willow or lichen component. Willow is the most important food for northern moose, and woodland caribou depend on lichens.

Two species are considered to be in competition when the presence of one leads to a reduced population of the other. They may be in 'exploitative competition' for resources or exhibit 'apparent competition' if they share a common predator (Holt 1977). A single prey type limits a predator's numbers by one feedback pathway. Apparent competition, also known as 'competition for enemy-free space' (Holt and Lawton 1994) may occur if the entry of an alternate prey species increases the density of the predator by expanding its resource base.

When there is a choice between two ungulate prey species that range in body size, wolves tend to select the smaller species (e.g., Murie 1944; Mech and Frenzel 1971; Carbyn 1983; Bjorge and Gunson 1989). This may also apply to the choice between bison and smaller ungulates. MacNulty (2002) found that bison in Yellowstone National Park were twice as likely as elk to charge wolves, and elk were five times more likely to be attacked by wolves. He also reported that wolves had a 20% kill success rate when attacking elk, but only 2% success with bison. Garrott *et al.* (2007) found that higher vulnerability and stronger wolf selectivity for elk resulted in an abrupt dietary shift occurring only when elk became very rare relative to bison.

When Soper (1941) carried out his studies in Wood Buffalo National Park during the early 1930s, woodland caribou were distributed mainly in the Caribou Mountains and barely reached the bison range from the west, much the same as it is today. He stated that in former years, presumably when the bison population was extremely small, woodland caribou occurred throughout the bison range. Joly and Messier (2005) suggested that wolves relying on moose (possibly in the Nyarling range where predation on bison was low) would incorporate bison into their diet if they rose to some threshold density, and continue until bison reach very low density.

According to Jacobson (1976), Kimble (pers. comm. 1981), and Calef (1984), woodland caribou and moose were abundant, and wolf numbers were very low on the bison range in the 1960s and 1970s. Compared to surveys in 1965 and 1971, woodland caribou and moose populations of the Mackenzie Bison Sanctuary appear to have dropped precipitously to 1987, while the resident wood bison population grew exponentially from a few dozen to 1,718 animals during the same time period (Gates and Larter 1990). A study in the Mackenzie Bison Sanctuary and Mink Lake area provided evidence that wolf populations that are buoyed by high bison densities can destabilize the moose populations and exacerbate their decline (Larter *et al.* 1994). A significant decline in the moose population seemed to be confirmed by Bradley *et al.* (1998) and Bradley and Johnson (2000).

In the Nahanni bison range, moose are abundant and are the primary prey of wolves. Evidence of wolf-killed bison has yet to be reported (Larter pers. comm. 2012). The population of about 400 bison may not yet be near the threshold that changes predator-prey relationships and results in a prey switch for wolves.

STATE AND TRENDS

Population

Abundance

Table 2. Population estimates from surveys between 1971 and 2014 (the Nyarling River, Grand Detour, and Hook Lake subpopulations are the only Greater Wood Buffalo Ecosystem subpopulations that occur within the NWT).

			Greater Wood Buffalo Ecosystem		
Year	**Nahanni**	**Mackenzie**	**Nyarling River**	**Grand Detour**	**Hook Lake**
1971	-	-	-	336	1701
1972	-	111	-	-	-
1973	-	122	-	-	-
1974	-	152	-	338	1516
1975	-	237	-	232	1013
1976	-	-	-	167	736
1977	-	356	-	149	605
1978	-	410	-	196	558
1979	-	580	-	94	444
1980	28	645	-	240	386
1981	14	668	22	231	361
1982	-	712	-	-	-
1983	-	980	48	198	316
1984	-	-	35	144	-
1985	-	-	12	58	-
1986	20	-	-	-	-
1987	25	1718	145	6	183
1988	-	-	5	71	-
1989	40	2431	36	118	-
1990	-	-	112	56	-
1991	-	-	144	3	-
1992	55	2026	236	4	228
1993	-	-	-	-	-
1994	-	-	196	463	212
1995	64	-	174	356	-
1996	78	1857	173	288	508
1997	107	-	49	282	-
1998	160	1908	229	148	-

1999	-	-	184	95	-
2000	-	1998	-	235	283
2001	-	-	-	-	-
2002	-	-	233	-	-
2003	-	-	652	-	-
2004	403	-	-	-	-
2005	-	-	518	-	-
2006	-	-	-	-	-
2007	-	-	717	-	-
2008	-	1555	-	-	-
2009	-	-	576	888	902
2010	-	-	-	-	-
2011	431	-	-	-	-
2012	-	1531	-	-	-
2013	-	714	-	-	-
2014	-	-	326	368	715

The most recent population estimates for wood bison in the NWT are as follows:

Table 3. Population estimates (the Nyarling River, Grand Detour, and Hook Lake subpopulations are the only Greater Wood Buffalo Ecosystem subpopulations that occur within the NWT).

POPULATION	NUMBER	YEAR	REFERENCE
Nahanni	431	2011	Larter and Allaire (2013)
Mackenzie	714	2013	Armstrong (2013b)
Greater Wood Buffalo Ecosystem			
Nyarling River	326	2014	Cortese and McKinnin (2015)
Grand Detour[2]	368[3]	2014	Armstrong (2014)
Hook Lake	715	2014	Armstrong (2014)
Total	2,554		

From Table 2, the total population for the NWT is approximately 2,554. The proportion of these animals that are non-breeding calves and yearlings has not been accurately determined and is expected to vary among populations. Using overall summer herd composition averages since 1999 (calves 15%, yearlings 8%, bulls 36%, cows 41%) and assuming animals 2+ years of age

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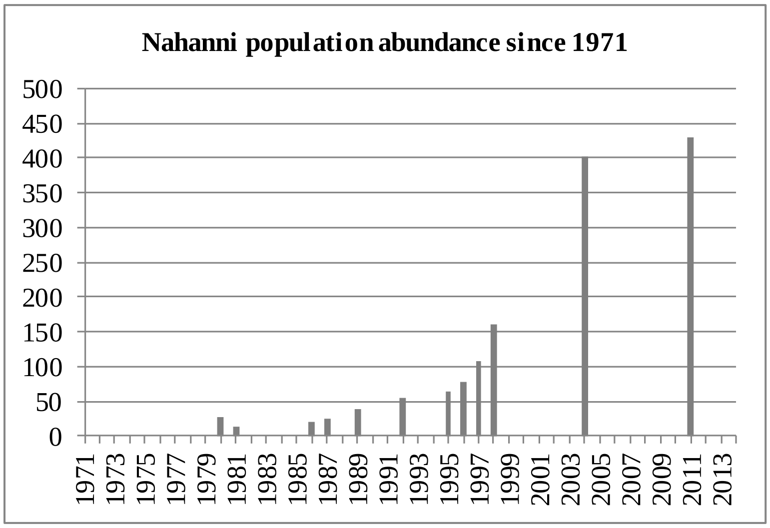
[2] The Grand Detour subpopulation sometimes moves between the NWT and Alberta. The survey area sometimes doesn't capture the core of the subpopulation.

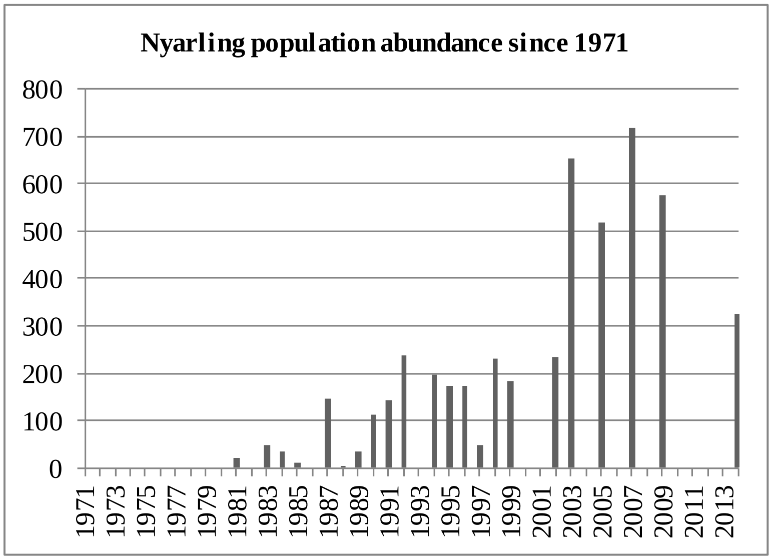
[3] Note that this number includes only the Government of the Northwest Territories' estimate of the Grand Detour subpopulation (Armstrong 2014) and not the results of Parks Canada's survey of Wood Buffalo National Park (Cortese and McKinnin 2015).

are capable of reproducing (Armstrong pers. comm. 2015), the number of mature individuals capable of reproducing would be approximately 1,966. Figure 9 (a-e), below, shows abundance since 1971 for NWT populations and subpopulations and Figure 10, p. 96, shows comparative abundance of all NWT populations and subpopulations since 1971.

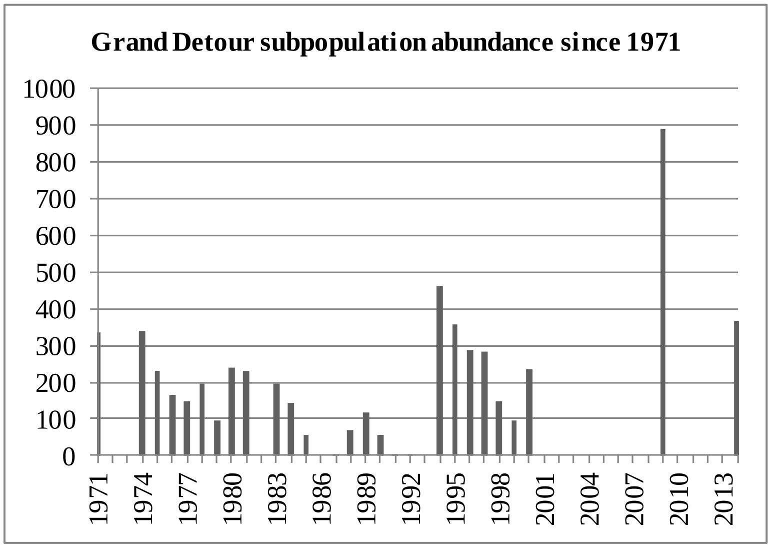
a)



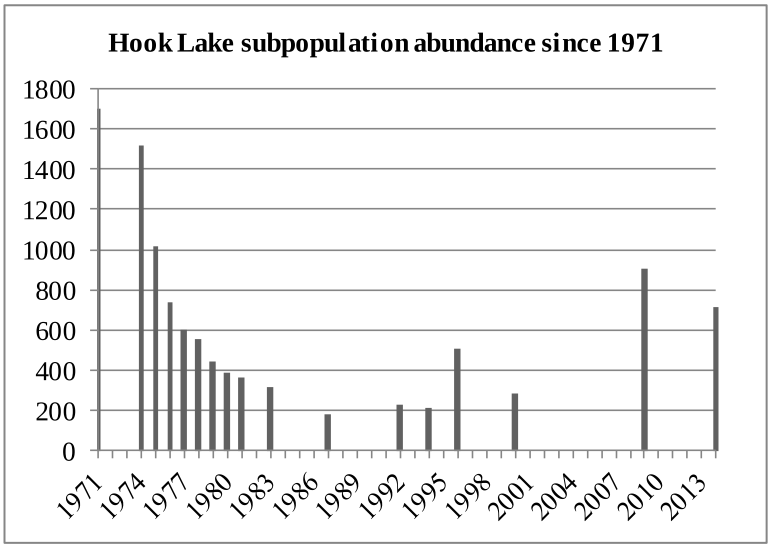
b)



c)


Grand Detour subpopulation abundance since 1971
1000
900
800
700
600
500
400
300
200
100
0
1971
1974
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004
2007
2010
2013

d)


Hook Lake subpopulation abundance since 1971
1800
1600
1400
1200
1000
800
600
400
200
0
1971
1974
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004
2007
2010
2013

e)

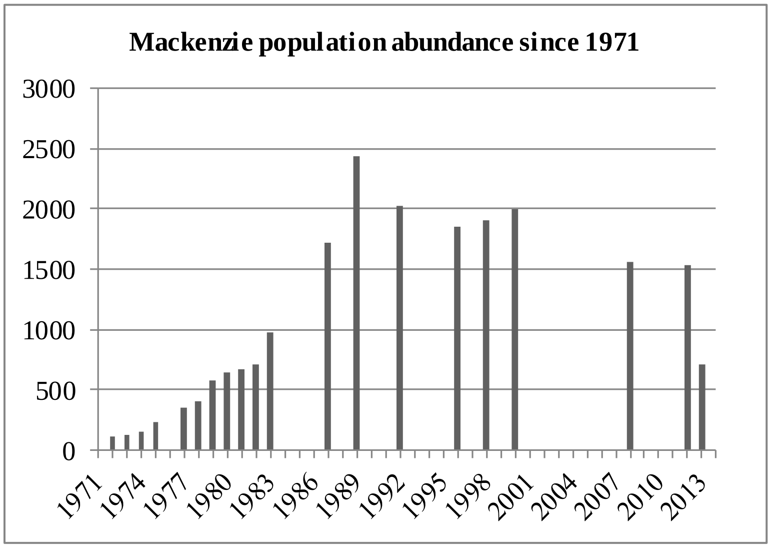


Figure 9a-e. Wood bison abundance since 1971: (a) Nahanni population, (b) Nyarling River subpopulation, (c) Grand Detour subpopulation[4], (d) Hook Lake subpopulation, (e) Mackenzie population. Figures 8b-d constitute the NWT portion of the Greater Wood Buffalo Ecosystem population. Fluctuations in numbers for the Grand Detour subpopulation may be related to movement of animals inside and outside (Alberta) the survey area. Data was obtained from Baker (1974), Jacobson (1974), Calef (1976), Jalkotzy (1979), Calef (1984), Chowns and Graf (1987), Gates and Larter (1990), Graf *et al*. (1990), Gates *et al*. (1991), Larter *et al*. (2000), Gates *et al*. (2001b), Joly and Messier (2004b), Larter *et al*. (2007), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Armstrong (pers. comm. 2013), Larter and Allaire (2013), Armstrong (2014), and Cortese and McKinnin (2015).

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[4] The Grand Detour subpopulation sometimes moves between the NWT and Alberta. The survey area sometimes doesn't capture the core of the subpopulation.

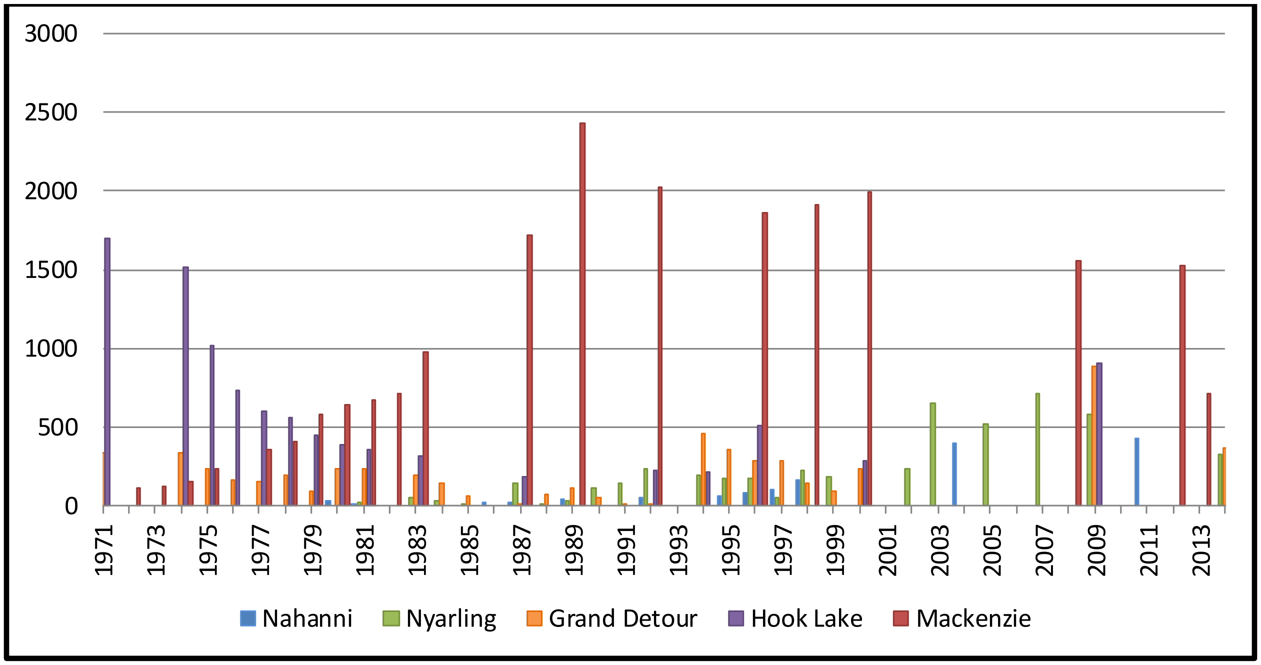

Figure 10. Comparative abundance of NWT wood bison populations and subpopulations since 1971. Data was obtained from Baker (1974), Jacobson (1974), Calef (1976), Jalkotzy (1979), Calef (1984), Chowns and Graf (1987), Gates and Larter (1990), Graf *et al*. (1990), Gates *et al*. (1991), Larter *et al*. (2000), Gates *et al*. (2001b), Joly and Messier (2004b), Larter *et al*. (2007), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Armstrong (pers. comm. 2013), Larter and Allaire (2013), Armstrong (2014), and Cortese and McKinnin (2015).

Compared to the combined total of all other free-ranging populations in Alberta (3,800; Vassal and Kindopp 2010; Aune and Gates 2010), Yukon (1,230; Yukon Wood Bison Technical Team 2010), British Columbia (100; Larter *et al*. 2007), Manitoba (300; Joynt 2010), and Russia (120; CBC News 2013), the proportion of the global and/or continental population occurring in the NWT is approximately 32%.

Refer to *Search Effort* (p. 72) and *Appendix A3* (p. 221) for more detail on population survey methods.

Density

Bison densities have been calculated in Table 4 (p.98) using the total area of occupancy for their populations, which avoids subjective partitioning of primary from secondary ranges. In accordance with the Species at Risk Committee’s (2012) definition, each area of occupancy will always have a certain mix of habitats at variable and changeable levels of quality.

If there is a strong allometric relationship between body mass and population density of bison, then an allometric calculation can be used to provide a standard of comparison for deciding whether wood bison are particularly common or rare in certain areas. Peters and Raelson (1984) reported that mean population density (D) of herbivorous mammals scales to body mass (W) allometrically as $D = 67.9(W)^{-0.882+/-0.04}$. However, population densities of mammals can vary by more than three orders of magnitude from prime to marginal habitats (Silva and Downing 1995).

Environmental factors that affect an animal's ability to survive and reproduce include weather, food, other animals, pathogens, and habitat, but Peters and Raelson (1984) have shown animal size to be a powerful factor in predicting density of herbivorous mammals. Recognizing the difficulties of defining carrying capacity and to help decide whether the decline of bison in Wood Buffalo National Park is necessarily a concern, Nudds (1993) used allometrics to estimate an expected population density and appropriate number of bison for the principal bison habitat in Wood Buffalo National Park. Similarly, Plumb *et al*. (2009) used allometrics for bison of Yellowstone National Park that would satisfy concerns regarding forage base, movement ecology, retention of genetic diversity, brucellosis risk management, and other societal constraints. Using a mean body mass estimate of 590 kg derived from Olson (2002) the allometric population density for wood bison is expected to be 0.24 bison/km^2.

The distribution of wood bison populations represents a fraction of the original range, and it is not known how much habitat capable of supporting high densities of wood bison has been lost. Table 4 (p.98) shows all current densities of wood bison to be under the allometric estimate of 0.24 bison/km^2. After the 1925-1928 addition of plains bison to Wood Buffalo National Park was completed, Kitto (1930) estimated the mixed population at 10,000 bison. In the early 1930s, Soper (1941) thought that bison occupied 8,200 miles^2 (21,240 km^2) within Wood Buffalo National Park. He also provided evidence that some of them were using the Slave River Lowlands between the Park and the Slave River, bringing the total range of the Greater Wood Buffalo Ecosystem up to 23,740 km^2. Soper (1941) estimated the bison population of 1934 to be 12,000, giving a density of 0.51 bison/km^2, but Fuller (1950) had reason to believe that this population estimate was too high. It appears that the Greater Wood Buffalo Ecosystem population had reached the limits of its current range by 1949 (Fuller 1950). Fuller (1961) estimated the total Wood Buffalo National Park population, plus those that had left the confines of the Park (now known as the Greater Wood Buffalo Ecosystem) to be 14,000-16,500 bison. Accepting the conservative figure of 14,000, the resulting 0.30 bison/km^2 density value is still higher than the allometric projection of 0.24 bison/km^2. The historical maximum population of 1,700 animals for the Hook Lake subpopulation (Rippin 1971 *in* Nishi 2010), which has always been surveyed separately, is also above the allometric projection. Environmental conditions from 1930 to 1971 seem to have been favourable for the Greater Wood Buffalo Ecosystem population to maintain a density consistent with or higher than mean densities of herbivores, scaled to body mass. Since 1971, observed densities have been suppressed, apparently by one or more overwhelming factors that have affected the animals' ability to survive and reproduce.

Immediately prior to dispersal episodes, densities have been reported to exceed 0.70 bison/km^2 for the Mackenzie population (Gates and Larter 1990; Larter *et al*. 2000). Until 1968, the bison population was primarily restricting its distribution to prime habitat on the marl basin of Falaise Lake, and then extended its range to other marl lakes. In 1980, the range expanded to the Mink Lake area. Larter *et al*. (2000) plotted population density against the instantaneous rate of growth from 1963 to 1998 and found a cyclical pattern during the eruptive population increasing phase; both density and population growth rate increased until population density exceeded circa 0.55 bison/ km^2. Once this point was reached, both density and growth rate decreased and the cycle began again. The cycle was completed twice with both dispersal episodes coming the year following peak population density. During the eruptive phase of population growth, there was pulsed dispersal of animals and an increasing area of occupancy. Current density is well below allometric projections, which may be a reflection of high quality sedge-grass meadows covering less than six percent of the range, often separated by tens of kilometres of marginally productive forest (Mychasiw 1987; Larter and Gates 1990; Matthews 1991), and the limited high quality sedge-grass meadows left in the range after recent increases in the water table (Armstrong pers. comm. 2012).

Because the Nahanni population has such a brief history, allometric projections cannot yet be made.

Table 4. Wood bison density (bison/km^2), where 'maximum population' refers to the maximum number a population has ever attained in the past and maximum density is calculated based on the area of occupancy and the 'maximum population'. 'N/A' is used to indicate where data are missing, and when populations are on an upward trajectory or undergoing a range expansion; in these cases, no maximum population can yet be calculated. Population data was obtained from Fuller (1961), Calef (1976), Larter *et al*. (2000), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Larter and Allaire (2013), Armstrong (2014), Cortese and McKinnin (2015).

Population	Area of Occupancy (km^2)	Current Population	Current Density	Maximum Population	Maximum Density	Allometric Population	Allometric Density
Nahanni	11,713	431	0.04	N/A	N/A	2,811	0.24
Mackenzie	21,695	714	0.03	2,431	0.11	5,207	0.24
GWBE	46,176	3,112	0.07	14,000	0.30	11,082	0.24
Nyarling R.	7,177	326	0.05	N/A	N/A	1,722	0.24
Grand Detour	4,915	368[5]	0.07	N/A	N/A	1,180	0.24
Hook L.	5,105	715	0.14	1,701	0.33	1,225	0.24

Carrying capacity

Ecological carrying capacity is defined as the population size at which the population no longer increases (Caughley 1979). This upper limit is reached when removal of forage by herbivores equals the forage produced annually, and juvenile survival equals adult mortality. However, these may be indicators that the population density is too close to exceeding what the range can support. Fuller (1966) suggested that the ideal situation for bison was to have a stable population below the ecological carrying capacity. Estimates of wood bison carrying capacity based on standing crop and productivity of the forage (e.g., Townsend 1972; Reynolds *et al*. 1978;

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[5] Note that this number includes only the Government of the Northwest Territories' estimate of the Grand Detour subpopulation (Armstrong 2014) and not the results of Parks Canada's survey of Wood Buffalo National Park (Cortese and McKinnin 2015).

Reynolds *et al*. 1980; Peden and Reynolds 1981) have been much higher than levels ever attained by the real populations.

A population surpassing 400 approaches an acceptable level for the long-term retention of genetic diversity (McFarlane (Zittlau) *et al*. 2006). A population greater than 1,000 would give a 90% probability of retaining 90% of allelic diversity for 200 years (Gross and Wang 2005) and satisfy the recommendations from the Bison Conservation Initiative (Dratch and Gogan 2010) (see *Trends and fluctuations – Population viability analysis* for further information, p. 102).

Trends and fluctuations

Rate of growth

Table 5 (p. 100) shows approximate instantaneous rates of growth for the last three generations and the three generations before that, using survey data in Table 2 (p. 91). From Table 5 (p. 100), three of the five wood bison populations/subpopulations in the NWT are showing growth (Nahanni population, Nyarling River subpopulation, and Hook Lake subpopulation) and two (Mackenzie population and Grand Detour subpopulation) are in decline. The Nahanni population has been fairly stable for the past decade. The Nyarling River subpopulation (Greater Wood Buffalo Ecosystem population) is a small, low density herd that has generally been stable. Both Hook Lake and Mackenzie population numbers have undergone the most substantial population changes over time. The Hook Lake subpopulation (Greater Wood Buffalo Ecosystem population) increased from 350 animals in 1949 (Fuller 1950) to 1,701 in 1971 (Calef 1976) (r = 0.072)[6]. This was followed by a decline for the next similar period (r = -0.096), and then growth for the last three generations (r = 0.052). From its establishment, the Mackenzie population increased from 18 animals in 1966 (Larter *et al*. 2000) to 111 animals by 1972 (r = 0.303), and then continued to increase to 2,026 animals to 1992 (r = 0.145). The last three generations however, have seen the Mackenzie population decline at a rate of r = -0.050. Although the Mackenzie population decline can, in part, be attributed to the 2012 anthrax outbreak, it is important to note that the population was declining for approximately 12 years prior to this event as well (Armstrong pers. comm. 2015). Overall, the NWT population of wood bison has declined over the last three generations at an instantaneous rate of r = -0.012 (Table 5, p. 100).

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[6] Instantaneous rate of growth (r) is a measure of the per capita rate of change in population size for a particular period of time. In a closed population it equals the birth rate minus the death rate. A stable population has $r = 0$. It was calculated using the formula $r = (\ln N_{(t+n)} - \ln N_{(t)})/n$; where t is the initial time (year), n is the number of years from the initial time, and N is the population estimate for each time period.

Table 5. Instantaneous rate of growth (*r*) data was derived from Baker (1974), Jacobson (1974), Calef (1976), Jalkotzy (1979), Calef (1984), Chowns and Graf (1987), Gates and Larter (1990), Graf *et al*. (1990), Gates *et al*. (1991), Larter *et al*. (2000), Gates *et al*. (2001b), Joly and Messier (2004b), Larter *et al*. (2007), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Armstrong (pers. comm. 2013), Larter and Allaire (2013), Armstrong (2014), and Cortese and McKinnin (2015).

POPULATION	LAST 3 GENERATIONS (approx. 1993-2014)	PRIOR 3 GENERATIONS (approx. 1972-1993)
Nahanni	0.076[7]	N/A
Mackenzie	-0.050	0.145
Greater Wood Buffalo Ecosystem		
Nyarling River	0.015	N/A
Grand Detour	-0.011	0.014
Hook Lake	0.052	-0.096
NWT pop average	**-0.012**	**N/A**

Using available survey data, the three generation (1993-2014) decline was calculated with an exponential assumption and only two years of data for each subpopulation (IUCN Criterion A, exponential assumption, two data point calculator). An overall wood bison decline was estimated at approximately 11%. Refer to *Appendix A4* (p. 228) for further detail on these calculations.

Figures 11 (p. 101) and 12 (p. 102) show trends in total wood bison numbers for the NWT, with estimates for years without population surveys derived by calculating the annual growth rate between successive population estimates and projecting that forward. Figure 11 shows the trend lines for each generation for all wood bison in the NWT. An increase of 45% in the first generation (1980-1986) includes the effect of active reintroduction in the Mackenzie and Nahanni populations. For subsequent generations increases were 31% (1987-1993), 3% (1994-2000), and 37% (2001-2007). During the last generation, the population decreased by 51% (2008-2014). Using those derived values, a 23% total decline can be calculated for wood bison in the NWT over the last three generations (1993-2014). For more information on the methodology used to construct these figures, refer to *Appendix A4* (p. 228).

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[7] Owing to bison introductions in the mid-1990s, the instantaneous rate of growth for the Nahanni population was not calculated over a full three generations (1993-2014); rather, it was calculated from the 1998 estimate of 160 bison.

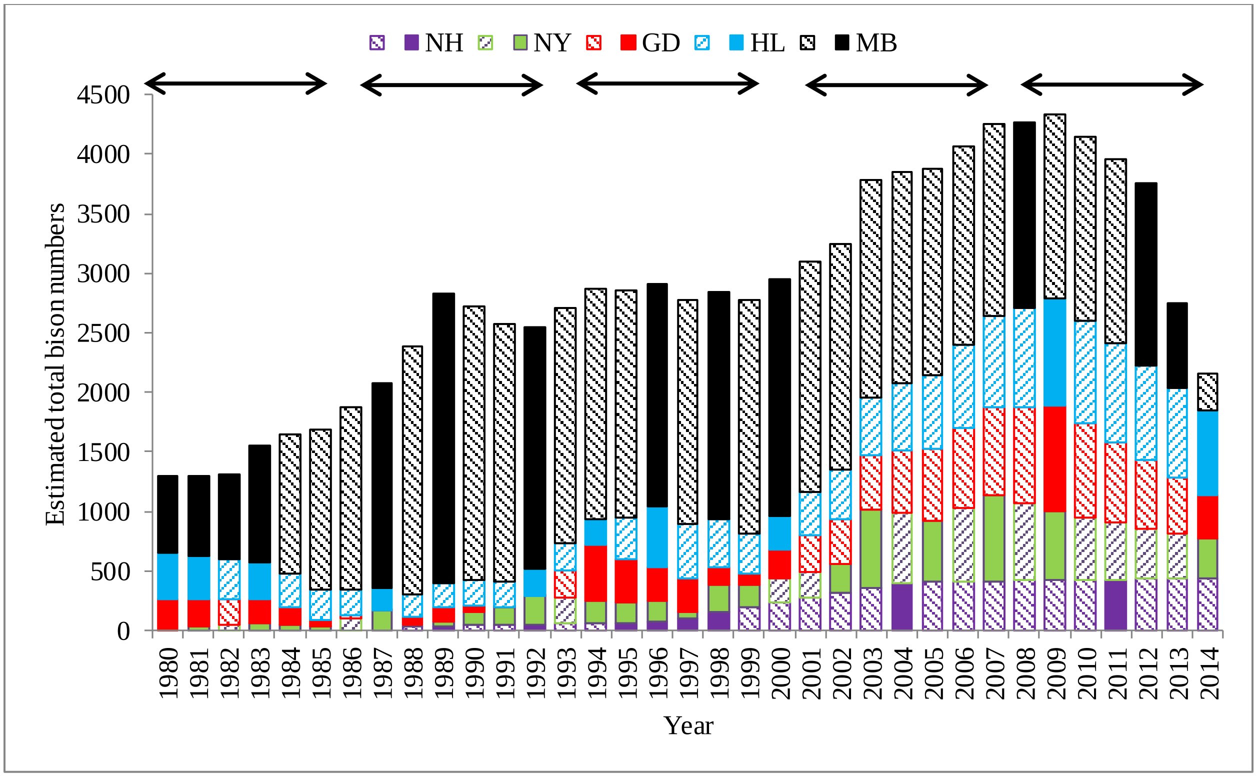

Figure 11. Estimated total NWT bison numbers, stacked by population/subpopulation (NH = Nahanni population, NY = Nyarling River subpopulation, GD = Grand Detour subpopulation, HL = Hook Lake subpopulation, and MB = Mackenzie population). Numbers from surveys are shown with solid fill and extrapolated numbers are shown with hatched fill. The 7-year periods shown with arrows indicate 'bison generations'. Data was obtained from Baker (1974), Jacobson (1974), Calef (1976), Jalkotzy (1979), Calef (1984), Chowns and Graf (1987), Gates and Larter (1990), Graf *et al*. (1990), Gates *et al*. (1991), Larter *et al*. (2000), Gates *et al*. (2001b), Joly and Messier (2004b), Larter *et al*. (2007), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Armstrong (pers. comm. 2013), Larter and Allaire (2013), Armstrong (2014), and Cortese and McKinnin (2015).

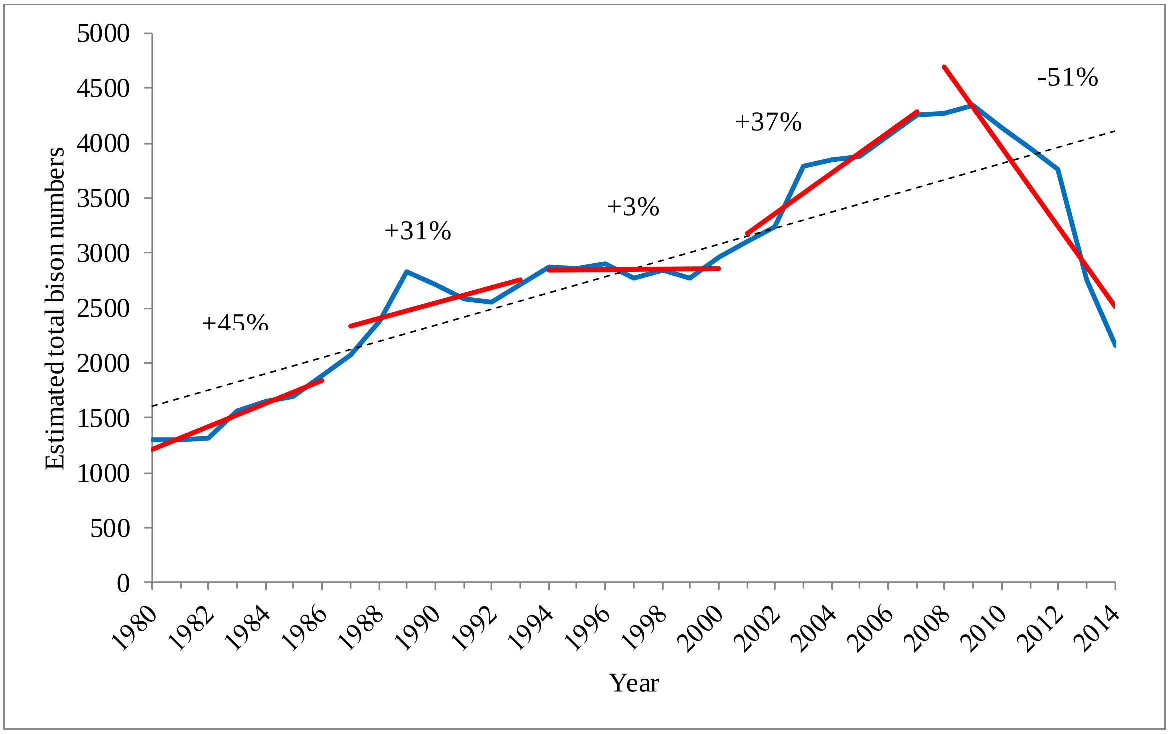

Figure 12. Estimated total NWT bison numbers summed for all NWT populations from 1980-2014 (blue line). Linear trend lines are shown for 1980-2014 (dashed line) and for each 7-year bison generation (red lines). Percent change is included above each generation trend line. Data was obtained from Baker (1974), Jacobson (1974), Calef (1976), Jalkotzy (1979), Calef (1984), Chowns and Graf (1987), Gates and Larter (1990), Graf *et al*. (1990), Gates *et al*. (1991), Larter *et al*. (2000), Gates *et al*. (2001b), Joly and Messier (2004b), Larter *et al*. (2007), Vassal and Kindopp (2010), Armstrong (2011), Armstrong (2013b), Armstrong (pers. comm. 2013), Larter and Allaire (2013), Armstrong (2014), and Cortese and McKinnin (2015).

For information on instances of eruptive oscillation in wood bison populations, which typically occurs after a population has been significantly reduced or has been introduced, refer to *Appendix A5* (p. 230).

Population viability analysis

Although metapopulations may be large, subpopulations colonizing new areas are usually small and face significant risks. Stochastic events are capable of causing extinctions in small numbers of individuals haphazardly that would otherwise be buffered against in large populations. An example of demographic stochasticity might be the death of every male during an anthrax outbreak. An example of environmental stochasticity might be the loss of an entire population to a drowning event. In small populations, loss of genetic diversity in these types of instances may be particularly acute.

Feedback between demographic and genetic decline that leads rapidly toward extinction is called an ‘extinction vortex’ (Gilpin and Soule 1986). The threshold below which a population is likely to be drawn into an extinction vortex is its ‘minimum viable population’ or MVP.

Using a simulation model, Gross and Wang (2005) demonstrated that an MVP of about 400 bison was needed to retain 90% of selectively neutral variation with a 90% probability for 200 years. Longer generation times allow older animals to eventually or continually contribute to the gene pool. As population sizes approach 1,000, the simulated effects of population management on genetic variation become small. Gross and Wang (2005) concluded that populations exceeding 1,000 should be more resilient than smaller populations.

Recognizing that few bison herds in North America play the significant roles they once did in the ecosystems when they competed with other grazers, interacted with predators, shaped landscapes, and roamed without impediment, Sanderson *et al*. (2007) questioned whether bison restoration should ideally encompass the interactions between bison and their environment. A statement jointly written by scientists and stakeholders from throughout North America, known as the 'Vermejo Statement' is as follows: "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." (Sanderson *et al*. 2007: 254). They defined the following population size classes as a scorecard for ranking contributions of bison herds to the concept of ecological restoration:

- small contribution – fewer than 400 animals;
- modest contribution – 400 to 1,000 animals;
- large contribution – 1,000 to 5,000 animals;
- exceptional contribution – more than 5,000 animals.

Accordingly, both the Nahanni and Mackenzie populations would be ranked as modest contributors. The Greater Wood Buffalo Ecosystem population would be ranked as a large contributor to ecological restoration of bison herds, and the only wood bison population that can be considered ecologically restored (thousands of individuals).

Population dynamics

Population dynamics typically show considerable annual variation; therefore, long term averages are required for an accurate assessment at the population level. Parameters used here to describe population dynamics (natality, recruitment, adult survival, and immigration/emigration) have not been measured consistently among all wood bison populations, or during comparable time intervals. Recent time periods are the most important for evaluating the current status of wood bison in the NWT. Fortunately, the methodology among jurisdictions has become standardized.

Natality

Estimation of calf crop in a population is very sensitive to the timing of the census. Early counts miss later births and late counts fail to detect the calves lost during the intense neonatal predation period. A series of counts through the duration of the calving season determines when peak calving occurs and provides the most accurate estimate of birth rate.

From Wood Buffalo National Park slaughters between 1950 and 1953, Fuller (1961, 1966) estimated the pregnancy rate of adult females to be over 50%, but the observed calf crop was only 20-25% of the total population. He considered abortion in late pregnancy and post-partum mortality as explanations for this discrepancy.

Because of the difficulty in accurately accounting for the adult male component of the population, it has become conventional for the birth rate to be expressed in terms of the number of calves per 100 adult cows. In Wood Buffalo National Park, the natal trajectory trended from approximately 28 calves: 100 cows (1986-1989), upward to 38 calves: 100 cows (1989-2003) (Bradley and Wilmshurst 2005).

Larter *et al*. (2000) estimated the average birth rate for the Mackenzie Bison Sanctuary from 1984 to 1998 at 41 calves: 100 cows. As expected, the average for the expanding number of bison in the Mink Lake area (Mackenzie population) from 1989 to 1998 was higher at 51 calves: 100 cows. In 2013, the Mackenzie birth rate was 11 calves: 100 cows, which is the lowest ever reported for this population. Since 1999, the birth rate has averaged 34 calves: 100 cows and ranged between 11 and 47 calves: 100 cows (Armstrong 2013a).

Although the mean birth rate for the Nahanni population was 37 calves: 100 cows (Larter and Allaire 2007), it was only for six consecutive years (2002-2007) and there are little comparative data prior to 2002. However, the ratio is 42 calves: 100 cows for 11 consecutive years (2002-2013) and if the only other data point from 1999 is added, 41 calves: 100 cows would be the mean over two generations, with a range of 20-65 calves:100 cows (Larter pers. comm. 2014).

Recruitment

Recruitment is generally defined as the percentage of juveniles entering the reproductive segment of the population. Although this does not usually occur in bison until after the second year, bison in this age class are difficult to segregate. Recruitment has been considered synonymous with survival to the age of one year, partly because high calf mortality levels do not continue into the yearling and older age classes (Fuller 1961, 1966). Recruitment rates are very sensitive to predation levels.

When Gaillard *et al*. (1998) reviewed long-term population studies of large herbivores in contrasting environments, they found that juvenile survival typically shows high yearly variability, and may play a predominant role in population dynamics. Predation, drought, rainfall, harsh winters, low birth weight, low early growth rates, late parturition, poor calving areas, lack of suitable bedding sites, genetic factors, and altered immunocompetence of neonates were reported as causes that decrease juvenile survival in ungulates. Recruitment is the main target of limiting factors, both density-dependent and density-independent, although variable juvenile survival is probably as important in bison population dynamics.

From slaughtered animals (1950 to 1953) in Wood Buffalo National Park, yearlings averaged 7.6% of the total population (Fuller 1961, 1966). This figure was from a time when the bison population was fairly stable at relatively high numbers. Since then, expressing recruitment in terms of the number of yearlings per 100 adult cows (instead of percentage of the total population) has become standard. For all of Wood Buffalo National Park, the recruitment trajectory has risen from about 5 yearlings: 100 cows (approx. 1991) to about 20 yearlings: 100 cows (2004) (Bradley and Wilmshurst 2005).

The estimated recruitment for the Mackenzie Bison Sanctuary from 1984 to 1998 was 22 yearlings: 100 cows and the expanding number of Mackenzie population bison located near Mink Lake produced 30 yearlings: 100 cows from 1989 to 1998 (Larter *et al*. 2000). In 2013, the Mackenzie recruitment rate was 9 yearlings: 100 cows, which is one yearling more than the lowest ever reported for this population in 2003. Since 1999, recruitment has averaged 19 yearlings: 100 cows and ranged between 8 and 31 yearlings: 100 cows (Armstrong 2013a).

For the Nahanni population, the estimated recruitment is 21 yearlings: 100 cows for the last two generations, with a range between 10 and 31 yearlings: 100 cows (Larter pers. comm. 2014). Larter and Allaire (2007) estimated an overwinter survival of calves by dividing the ratio of yearlings: 100 cows determined in a given year by the ratio of calves: 100 cows from the previous year. If recruitment is synonymous with survival to the age year one then the mean overwinter survival of calves from 2002/03-2012/13 was 57.2% (range 22.8-88.5%) (Larter pers. comm. 2014).

Adult survival

The review by Gaillard *et al*. (1998) also indicated that survival of prime-aged, large mammal females varies little from year to year, or across populations. Adult female survival appeared to be buffered against temporal variation regardless of the causes of mortality, with the exception of disease. The calculation of meaningful survival rates for adult wood bison in the NWT is hampered by several factors, such as small sample sizes, short collection periods, and a paucity of data from marked individuals. Survival rates are most sensitive to the age structure of the adults.

In Wood Buffalo National Park, Joly and Messier (2005) found that annual survival of adult bison varied from a low of 77% in the Delta subpopulation (located in Alberta) (1998/99) to nearly 100% in the Nyarling River subpopulation from 1997-2000. For the Mackenzie population, the probability of annual adult survival was 92.9% between 1986 and 1991 (Larter *et al*. 2000).

Immigration and emigration

There has been no evidence of immigration or emigration other than among the subpopulations of the Greater Wood Buffalo Ecosystem population. Wilson and Strobeck (1999) detected significant gene flow throughout the Greater Wood Buffalo Ecosystem population, but not enough to totally obscure genetic differences. Joly (2001) did not discover any significant trends regarding interchange among any subpopulations. Calef and Van Camp (1987) found that the ratio of bison numbers east (Hook Lake) and west (Grand Detour) of the Slave River remained fairly constant at 4:1 between 1966 and 1977 and none of the animals collared at Hook Lake were ever relocated west of the Slave River. None of the thousands of tagged animals at the Hook Lake anthrax round-ups reappeared at any Wood Buffalo National Park round-ups, or vice-versa (Calef 1976). An anomaly was reported by Calef and Van Camp (1987) when the Hook Lake subpopulation appeared to lose about 50 bison in 1978 to the west side of the Slave River, then regained the same number in 1979.

Possibility of rescue

Rescue effect is the process by which a species may move through its range in a way that would mitigate an NWT extirpation or population decline. Some wood bison herds in the NWT share distributions with Alberta, British Columbia and the Yukon. Because tuberculosis and brucellosis present in the bison in the Greater Wood Buffalo Ecosystem population pose a threat to wood bison recovery (Gates *et al*. 1992b), bison exclusion zones are maintained in northern Canada that deny wood bison from using 50% of their historic range (Reynolds and Gates 1991). The NWT Bison Control Area enforces an anthropogenic separation of the Nahanni and Mackenzie populations from the Greater Wood Buffalo Ecosystem population. Although this stifles gene flow and rescue, exclusion zones are presently the only protection available against infection of disease-free herds and must continue indeterminately, or until they fail.

In the event that the Nyarling River, Grand Detour or Hook Lake subpopulations should disappear or experience a decline, the likelihood of rescue from other subpopulations in the Greater Wood Buffalo Ecosystem is high. There is virtually no probability that dispersal from elsewhere could re-establish the Mackenzie population because of the Bison Control Area, and the Mackenzie range is too remote from any others for immigration to be a factor. The likelihood of the Nahanni population being rescued by dispersal from elsewhere is also remote even though it is not far from the Nordquist herd in northern British Columbia. The Nordquist herd is small, estimated at 117 animals in 2010 (Thiessen 2010), and there has been no known or reported movement between the two populations. The Aishihik population in southwestern Yukon is remote from the Nahanni population and therefore provides virtually no potential for rescue.

Habitat

Habitat availability

Present habitat

The main landscape features providing the highest forage biomass for wood bison are marl lake basins, fens, floodplains, and salt plains. All are wetlands and if peat accumulates in marl lake basins, floodplains, or salt plains, they may transform into fens. Marl lake basins occupy large parts of the Mackenzie and Nyarling River bison ranges, generally at elevations exceeding 190 m above sea level. Fens are mainly associated with the Mackenzie population range below 190 m and the Nyarling River subpopulation range, although they may be found in all areas of bison occupation. Floodplains of the Slave, Mackenzie, Liard, South Nahanni and Horn rivers have perched basins and channels that are at slightly higher relief than present water courses and were formerly more active in the drainage systems. Floodplains also occur below 170 m along low-lying shores of Great Slave Lake. The Salt Plains of Wood Buffalo National Park lie within Alberta, except for a northern extension into the NWT (locally known as the 'Foxholes') west of Fort Smith, where this landscape feature merges with the Slave River Lowlands. It appears to be a zone of overlap between the Grand Detour and Hay Camp subpopulations. North of the Mackenzie River, there are extensive foxtail (*Hordeum jubatum*) meadows (Chowns 1986; Matthews 1991), which are indicators of saline soils (Raup 1935).

Potential habitat

There are areas of the NWT that appear to have suitable habitat, but are not occupied by wood bison. The historical range of wood bison extends to Lac La Martre (Richardson 1829) and bison may now be re-entering this region (Cluff pers. comm. 2012). There is a considerable amount of former range contained within the Bison Control Area. Historically, bison were found along the south shore of Great Slave Lake (Allen 1877; Hanks and Irving 1987), but when animals re-appear, they are routinely removed in accordance with disease control protocols. The alluvial formations on the south shore of Buffalo Lake contain sedge meadows within 50 km of the Nyarling River subpopulation (Chowns 1979), but some of this habitat extends into the Bison Control Area. North of the range of the Nahanni population, there are many mountain valleys that resemble those in the Yukon and British Columbia where bison are thriving (Ecosystem Classification Group 2010). The combined potential habitat for Lac La Martre, the south shore of Great Slave Lake, Buffalo Lake, and the mountain valleys may exceed 3,000 km^2, but requires further investigation.

Perhaps the largest tract of potential habitat lies within the 12,000 km^2 former basin of Glacial Lake Mackenzie, which was named and described by Smith (1992). Occupying the middle three-quarters of the Mackenzie Valley, this 800 km-long water body was separated from Glacial

Lake McConnell by an ancient delta at the mouth of the Liard River, and extended northward to where it was partially dammed by a limestone upland known as the ‘Ramparts’ near Fort Good Hope. Perched deltas in most of the Mackenzie tributaries mark upper levels of Glacial Lake Mackenzie. As with other glacial lakes, dense soils in the former basin and its delta provide favourable conditions for sedge-grass vegetation. The Mackenzie River carved an inner valley into the lacustrine sediments and its floodplain and wet sedge fens resemble habitat found in current wood bison range (Ecosystem Classification Group 2007, 2010).

The southernmost section of the former basin, extending from the mouth of the Rabbitskin and Spence river deltas (50 km east of Fort Simpson) to the mouth of the Willowlake River, is 30 km wide and reaches into the lower valleys of the North Nahanni, Root and Willowlake rivers. Where the Mackenzie River turns northward at Camsell Bend, the surrounding area has extensive meadows containing *C. atherodes* (Porsild and Cody 1980). River islands and tributary streams are disturbed frequently by flooding and ice scouring, which maintains early successional vegetation (Treseder and Graf 1985). The last record of bison in this area was at the mouth of Martin Creek in 1831(Preble 1908). This section is nearest to existing wood bison populations, but dense forest, extensive bogs, and mountains are barriers to reoccupation. Natural corridors along the lower Liard and upper Mackenzie rivers are constricted in the Fort Simpson area by islands and shorelines that lack floodplains and have steep unvegetated banks (Walton-Rankin 1977).

The northern half of the former basin is the most extensive and ascends several kilometres up into the valleys of the Redstone, Keele, Great Bear, Little Bear, Carcajou, and Mountain rivers. A 50 km embayment east of Tulít’a includes Kelly and Brackett lakes east of the Norman Range. The widest embayment extends 75 km from the Mackenzie River into the Arctic Red Plain (Low Subarctic) Ecoregion, encompassing the lower Hume and Ramparts rivers, and also extends 25 km east of the Mackenzie River. A study of historical bison range in Alaska, Yukon, and adjacent NWT by Stephenson *et al*. (2001) provided the most comprehensive summary of bison evidence from the past for the northern half of the former Glacial Lake Mackenzie basin and its delta.

None of the potential habitats listed above have ever been evaluated. Because bison range has largely been a function of long term climatic effects that shift the extent of forest, grassland and peatland on the landscape, former range does not necessarily predict potential range for the near future. All bison remains discovered at latitudes higher than current limits in the NWT have been dated to times when the climate and vegetation were different from today. The climatic thresholds of wood bison physiology for higher latitudes are unknown. Beringian bison were able to thrive in periglacial areas where the winters were cold, but snow was shallow and exceptional summer growing conditions produced an abundance of food (Guthrie 2001).

Habitat fragmentation

The emergence of discontinuities in the preferred environment of bison results in habitat and population fragmentation. Whereas natural processes slowly alter the layout of the physical environment, land conversion by humans tends to have much more immediate impacts on habitat fragmentation. The clearing of native vegetation for agriculture, rural development, urbanization, mining, fossil fuel exploration, timber harvesting, roads, and hydroelectric reservoirs are the usual forces detrimental to contiguous wildlife habitat. However, wood bison often derive foraging opportunities from disturbances that revert mature forest into early successional vegetation, and these animals readily use road right-of-ways and seismic lines as travel routes. Although agriculture has probably been an important form of habitat fragmentation for wood bison in the western provinces, this activity is relatively undeveloped in the NWT.

Natural habitat fragmentation is caused by expanses of dense forest, muskeg and steep mountains. Wood bison have a limited ability to overcome some of these physical obstacles by developing trails many kilometres in length through forests, across bogs, and along mountain valleys and passes. Meagher (1973) described well-defined travel routes in montane areas at elevations exceeding 3,000 m.

Habitat trends

Wood bison habitat is constantly changing in area and quality in the NWT through vegetation succession and retrogression, which progresses differently in lowlands and uplands. When moisture levels are most favourable, *C. atherodes* meadows provide the greatest volume of high quality bison forage; however, sedge meadows and grasslands in wood bison range are inherently unstable. These early seral stages of vegetation succession must be revitalized and maintained by frequent cycles of floods and drawdowns, and fires.

Recruitment of *C. atherodes* in wetlands occurs primarily during periods when the substrate is free of standing water, referred to as ‘drawdowns’ (Van der Valk and Davis 1978). Seeds of *C. atherodes* from the soil seedbank germinate on the exposed substrate, and when flooding returns, *C. atherodes* and other emergents survive and reproduce vegetatively (asexually, without need for seeds or spores), while other plants are eliminated (Welling *et al*. 1988). However, if desiccation is prolonged, woody perennials often invade. Large fluctuations in water levels also favour decomposition of dead plant material, which impedes excessive peat accumulation (Damman 1979). Accordingly, high amplitude flood/drawdown cycles are important for maintaining wood bison habitat.

Higher quality bison habitat probably existed in periods in the past when climatic conditions were most optimal, native use of fire was customary, and in the Slave River Lowlands, when overbank flooding by the Slave River due to ice-damming in spring still occurred in some years.

Flood plains

Rivers are powerful forces of disturbance across their floodplains. They continually erode their banks, deposit sediments into island/bar complexes, carve new channels and abandon old ones, scour shoreline areas and occasionally flood the plain. These processes provide new substrates for riparian plant communities and reset succession to early seral stages. The Slave River Lowlands is composed of deltaic deposits that filled the former southern arm of Great Slave Lake after isostatic rebound separated it from Lake Athabasca (Craig 1965). The Slave River advances laterally through the relict portion of the delta (Vanderburgh and Smith 1988), and the new alluvial accumulations support very productive meadows. East of the river, where the deltaic deposits have been re-sorted by abandoned distributary channels, there are hundreds of shallow ephemeral lakes or sloughs containing emergent vegetation (Brock *et al*. 2008). At the outlet of Great Slave Lake, a widening of the Mackenzie River known as Beaver Lake regularly floods into extensive areas of low relief. Many broad former channels extend downstream to the Mills Lake - Horn River delta floodplain complex (Kemper *et al*. 1975).

Low-lying flat land adjacent to these rivers and Great Slave Lake are inundated by small rises in water level that may persist long enough to drown woody plants. Timoney and Argus (2006) determined that pulses of willow establishment coincided with drying periods. Willow die-back depended on species, water depth, duration of flooding, time since flooding, and size and age of the plant. High amplitude flood/drawdown cycles are necessary for retrogression of these habitats to stages favourable to bison. Although the distributary channel network responds to summer flooding, it appears that only spring ice jamming on a massive scale is capable of surpassing the natural levees and recharging the perched stream channels, floodplain lakes and wetlands (Peters *et al*. 2006; Brock *et al*. 2008; Pavelsky and Smith 2008). Low freeze-up levels, followed by rapid melt of a heavy winter snowpack, are conditions necessary for producing a spring flood-wave large enough for ideal massive ice jamming and extensive backwater flooding (Prowse and Conly 2002; Beltaos *et al*. 2006).

The main tributary of the Slave River, the Peace River, has much of its runoff captured by the W.A.C. Bennett Dam and the Williston Reservoir, which were constructed for hydroelectricity and filled between 1968 and 1971. Since then, there has been a concern about diminishing flood/drawdown cycles and detrimental effects on bison habitat downstream in Wood Buffalo National Park (Carbyn *et al*. 1998). By releasing more water than normal during winter when electricity demand is highest and reducing the flow of the Peace to recharge the reservoir in spring, the dam disrupts the natural amplitude of the flood/drawdown cycle (Peters and Prowse 2001). This concern may be heightened with the recent approval of the Site C dam by the Government of British Columbia (Government of British Columbia 2014). The Site C hydroelectric project would result in changes to the entire river flow regime during the construction phase (BC Hydro 2013). In addition, declining snowpacks in the catchments of other main tributaries since the mid-1970s (Prowse and Conly 1996) and a shorter ice season since the 1961–1990 period (Prowse *et al*. 2004) compound the problem. This trend may have actually begun in the late 19th century (Wolfe *et al*. 2005, 2006).

Approximately two-thirds of the water in the Slave River flows from the Peace River, and since the impoundment of the Peace River at the Bennett Dam, English *et al*. (1997) found that sediment loads in the Slave River have decreased by one-third, spring flow levels are lower, and a general drying trend has occurred in the Slave River delta. Consequently, growth of the geomorphological structure of the delta has slowed and herbaceous riparian communities are being replaced by woody vegetation and mosses that are intolerant of the sediment loading that accompanies frequent flooding. Gibson *et al*. (2006b) suggested that channel migration and climate variability have also had significant effects on the Slave River delta.

Since the last extensive fires in the Hook Lake bison range in 1952 and a generalised lowering of the water table, local residents have reported that the meadows have decreased substantially in size because of willow and tree invasion (Jalkotzy and Van Camp 1977).

Almost three-quarters of the inflow to Great Slave Lake originates from the Slave River, and Great Slave Lake is the source for nearly all of the water entering the upper Mackenzie River (Gibson *et al*. 2006a; Prowse *et al*. 2006). If upstream flow regulation can affect seasonal levels in Great Slave Lake, Woo and Thorne (2003) suggested that outflows to the downstream Mackenzie River would also experience some degree of seasonal dampening from regulation. However, their analysis also indicated that these effects would likely be partially offset by climate variability.

Ecological changes in the upper Mackenzie River from flow regulation and climatic anomalies are unclear, as no long term studies are being carried out. Comparison of aerial photos of the Mills Lake – Beaver Lake area from 1970 to present shows encroachment of willows and aspen into former sedge meadows, but the extent has never been measured. Cycles that occur along the Slave and Mackenzie rivers and Great Slave Lake are driven largely by precipitation variability in the Peace-Athabasca basins (Prowse *et al*. 2006). Consequently, floods and drawdowns on these major watercourses are often out of synch with the local precipitation cycles that affect inland areas.

While the nearby inland basins were drying out in 1974, Mills Lake was flooded until autumn and water levels rose to within six inches (15 cm) of the historic high water mark (Kemper *et al*. 1975). This paralleled the 1974 large discharge peak on the Slave River (Brock *et al*. 2008) and the nearly complete inundation of the Peace-Athabasca Delta from spring until autumn that drowned about 3,000 bison that year (Carbyn *et al*. 1993; Peters *et al*. 2006).

In the early 1990s, the flood/drawdown difference between the Mackenzie River and inland areas to the north had reversed from 1974. Most of the high biomass sedge meadows regularly used to sustain this bison population through the winter appeared to be under water. Bison invaded the high and dry shoreline meadows extending from Mills Lake, and Beaver Lake on the Mackenzie River, to Lonely Bay on the west side of Great Slave Lake in great numbers (Gates *et al*. 1992b).

During the early 1990s, the Northern River Basins Study was initiated to determine the effects of the Bennett Dam on the Peace River, Slave River and Great Slave Lake ecosystems, and how they were being shaped by climate change, flow regulation and land use changes. Recommendations included modification of water release at the dam, which would attempt to maintain wetlands, including bison habitat, in a more natural state (Prowse and Conly 1996).

Marl lake basins

The origin and development of marl lakes has been described by Wentzel (1975). In closed basins receiving highly calcareous ground water from the limestone bedrock or glacial till, physico-chemical processes cause calcium carbonate, the main component of marl, to precipitate and render essential elements unavailable to plants. When the inundation of calcareous water is reduced, nutrients accumulate and the pH becomes less alkaline. Plant production is quite variable, as some basins in early stages of marl accumulation are nearly barren of vegetation, whereas others have developed a humus layer and reached ideal pH levels for *C. atherodes* and other forage plants.

Marl lake basins in wood bison range typically occupy closed depressions, well defined by ice-shoved shorelines (ramparts) and moraines. They apparently alternate between shallow lakes and relatively dry basins. During the early 1980s, when Mychasiw (1987) conducted his primary range survey in the Mackenzie Bison Sanctuary, only a relatively small part of most lake basins held any water. Because they contained driftwood, he suggested that the lake ramparts were of relatively recent origin and created by shoreward movements of ice. Aerial photos of marl lake basins from 1948 show that they were dry enough to support extensive sedge meadows (Mychasiw 1987). In preparation for bison reintroduction, Novakowski (1959) described the area from Falaise Lake to Lonely Bay as having no potential. That assessment may have been because higher precipitation in the 1950s flooded Falaise Lake and the other marl lake beds (Chowns 2002). After the release of 18 animals in 1963, surveys showed that the growing bison population had started using marl lake meadows by 1968 (Gates and Larter 1990). Low water levels shown by 1971 aerial photos of the marl lakes (Mychasiw 1987) suggest that a drying trend began in the 1960s.

Edward Lepine (pers. comm. 1979) stated that at the marl lake known as Boulogne Lake, he used to trap muskrats in “four feet of water” in the early 1960s, but those sites became “four feet of grass” by the 1970s. During the annual waterfowl survey of 1974, Kemper *et al*. (1975) observed that steadily receding water levels had transformed Falaise and Boulogne lakes into mere potholes surrounded by extensive, open sedge-grass meadows. Boulogne Lake formerly occupied approximately 12 square miles (31 km^2), but was reduced to an intermittent marsh that had become unimportant for waterfowl because of low water. Falaise Lake, once 50 square miles (130 km^2) in area, only had three small permanent wet areas remaining.

Through the 1970s until the late 1980s, the bison were mainly concentrated in a very small area of the Mackenzie Bison Sanctuary, primarily Boulogne, Falaise, Dieppe, Calais and other unnamed large marl lakes, where extensive *C. atherodes* meadows were available. Based on 1977 estimates, Peden and Reynolds (1981) suggested that the annual forage production in this area could support 14,000 bison. However, low water tables in the Mackenzie Bison Sanctuary led to concerns about loss of wet sedge meadow bison habitat. As drying of the soil progressed in the marl lake basins, Jacobson (1976) proposed that a plant succession pathway from sedge-grass meadow to shrubland and forest was occurring. Compared to 1948, Mychasiw (1987) documented that by 1971(latest aerial photos available for comparison), woody plant cover had encroached 11% into the sedge meadows of selected marl lakes. Woody encroachment had also been continuing unabated through to his 1983-1985 study of forage production and coverage of the major vegetation classes, but quantitative changes from 1971 aerial photos to 1980s satellite imagery could not be accurately assessed (Mychasiw 1987).

By the mid-1980s, precipitation started increasing in the Mackenzie Bison Sanctuary and water levels were rising incrementally (Gates *et al*. 1995). As water levels increased, woody plants were drowned, and dry grassy meadows were transforming into wet sedge meadows. After high levels had persisted for several years, sedge meadows in deeper parts of the lake basins also began to drown. This was exacerbated by the arrival of beavers and their dam building activities when flowing water returned to formerly dry creek beds (Chowns 1988). Water levels in the Mackenzie Bison Sanctuary reached a peak around 1992 (Gates *et al*. 1992a).

Precipitation began relenting in 1992, and by 1994 drought conditions had returned and the water table reached its lowest level in 1995 (Chowns *et al*. 1998). However, this period of drying was insufficient to allow the marl lake basins to return to mid-1980s water levels. Flooding has been prolonged and current levels have increased higher than those observed in 1992 (Armstrong pers. comm. 2012). Studies in Manitoba and Saskatchewan have shown that *C. atherodes* cannot survive longer than three years in water depths exceeding 76 cm (Harris and Marshall 1963; Millar 1973; Squires and Van der Valk 1992).

Since the time of optimal moisture levels and peak forage production in the 1970s and 1980s (Peden and Reynolds 1981; Mychasiw 1987; Smith 1990), there has been a net loss of marl lake bison habitat of unknown proportions (Armstrong pers. comm. 2012). At a decadal timescale, Sarmiento and Palanisami (2011) found that the precipitation effects of the Pacific North American circulation oscillation influenced Great Slave Lake and Lake Athabasca water levels, and the El Niño oscillation was phase coherent with Great Slave Lake only. Although climatic oscillations cannot be predicted, a drying trend can be expected to recur in the future that could restore marl lake bison habitat.

Fens

These landscape features evolve in shallow basins where the water table remains close to the ground surface throughout the growing season, and a shallow peat layer forms when accumulation of dead plant matter exceeds decomposition (National Wetlands Working Group 1997). *C. atherodes* may be very abundant until increasing depth of peat and decreasing pH shifts the competitive advantage to water sedge, *C. aquatilis* (Jeglum 1971), which has less food value for bison in summer and winter (Larter and Gates 1991).

The high precipitation that flooded the marl lake basins also affected the fens in the Mackenzie Bison Sanctuary. The capacity of peat to absorb moisture buffers flooding, and the water table may fluctuate within the column of peat without producing standing water. Although sedge meadows were not drowned, flooding appeared to temporarily render forage unavailable for bison in the early 1990s (Gates *et al*. 1992b).

If dead plant material accumulates above the water table and is able to decompose into well-humified peat, conditions improve for a diversity of woody species, including willows, dwarf birch and aspen, which out-compete sedges and grasses (Moss 1953). Increased peat decomposition and tree cover also occurs when drought lowers the water table (Gignac and Vitt 1994).

Only during drought conditions can fire penetrate the rooting layers of peat and cause significant retrogression. In experiments conducted by Hogenbirk and Wein (1991), deep burning reduced *C.atherodes* and *Calamagrostis canadensis* by up to 90%, and fire-scoured plots were often invaded first by pioneering plant species before graminoids returned.

In the Slave River Lowlands, Jalkotzy and Van Camp (1977) observed the major effect of fire in meadow habitats to be removal of dead plant material, which comprised over 50% of the standing plant biomass. This fire improved bison range by removing low quality plant material from the diet, and increasing the availability of new forage in spring by accelerating green-up. Reynolds (1976) suggested that periodic fire in the Hook Lake area would improve forage production by creating faster nutrient cycling. Although repeated surface burns appeared to reduce willow vigour in Slave River Lowlands meadows studied by Quinlan *et al*. (2003), survival remained high and less palatable bison forage species became more abundant.

The Bluefish River – Deep Bay area that was recommended for the 1963 Mackenzie bison transplant, is dominated by fens and intervening forest. Novakowski (1959) cautioned that because much of this had burned over in 1946, its value in terms of bison forage would be temporary as the trees return. In an attempt to reverse woody shrub invasion that was diminishing bison habitat value, prescribed fires were designed in 1991for the fens between Fort Providence and Deep Bay (Chowns 1992). The methodology used was to mimic native use of fire in historic times. More than 55,600 hectares were treated in this manner (Chowns *et al*. 1998).

Plant succession was being offset by a series of severe fires (1973, 1979, 1980, and 1995) that scoured out large fens in the Mink Lake area and northeast of Fort Providence (Chowns 1986; Chowns 1995). Drought conditions allowed fire to penetrate deep into the peat, burning out entire root systems of trees, willows and dwarf birch, which permitted sedges and grasses to invade. Eventually, the burns were producing a much greater diversity of herbaceous plants. *C. atherodes* was still favoured where it was encountered, but bison broadened their diet when foraging in these areas (Larter and Gates 1991).

Loss of sedge-grass meadow in fens through peat aggradation and woody shrub invasion is a relatively slow process measured over decades and centuries, but retrogression has often been established by a single fire. Because of flooding in the early 1990s and several large fires in the mid-1990s that caused retrogression of shrubland to meadow, there has probably been a net gain in fen habitat. Future habitat change depends on the frequency of these events.

Bogs

If dead plant material accumulates under cold, anaerobic conditions and *Sphagnum* moss species invade at the expense of sedges, fens may transform into bogs (Heinselman 1963). The most extensive bogs (also known as muskegs) occur on the Taiga Plains beyond the confines of the glacial lake beds (Ecosystem Classification Group 2007). Although peat accumulation is measured in centimetres per century, pH and plant species composition can change over a time scale of decades (Seischab 1984). *Sphagnum* actively lowers the pH of its environment by exchanging hydrogen ions for cationic nutrients such as calcium and potassium, which hampers microbial decomposition (Wentzel 1975). Accordingly, these plants are the most rapid producer of peat (Heinselman 1963). Poorly decomposed peat may spread beyond its original confining basin and rise above the surrounding landscape. Insulation of lower layers from solar radiation in summer, and increased cold penetration in winter because of snow interception by trees, results in the formation of permafrost (Zoltai 1995). As peat depth and permafrost prevent roots from reaching the mineral rich ground water, ericaceous shrubs and other plants adapted to these low nutrient environments must rely on precipitation for their moisture requirements (National Wetlands Working Group 1997). Such shallow rooted plants are intolerant to grazing and have developed chemical defences rendering them unpalatable to bison (Guthrie 2001).

Bogs grow in cool, moist climates. As poor providers of cover or forage, the growth of bogs is considered as a loss of habitat. However, their distribution may be related to past climate and bogs in latitudes of wood bison distribution are showing some evidence of degradation (Zoltai 1995).

Salt plains

Where brackish water seeps from uplands and is partially trapped in shallow depressions, the salinity may be prohibitive for plant growth. This is known to occur in the Salt Plains and the Slave River Lowlands, especially east of the Little Buffalo River (Raup 1935; Pringle *et al.* 1975). However, beyond these salt pans, decreasing salinity levels allow slender reedgrass (*Calamagrostis inexpansa)*, foxtail (*Hordeum jubatum*), Baltic rush (*Juncus balticus*), and other halophytic plants to establish (Raup 1935). In addition, some dense stands are formed by species such as alkali cordgrass (*Spartina gracilis*) and horned sea-blite (*Suaeda calceoliformis*), which are more often associated with halophytic grasslands in central North America (Schwarz *et al*. 1986). Trees are restricted to slight elevations of relief. Low forage biomass precludes much of the Salt Plains as winter bison range, and the availability of fresh drinking water limits use in late summer. Meadows containing dense stands of sedges and grasses extend into the soils of lowest salinity and are the most attractive to bison. The outer transition zone between herbaceous and woody vegetation is poorly defined on level terrain where the water table remains close to the soil surface.

Despite heavy precipitation that flushes the highly soluble salts and improves conditions for woody encroachment, and excessive flooding that causes retrogression to meadow, Schwarz *et al*. (1986) found no evidence of substantial vegetation change from examination of aerial photos between 1945 and 1982. This suggests that there has been no net gain or loss in bison habitat in the Salt Plains.

Karst terrain

An extensive area of karst terrain stretches through the Nyarling River subpopulation range of north-central Wood Buffalo National Park, continuing to the southern shore of Great Slave Lake. It appears to re-emerge in the Mackenzie range north of Lonely Bay, on the west side of Great Slave Lake (Ecosystem Classification Group 2007). This type of geological formation is described by Parks Canada (2012). It is shaped by the dissolution of soluble carbonate bedrock such as limestone, gypsum or dolomite by rain water that forms a weak carbonic acid solution. Sulphide oxidation may also be a corrosion factor. Subsurface drainage develops as rock is removed. If spaces develop underground, collapse sinkholes appear when the roofs cave in after being weakened by circulating water. Formations range from steep-sided bedrock chasms to gently sloped soil-lined bowls. The most widespread surface karst landforms are solution sinkholes that are created when water pools in shallow depressions and dissolves bedrock layers nearer the surface. Individual features frequently coalesce where they are densely clustered or aligned.

Valleys have been carved by past rivers, which may now flow underground, and these river beds become sunken when they are undermined. Characterized by the lack of integrated surface drainage, most of these valleys have dry stretches and blind pockets. The most notable karst valley is the Nyarling River, which disappears from the surface to flow underground for 26 km. A similar unnamed drainage way flows from west to east, north of Lonely Bay.

These formations may contain periodic or permanent water, and often support forage preferred by bison, especially in summer (Fuller 1966). Raup (1935) described the development of meadow vegetation in shallow sinkholes. Although they are relatively small food patches, hundreds of them pock-mark the bison ranges, and the sunken valleys are tens of kilometres in length. Karst depressions providing sustenance may be likened to “oases” for bison in densely forested landscapes where most water is subsurface. In addition, the valleys provide important travel corridors for these animals. Karst terrain in the bison ranges is very unstable and trees tilting haphazardly are signs of recent activity. There is no evidence suggesting any net gain or loss of bison habitat in karst terrain.

Uplands

High ground in wood bison range of the NWT is generally forested and characterized by coarser soils and greater depths to the water table. Raup (1933) was one of the first to recognize that forests are most valuable as bison feeding habitat when they are at early seral stages, usually as a result of fire. Timber harvesting also has the potential to improve habitat on a small scale. Clearcuts examined in northern Alberta provided adequate forage for wood bison during the summer, and capacity typically started decreasing eight years after the harvest (Redburn *et al.* 2008).

Early travelers in wood bison range (Mackenzie 1801; Russell 1898; Preble 1908; Seton 1911; Blanchet 1926) commented on the extent of treeless prairies that now seem to be much diminished. Alexander Mackenzie (1801) remarked about hunting bison at Mills Lake and the extensive prairies on both sides of the Horn River abounding with bison. Blanchet (1926) mentioned large prairies within 50 miles (86 km) of Fort Providence. When leaving that settlement for the winter trail to Fort Rae, travelers were cautioned to allow themselves plenty of time to cross the first three prairies, otherwise they would be unable to find enough wood for a camp fire (Russell 1898). Today, almost all of this prairie land has been usurped by early successional forest.

In his rejection of areas at the Horn River and westward as a potential site for bison reintroduction, Novakowski (1959) commented that their value would be temporary as these were burns that would revert back to forest. Holsworth (1960) described areas of Wood Buffalo National Park where fires had been of adequate frequency to firmly establish grassland for considerable periods of time. He also commented that some of the large grassy meadows described by Raup (1933) and Soper (1941) from the 1930s had almost disappeared by the 1950s.

Holsworth (1960) suggested that after a forest fire, transpiration may be reduced to the point where a higher water table hinders tree regeneration. Rowe and Scotter (1973) found that *Calamagostis canadensis* and various sedge species frequently move into recently burned areas of the boreal forest as they are fast growing and capable of rapid invasion by seed and vegetative means, and burning seems to stimulate flowering and seed production. They also noted that a vigorous growth of sedges, grasses and forbs may continue for about ten years.

Campbell and Hinkes (1983) reported that a fire in black spruce forest expanded sedge-grass winter range of the Farewell bison herd in Alaska. The fire also removed belts of dense black spruce allowing insular meadows to become more accessible. Connectivity with summer range was also enhanced.

Anthropogenic burning has been well documented in North America by Pyne (1997) as a means of improving bison habitat by transforming large areas from forest to grassland. Until the 20th century, lightning fires burned unchecked across the range of wood bison in summers of low precipitation, and aboriginal people were adding to the burn pattern on the landscape by igniting fires in the spring, fall, and wet summers to suit their needs. With fire, they could easily maintain grasslands where conditions would normally allow invasion by trees and shrubs. Modification of the environment by native people was the result of repeated controlled surface burns every few years, broken by occasional large, stand-replacing fires in times of drought. Habitats were to a large extent maintained by controlled burning practiced by native peoples in the wood bison range of northern Alberta (Lewis 1977; Lewis 1982; Lewis and Ferguson 1988).

To help understand the structure of past and present vegetation communities, and natural fire frequency in this area, Chowns (2002) carried out a fire history study of the Mackenzie bison range. Over a 200 year time span, the average fire interval was found to be 40 years, and appeared to be much shorter in the lowland sector lying below 190 m elevation (33 years), than the upland sector (46 years) above 190 m elevation. The larger, more frequent fires in the lowland sector may be explained by higher fuel connectivity and aboriginal use of fire. A grassy understory enables fire to spread faster over large areas and recur more frequently than a fuel bed with higher bulk densities (Miller and Urban 2000). In the study area, multi-year layers of grass and sedge often accumulate and provide heavy potential fire fuel loads. The lowland sector, which has always attracted the most human activity, showed considerable evidence of fire in years that may not have been subjected to particularly dry weather. According to Petitot (1891), aboriginal people in the Fort Providence area used fire to manage the environment to their advantage.

Although high fire frequencies produced optimal upland bison habitat before the implementation of organized fire suppression, several large fires in the mid-1990s have contributed to a net gain in upland bison habitat over the past three generations.

Distribution trends

Originally, all wood bison in the NWT and adjacent areas probably existed as one extensive metapopulation (Roe 1970; Reynolds *et al*. 2003). The following is the approximate sequence of extirpation from historical distribution: Alaska and the Yukon – early 1800s (Stephenson *et al*. 2001), upper Hay River – 1860s (Preble 1908), middle Peace River – 1870 (Butler 1873), Grande Prairie district – 1870s (Dawson 1881), eastern Slave River Lowlands – 1880 (Radford 1911), west of Great Slave Lake – early 1880s (Blanchet 1926), Clearwater River of Alberta and Saskatchewan – 1888 (Seton 1927), lower Athabasca – 1896 (Jarvis 1897), Liard-Nahanni – late 1890s (Rhoads 1897), south of lower Peace – 1898 (Radford 1911), Fort St. John district – 1906 (MacGregor 1952) and western Slave River Lowlands – 1911 (Mulloy 1912). The total number of bison probably stopped declining between 1896 and 1900 (Soper 1941), even though isolated herds were continuing to disappear. The two last remaining herds west of the Salt and Little Buffalo rivers were able to reverse the decline and grew to about 1,500 by 1922 (Seibert 1925).

In the NWT, it appears that the Nyarling River subpopulation of the Greater Wood Buffalo Ecosystem has always been intact. Bison that moved from Wood Buffalo National Park to the western Slave River Lowlands (Grand Detour subpopulation) in the early 1930s (Soper 1941), and continued across the Slave River to the eastern Slave River Lowlands (Hook Lake subpopulation) in the late 1930s or early 1940s (Fuller 1950), quickly reoccupied all of their former range.

After its reintroduction in 1963, the Mackenzie population has been undergoing range expansion to the west and north. Bison became well established in habitat east of Mink Lake after a fire in 1980. Frequent fires had been maintaining these sedge-grass meadows. Mills Lake was occupied a few years later. Before the 1994 fire north of Lonely Bay, a few bison had wandered to some of the marl lake beds in that area. The fire enhanced movements from core areas in the south and facilitated further range expansion northward into unoccupied habitat (Chowns 1996). Until 1995, bison seldom wandered west of Mink Lake, even though there had been frequent fire in the past and unforested tracts were very widespread. After an extensive fire that summer, bison surged into this new habitat, and it was soon occupied by hundreds of animals. Even while the plains west of Mink Lake were still largely devoid of vegetation, large numbers of bison were very attracted to this open habitat (Chowns 1997).

The Nahanni population was reintroduced into part of its former range near Nahanni Butte in 1980 with 28 animals being released. This founding population fragmented and dispersed widely into northeastern British Columbia. Augmentations of 12 animals in 1989 near Nahanni Butte and 59 animals in 1998 near Fort Liard bolstered the population along the Liard Valley between the two communities (Larter and Allaire 2007). More recently, the population has expanded to the west up to the Kotaneelee Valley and to the northeast down the Liard River to Poplar River (Larter and Allaire 2013).

THREATS AND LIMITING FACTORS

Human-caused mortality (e.g., harvesting) and disease management actions like vaccination round-ups and culls for disease control, represent an important historical threat to wood bison; one that populations have not yet recovered from. Today, infectious disease, human-caused mortality, vehicle collisions, habitat loss (e.g., diminishing flood/drawdown cycles), low genetic diversity, fire management, predation, and episodic catastrophes (e.g., drowning) are considered the most important threats to wood bison in the NWT. These are discussed in more detail in the pages that follow.

Human-caused mortality

Human-caused mortality is primarily due to overhunting of severely reduced bison populations in the past, from which populations have not yet recovered. Humans are very efficient predators of large mammals, and even before firearms, subsistence use may have influenced bison abundance and distribution (e.g., Van Vuren 1987). Humans preferentially used the most profitable food available, which often meant large mammals such as bison.

The long-term decline in wood bison was exacerbated by the advent of the fur trade, which relied heavily on the meat provided by wood bison (Chowns 1990; Ferguson 1993). Commercial exploitation for hides was not a contributing factor. After witnessing the tragedy of plains bison, the Hudson Bay Company refused to trade in wood bison hides (Russell 1898; MacFarlane 1908).

Hornaday (1889) chronicled the disappearance of plains bison across North America as firearms arrived, and predicted the demise of wood bison in the same manner if conservation measures were not taken. He also mentioned the character of their habitat as an advantage for wood bison that prevented hunting on horseback. According to fur traders and records in the Mackenzie District (Chowns 1990) and Athabasca District (Ferguson 1993), trading posts had a huge appetite for meat. Although the species of animal was not always recorded, efforts focused on large mammals. Ferguson’s (1993) analysis shows that this factor may have initiated the great decline of wood bison between 1800 and 1820 when rivalry between competing trading companies was most intense and creation of new posts was prolific. By 1830, it was evident that bison depletions were quite widespread and populations were not recovering.

The change from hunter-gatherer societies to a fur harvesting lifestyle that led to greater mobility, more dogs to feed, and the earnings to acquire firearms meant greater pressure on bison that were already in serious decline. By the late 1800s, ever increasing distances to find bison were seen as warning signs of imminent extermination (e.g., McConnell 1891; Pike 1892; Russell 1898; Whitney 1898; MacFarlane 1908; Radford 1911).

The *Unorganized Territories Game Preservation Act* of 1894 banned the hunting of bison, but it was not publicized or enforced north of 60° latitude until Royal North West Mounted Police officers came to Fort Smith (Jarvis 1897). The creation of Wood Buffalo National Park in 1922, along with hunting and trapping restrictions, was a further measure to discourage human access to the bison range.

Management actions are also a source of human-caused bison mortality. From November 1964 to March 1965, 522 bison of the Grand Detour subpopulation were slaughtered in a futile attempt to prevent the disease from spreading through Wood Buffalo National Park (Novakowski 1965). Untainted meat was sent north to Inuit communities for human consumption (Beck pers. comm. 2016). At Hook Lake and Wood Buffalo National Park, large scale annual round-ups were carried out for vaccinations from 1965 to 1977. This was very disruptive to the herds at a critical time when calves were young, and the average mortality from these round-ups was estimated at two percent of the animals handled (Millette and Sturko 1977). Present-day management includes slaughtering bison that cannot be deterred from entering communities, as well as those that venture into the Bison Control Area. Removals from the Mackenzie population in Fort Providence have ranged from 0 to 8 annually in recent years, and 0 to 3 annually from the Nahanni population in Fort Liard (Armstrong pers. comm. 2015)

As bison reappeared in the Slave River Lowlands during the 1930s and 1940s, the Slave River Preserve was in effect (Robinson and Robinson 1946; Ogilvie 1979), which protected the game and fur harvesting rights of General Hunting Licence (GHL) holders who were mainly aboriginal people. The newly founded Hook Lake and Grand Detour subpopulations were considered surplus hybrids from Wood Buffalo National Park, and when the Slave River Preserve was abolished in 1955, the implementation of a harvest season on bison for non-native residents was allowed (Van Camp 1987). In 1959 and 1970, outfitters were licensed to guide non-resident hunters. When meat was no longer available from slaughters in Wood Buffalo National Park, northern residents turned more attention to hunting the animals that had moved outside of the Park.

Harvest of the Hook Lake and Grand Detour subpopulations exceeded 165 per year from 1968 to 1974 (Calef 1976). As the Hook Lake subpopulation declined drastically between 1974 and 1976, the absolute numbers killed by hunters also dropped, but the hunter harvest rate continued at 8-10% of the subpopulation per year, as it had since 1969 (Van Camp 1987). After non-GHL hunting was terminated in 1977, GHL holders harvested 4-8% of the population, which, without the additive effects of predation and other sources of mortality, was still higher than the 3.9% recruitment rate. Calef (1976) suggested that overhunting may have been a contributing factor to the 1974-1976 decline, which was aggravated by the preference of hunters for young cows, the most productive segment of the subpopulation. Because bison of the Hook Lake and Grand Detour subpopulations were considered hybrids, more restrictive legislation for GHL holders was never introduced.

Today, the Nyarling River and Hay Camp subpopulations in Wood Buffalo National Park are completely protected from hunting in the NWT by the Canada *National Parks Act* (2000), except for animals that wander outside of national park boundaries. Because wood bison in the NWT were designated as a species in danger of becoming extinct under regulation (Game Declared in Danger of Becoming Extinct, C.R.C., c. 1236, enabled by the *Northwest Territories Act*), the reintroduced Nahanni and Mackenzie populations were also granted special protection from unrestricted hunting. Protection measures were carried over in the regulations when the new NWT *Wildlife Act* (SNWT 2014, c 31) came into force in November 2014. Harvest levels of these animals are managed through quotas (ENR 2010; Big Game Hunting Regulations, R-019-92). Harvest of the Nahanni population has ranged from 2-5 animals annually since 2008 (Larter pers. comm. 2016a). Quotas for the Mackenzie population were adjusted after the 2012 anthrax outbreak, and all hunting of the Mackenzie population was halted until the population shows recovery (with the exception of 4-5 males harvested annually by the Deh Gah Gotie First Nation under a Wildlife Permit). Resident harvest of the Slave River Lowlands subpopulations (Hook Lake and Grand Detour) is typically 3-5 animals annually (Aboriginal harvest from these subpopulations is not recorded) (Armstrong pers. comm. 2016a).

During the Hook Lake decline in the 1970s and 1980s, the territorial government sought a voluntary reduction in GHL harvest (Van Camp 1987). This endeavour failed to achieve its objectives.

Disease

Of the nine diseases of concern listed by the American Bison Specialist Group, there are four infectious bacterial diseases that are currently of concern to the conservation of wood bison (Aune and Gates 2010). The American Bison Specialist Group considered anthrax (*Bacillus anthracis*) and bovine tuberculosis (*Mycobacterium bovis*) to have the most serious disease implications for bison restoration. They ranked bovine brucellosis (*Brucella abortus*) as a significant impediment and Johne’s disease (*Mycobacterium avium* subspecies *paratuberculosis*) as a medium impediment (Aune and Wallen 2010). No highly effective vaccines are available for preventing diseases in free-roaming bison (Aune and Gates 2010).

While the Greater Wood Buffalo Ecosystem population has been co-evolving with tuberculosis and brucellosis for several generations, and has a broader genetic diversity to draw upon for pathogen resistance, the Mackenzie and Nahanni wood bison populations, relatively unexposed to these diseases and with less genetic diversity, may be more vulnerable to the lethal effects of the two diseases.

Anthrax

Anthrax is a naturally occurring disease that is endemic in northern bison. Outbreaks of varying proportions have arisen periodically in the Greater Wood Buffalo Ecosystem and Mackenzie populations, and many years may elapse between epidemics of high mortality (Elkin *et al*. 2013). Between 1962 and 2015, there have been eight documented outbreaks in the Slave River Lowlands, 13 in Wood Buffalo National Park, and three in the Mackenzie population. These outbreaks have killed at least 2,266 bison in total; additional outbreaks and anthrax cases may have gone undetected (Elkin *et al*. 2013; New 2014; Elkin pers. comm. 2016; see *Appendix A6*, p. 233, for details). No cases of anthrax have been documented in the Nahanni population (Larter pers. comm. 2016a).

In past occurrences, even though mass mortality was sudden, it was generally infrequent (Gates *et al*. 1995). Anthrax epidemics only occur in summer, and mainly affect mature bulls when wallowing, mating, and biting insects are most intense, and high densities of bison compete for diminishing water and food supplies (Gainer and Saunders 1989; Dragon and Rennie 1995). Although poorly understood, transmission pathways for anthrax include ingestion and inhalation from the environment (Elkin *et al*. 2013). Determining how bison ingest or inhale enough spores to trigger new epidemics and spread the disease however has been problematic (Elkin *et al*. 2013).

The first documentation of yearling and calf losses to the disease was at the Salt Plains of Wood Buffalo National Park in 1991, when 9 of the 34 bison that died were female (Broughton 1992). Another narrower spread between deaths of bulls and cows was a 3:2 ratio after the 2001 outbreak in Wood Buffalo National Park. Although the 2012 outbreak in the Mackenzie population also claimed juveniles and an unusually high number of females (Armstrong pers. comm. 2012), epidemics have always affected more mature bulls in the population. The 2012 outbreak in the Mackenzie population has been the most serious to date, killing an estimated 30% of the population, across all age groups, with 40% of these being mature females (Armstrong pers. comm. 2012). For more information on anthrax, refer to *Appendix A6* (p. 233).

Brucellosis

Bovine brucellosis arrived in North America with European cattle. Infected plains bison from Wainwright were likely the origin, and although brucellosis was not discovered in Wood Buffalo National Park until 1956, it has surely been present since the 1920s. It is present only in the Greater Wood Buffalo Ecosystem. This disease mainly impacts female bison reproduction by causing abortion of the foetus by the third trimester of pregnancy (Tessaro 1989). Most animals abort during the first pregnancy following infection, but will carry subsequent pregnancies to term (Canadian Food Inspection Agency [CFIA] 2012). Both sexes are susceptible to inflammation of the reproductive tract, and sterility in advanced cases. Bursitis and arthritis caused by concentrations of *B. abortus* in the joints results in lameness (Tessaro 1989, 1992). The disease may be transmitted through oral contact with aborted foetuses, infected placentas, uterine discharges and contaminated forage (Tessaro 1989). Although bulls may excrete large numbers of *B. abortus* in their semen, no evidence of venereal transmission of the disease has been found (Robison *et al*. 1998).

Even if the pathology of brucellosis in bison is fairly well understood, the effects at the population level have only been investigated in Yellowstone National Park. Dobson and Meagher (1996) suggested that brucellosis needs a population threshold of 200 bison to persist. In Wood Buffalo National Park, Joly and Messier (2004a) did not detect any decrease in prevalence rates since the 1950s, despite a major decline in population size. This observation included the Nyarling River subpopulation, which maintained its numbers between 112 and 236 bison. Since brucellosis appears endemic in this subpopulation, the threshold number may be lower than what Dobson and Meagher (1996) suggested.

A difficulty in brucellosis diagnosis is that a bison testing seropositive does not necessarily signify that it has the disease. Serology testing also detects the presence of antibodies in animals that have acquired resistance or immunity. Infection can only be proven if the disease organism is cultured from the animal's tissues. Yellowstone National Park bison have an antibody prevalence of approximately 50% (Rhyan *et al*. 2009). Fuller *et al*. (2007) found that brucellosis status and age of the maternal females in Yellowstone National Park affected birth rate. Calf production was lowest for three year old females infected that year, higher for females already brucellosis positive, and highest for females brucellosis negative. Females older than four years had the highest birth rates for every class of disease status. Modeling simulations by Fuller *et al.* (2007) suggested that brucellosis eradication would result in a 29% increase in population growth rate for the Yellowstone National Park bison population because of higher birth rates.

In a serological survey of 2,365 bison in and around Wood Buffalo National Park, sampled from 1959 to 1974, Choquette *et al.* (1978) found that 31.2% were seropositive for brucellosis. The discovery by Joly and Messier (2004a) that 30.9% of 342 bison tested positive from 1997 to 1999 shows that a seropositive rate of approximately 30% for the Greater Wood Buffalo Ecosystem has been fairly constant over a 50 year time span. Comparing these effects with Yellowstone National Park bison is complicated by the fact that 10% of these animals test positive for both brucellosis and tuberculosis (Joly and Messier 2001) and the two populations have a much different relationship with predators.

Tuberculosis

Bovine tuberculosis, like brucellosis, arrived in North America with imported cattle during European settlement, and has been endemic in the Greater Wood Buffalo Ecosystem since the introduction of plains bison from Wainwright in the 1920s. Almost all modes of infection are through the respiratory and digestive systems (Tessaro *et al.* 1990) and it occasionally passes from mother to offspring via the placenta or milk (Tessaro 1992). The Hook Lake Wood Bison Recovery Project was an experimental attempt to salvage bison from a diseased population (Himsworth *et al.* 2010). The detection of asymptomatic tuberculosis in some of the animals after nearly ten years of quarantine demonstrated the incubation capacity of this pathogen.

Based on the condition of carcasses from the 1952-1956 Wood Buffalo National Park slaughters, Fuller (1961, 1966) estimated the annual mortality of bison from tuberculosis at 5%. The small sample size examined by Tessaro (1987) indicated 6%, but it is impossible to know how many animals near death from the disease would succumb to other causes such as predation. Joly and Messier (2001) estimated the combined effects of tuberculosis and brucellosis on adult mortality at the population level to be much lower at about 1% per annum. Their number was derived from a 10% decrease in survival for the 10% of the bison that have both diseases. Carbyn *et al.* (1993) estimated from a sample size of 3,412 that 1% exhibited moderate to severe lameness, and that a further 1% showed various degrees of emaciation and debilitation.

From 1,508 bison examined at Hay Camp, Fuller (1961, 1966) noted the incidence of tuberculosis to be 39%, but it was significantly lower in the Delta subpopulation. Also, it had a tendency to rise rapidly in younger animals until about three years of age, and then more slowly in the older age classes. He suggested a possibility that this observation is the result of lethal removal of the most infected animals, and higher survival of those with genetic resistance.

Joly and Messier (2004a) found an incidence of 49% in the Nyarling River subpopulation (females only), Hay Camp and Delta subpopulations, and noted that the prevalence of tuberculosis was consistently 8-10% lower in the Delta subpopulation, compared to the Hay Camp animals. Also, males showed a higher prevalence than females, and it increased at a higher rate with age in males (1.26 times for each additional year of age) than females (1.1 times with each year of age). They were unable to detect an effect of age on prevalence in the Nyarling River subpopulation for females two years of age or older probably because of smaller sample sizes and fewer samples of younger adult females. In the Hay Camp subpopulation, prevalence of tuberculosis declined in females 11+ years of age relative to younger age classes. Rodwell *et al*. (2001) suggested a decline in prevalence of this disease in aged African buffalo relative to younger individuals due to a decline in relative survival in tuberculosis-positive buffalo in older age classes. Among Delta females, prevalence continued to increase with age. Carbyn *et al*. (1993) found that bison in the oldest age class were disproportionately represented in wolf kills in the Hay Camp area at 20.8%, though they only comprised 10.8% of the subpopulation. In the Delta area, the oldest age class formed 14.0% of wolf kills versus 10.8% of the subpopulation. If wolves in the Hay Camp area selected for aged bison, then there would be an expected decline in tuberculosis prevalence relative to younger age classes. An alternate explanation they offered was that general body condition of bison may be higher in the Delta subpopulation, resulting in a more robust immune system to slow progression of the disease.

During the 1952-1956 Hay Camp and Delta slaughters, Fuller (1961, 1966) observed, based on post-mortem examination, the pregnancy rate from a sample size of 654 females to be higher in tubercular bison, but not statistically different from non-tubercular animals. He suggested that the added physiological stress of pregnancy may have made cows more susceptible to the disease. Fuller did not indicate whether tubercular bison were showing clinical signs or merely testing positive for tuberculosis. Since brucellosis was not discovered in Wood Buffalo National Park until 1956, the interactive effect of both diseases could not be taken into account.

From a sample size of 205 bison collected from 1997 to 1999, Joly and Messier (2005) found a reduced probability of pregnancy for tuberculosis-positive females only in the Nyarling River subpopulation. However, they discovered in all Wood Buffalo National Park subpopulations that the probability of pregnancy was 30% less likely for females with both brucellosis and tuberculosis, compared to females with one or neither disease. Joly and Messier (2005) could not account for the difference in pregnancy rates of diseased females between the 1950s and the 1990s data. One suggestion was that their February-March sampling results were more impacted by late gestation brucellosis-induced abortion, than the December-January slaughters.

As with brucellosis, tuberculosis levels have not declined over time despite a major decline in population size, and prevalence rates were no different between high and low density populations (Joly and Messier 2004a). This stability in relative prevalence suggests that any decline in transmission does not occur until very low densities. The only feasible method for eradicating tuberculosis from a herd seems to be the removal of all infected animals, as well as all exposed susceptible animals (Northern Diseased Bison Environmental Assessment Panel 1990; Animal and Plant Health Inspection Unit – United States Department of Agriculture [APHIS USDA] 2005; CFIA 2012). In the Greater Wood Buffalo Ecosystem population, we can assume that all bison have been potentially exposed and are susceptible to infection.

Johne's disease

Clinical cases of this disease have never been documented in any free-ranging wood bison even though the causal organism is evident in all NWT populations (Elkin *et al*. 2006; Forde *et al*. 2013). It is mainly a chronic disease of domestic ruminants and clinical signs may lead to diarrhoea, weight loss, decreased milk production, and mortality (Buergelt *et al*. 2000). The origin of infections in wood bison is uncertain (Elkin *et al*. 2006). Forde *et al*. (2013) suggested that weakened animals might be quickly culled from the population through predation, and otherwise go undetected by wildlife managers. They also stated that it is unlikely that Johne's disease causes a high level of mortality in wood bison, but such chronic diseases can have a debilitating impact on a population.

Disease synergy

Disease synergy may be best described as an interaction between diseases where one enhances the pathological effects of another, or the immune response is too overwhelming for the host (Joly and Messier 2005). Although no brucellar lesions were reported among 1,000 bison slaughtered outside of Yellowstone National Park in 1996-97, these clinical signs are common among Wood Buffalo National Park bison where tuberculosis is also present (Tessaro *et al*. 1990). Compared to bison with one or neither disease, Joly and Messier (2005) found that bison testing positive for tuberculosis and showing a high titre for brucellosis, were 2.5 times more likely to die during the early winter season and 3.7 times more likely to die during the late winter season than bison testing negative for either or both diseases.

Vehicle collisions

Collisions between bison and vehicles are an important cause of mortality for wood bison populations in the NWT (Nishi 2004; ENR 2010). Wood bison use road rights-of-way for grazing and movement and are frequently found along roads. Collisions occur on all NWT highways that run through bison ranges (ENR 2010) and an average of about 20 vehicle-bison collisions are reported to police every year in the NWT (Department of Transportation 2012). Most collisions involve a single animal, although sometimes multiple animals are involved (Wildlife Collision Prevention Program 2016). The bison most frequently hit by vehicles are adult females, followed by calves, then adult males (ENR 2010; Wildlife Collision Prevention Program 2016). Collisions are most frequent from August to December (ENR 2010).

Most vehicle-bison collisions in the NWT involve the Mackenzie bison population (about 84%

of collisions; Wildlife Collision Prevention Program 2016). There have been up to 30 collisions reported in a single year on Highway #3 (Armstrong pers. comm. 2016b) and it is possible that others are unreported. There were over 380 bison killed in at least 270 vehicle-bison collisions on Highway #3 between 1989 and 2015, with an increasing trend in collisions until 2013. The increase was attributed to increased speed and volume of traffic, movement and expansion of the bison population, and improvement of the highway. It was expected that collisions would increase further with an increase in night-time traffic because of the new Deh Cho Bridge; however, there were fewer collisions recorded in 2014 and 2015 than in the two previous years (ENR 2010; Armstrong pers. comm. 2016b).

Vehicle-bison collisions also affect other wood bison populations in the NWT. About 15% of vehicle-bison collisions in the NWT involve the Nahanni population. Vehicle collisions resulted in 12 bison mortalities from 2000-2005 (Larter and Allaire 2007) and 9 bison mortalities from 2007-2015 (Larter pers. comm. 2016b) in the Nahanni population. Approximately 1% of vehicle-bison collisions in the NWT involve the Greater Wood Buffalo Ecosystem population along Highway #5 to Fort Smith (Wildlife Collision Prevention Program 2016) and the Government of the Northwest Territories' Department of Transportation has expressed concern about collisions along this highway (ENR 2010).

Loss and deterioration of habitat

Agriculture

The main loss of wood bison habitat in Canada has occurred in northern Alberta and northeastern British Columbia as fertile lacustrine and alluvial soils have been converted into agricultural land (Strong and Gates 2009).

Agriculture began in the Mills Lake – Horn River Delta meadows in the late 1960s and involved cattle ranching, haying and crop cultivation (Kemper *et al*. 1975). By 1974, there were three operations near the Horn River delta on the northeast shore of Mills Lake, and lease applications had been filed for the entire remaining area. Although agricultural activities halted after the 1974 flooding and the end of government assistance, the leases were still in place. By 1981, they were all acquired by an enterprising rancher from the United States hoping to start a beef cattle operation. After his endeavour failed, the leases again went dormant, waiting for a buyer. In the mid-1980s bison started to invade the Mills Lake – Horn River delta and this area has since become one of the most important core habitats for the Mackenzie bison population. Agriculture was a potential threat that did not quite materialize.

Agricultural interests have been apparent in the Liard Valley and Slave River Lowlands since the 1960s (Day 1966, 1972), although there have never been large scale initiatives.

River flow regulation

The Bennett Dam on the Peace River could represent a threat given its potential impact on floodplain habitats downstream, including the Slave River Lowlands, Great Slave Lake, and the Mackenzie River, although negative effects are probably obscured by long-term climate variation (for more information on the impacts of flow regulation on downstream floodplain habitats, refer to the section on *Habitat trends*, p.109). This concern may be heightened with the recent approval of the Site C dam by the Government of British Columbia (Government of British Columbia 2014). The Site C hydroelectric project would result in changes to the entire river flow regime during the construction phase (BC Hydro 2013).

Fire suppression

As described in the section on *Habitat trends* (p. 109), frequent fire is a component of wood bison habitat maintenance. The Dominion Forestry Branch emerged at the turn of the 20th century with the responsibility of protecting all natural resources in western Canada, including the last wild wood bison. There was a pervasive belief among the foresters in charge that fire was destructive to bison and threatening their range. As ‘buffalo patrols’ found little evidence that wolves or native people were affecting populations, locating and extinguishing fires throughout bison range became a top priority (Hewitt 1921). This may have contributed to the bison conservation problem that the government was trying to remedy, and the unintended consequence was that upland habitats may have started to deteriorate in the 1910s (McCormack 1992).

Forest expansion due to fire control after the mid-1900s likely contributed to a regional reduction in carrying capacity (Strong and Gates 2009). Suppression included fires caused by both lightning and humans. Consequently, northern sedge-grass habitat diminished in this century, replaced by forests resulting from fire suppression programs and new European-based land use patterns such as agriculture and timber harvesting (McCormack 1992). This is problematic from a bison management perspective, given their reliance on sedge-grass meadows. Holsworth (1960) stated that, at that time, the Wood Buffalo National Park forest management policy of total fire suppression conflicted with bison habitat objectives.

More recently, the natural role of fire in ecosystems has become better understood and is recognized in the NWT’s Forest Fire Management Policy (Government of the Northwest Territories [GNWT] 2005), and the Parks Canada policy on ecosystem-based management (Parks Canada 2015). Fire management actions that are considered for each fire include monitoring the fire, protecting values at risk, and fighting the fire. The actions that are taken depend on the location of the fire, availability of resources, fire behaviour and the potential to affect human life, property, natural resource values and cultural resource values (GNWT 2005). The number of fires and the area burned each year in the NWT fluctuate dramatically (ENR 2015a).

Frequent wildfires in bison range have produced the greatest results for habitat restoration. However, ignitions are impossible to predict and spread is often driven by weather. As resource managers and the general public develop a better understanding of the natural role of fire in the ecosystem, and how to use it safely for resource management, there may be greater confidence in using fire as a bison habitat improvement tool. The NWT and Parks Canada policies provide for the possibility of prescribed burning to achieve forest management, land use and ecosystem objectives (GNWT 2005; Parks Canada 2015). If fire is to be an effective tool for improving bison habitat, resource managers would also need to consider the risk to other values. For example, boreal caribou are a threatened species at both the national and NWT level and important boreal caribou habitat in the NWT is characterized by low fire frequencies (Gunn *et al*. 2004). There is a national critical habitat requirement in place under the *Species at Risk Act* to maintain at least 65% of boreal caribou habitat in the NWT as unburned within the last 40 years, as well as undisturbed by the human footprint (Environment Canada 2012). Thus the habitat needs of boreal caribou and wood bison may be seen as potentially incompatible where the species' ranges overlap, and a fire management strategy would need to accommodate the needs of both species.

Low genetic diversity

The fact that most wood bison herds have originated from only a few individuals has led to concerns about genetic variability. According to Nei *et al*. (1975), genetic variability is expected to decline rapidly in populations reduced to very small numbers, but if population size is restored, genetic variability starts to increase very slowly because of new mutations. If population size grows rapidly after going through a bottleneck, the reduction in average heterozygosity is low even if bottleneck size is extremely small. Conversely, the loss in the average number of alleles per locus is greatly affected by bottleneck size, but less so by the rate of population growth. A well-documented example is Przewalski's horse, descended from 13 founders. It may have lost 60–70% of the original alleles because of inbreeding and genetic drift, primarily during the early generations of captivity (Hedrick *et al*. 1999).

Founder effect

For every gene locus, there is at least one allele, and the more alleles carried by members of a population, the greater the genetic diversity. When a new population is established, it contains only a subset of the total alleles available from the parent population. If the number of founders is small, the subset of alleles will be a smaller fraction. In the late 1800s, many millions of plains bison were reduced to an effective founder number of less than 100 (Hedrick 2009). Even though the reduction in population size for wood bison from thousands to hundreds (Soper 1941) would likely have been less important to the genetic integrity of wood bison, all bison herds have been derived from remnants of much larger populations and the original gene pools may be poorly represented (Boyd *et al*. 2010). Further loss of genetic diversity is exacerbated if new parent populations are already genetically impoverished.

Wilson and Strobeck (1999) examined a number of bison herds and confirmed a positive correlation between the number of founders and the average number of alleles. The founder effect can foster genetic divergence in populations as shown by the genetic distance between the Mackenzie Bison Sanctuary and the Elk Island National Park Isolation Area wood bison populations. In the early 1960s, these two wood bison populations were founded from 18 and 11 individuals respectively, from the same Nyarling River area of Wood Buffalo National Park. However, their genetic distances show that their gene pools are quite distinct (Wilson and Strobeck 1999). Consequently, genetic diversity has not been well distributed among disease-free wood bison herds in Canada, especially herds started from the Elk Island National Park Isolation Area.

Continuing studies by McFarlane (Zittlau) *et al*. (2006) found that the average number of alleles was highest for Wood Buffalo National Park and Hook Lake subpopulations, indicating that they are the most genetically variable populations. Even though their founder number was probably the highest in North America (> 200 animals), Pertoldi *et al*. (2009) detected long chromosomal regions fixed for one allele in Wood Buffalo National Park samples, demonstrating that Greater Wood Buffalo Ecosystem bison are not very rich by normal genetic standards.

Halbert and Derr (2008) examined 11 federal bison herds in the United States and arrived at similar conclusions as Wilson and Strobeck (1999) regarding founder effects. Those populations with the highest genetic variation (National Bison Range and Yellowstone National Park) had many founders and multiple founder sources. The lowest variation was in the Theodore Roosevelt National Park – North herd, which was founded from 20 animals in 1962.

Inbreeding depression

Keller and Waller (2002) reviewed inbreeding effects in wild populations. Mating among closely related individuals causes a higher probability of recessive deleterious alleles being expressed in the progeny. The resulting decreased fitness, known as inbreeding depression, is often manifested by under-weight births, low survival and poor reproduction, as well as reduced resistance to disease, predation and environmental stress. These ill-effects may be sudden and severe on a population. Theoretically, recessive deleterious traits can be purged by natural selection acting against them, but the process is often inefficient.

In the large ancestral bison population, there would have been recessive detrimental genetic traits masked by dominant favourable alleles (Hedrick 2009). Hedrick (2009) suggested that the rapid reduction in population size of the late 1800s may have resulted in some detrimental alleles becoming fixed, or increasing in frequency by chance, resulting in lowered population fitness. The reproductive success of European bison has declined with inbreeding (Olech 1987). In North America, inbreeding depression has only been documented in the Goodnight Plains Bison herd, Texas, but suspected for the Badlands National Park herd in South Dakota (Berger and

Cunningham 1994). Because all re-established wood bison populations were founded by very low numbers from Wood Buffalo National Park, some degree of inbreeding would have been inevitable. Although there is no evidence of inbreeding depression in any wood bison populations, it is difficult to demonstrate without comparison to a control group.

Genetic drift

Genetic drift is the loss of alleles by chance and is intensified when populations remain small and isolated for many generations. The number of alleles available for each gene locus is limited by those present in the parental generation and can only decrease. Restoration of variation by mutation is too rare in small populations to be significant (Lacy 1987). The lower the frequency of an allele in the parent generation, the more likely it will be lost in the offspring generation.

Most of the U.S. federal bison herds have independently undergone genetic drift over a number of generations resulting in substantial differentiation among them (Halbert and Derr 2008). Even though the Mackenzie and Elk Island National Park Isolation Area wood bison both originated from the Nyarling River subpopulation, differences between allele frequencies have already developed over the past 50 years and these two populations contain less variation than their founding herd (Wilson and Strobeck 1999). Both the founder effect and genetic drift are probably responsible for the genetic status of these two herds.

As a population becomes more homogenous, it has fewer individuals with unique resistance traits to certain pathogens. Thriving populations with little genetic variation can be reduced to endangered levels by a single disease outbreak (O'Brien and Evermann 1988). Major histocompatibility complex (MHC) genes play a crucial role in pathogen recognition and are the most polymorphic genes in vertebrates (Borghans *et al*. 2004; Piertney and Oliver 2006). Loss of variation in these genes is a particular risk to the survival of some species. Population bottlenecks are the most likely explanation for the low MHC diversity observed in moose, muskoxen, roe deer, fallow deer (Mikko *et al*. 1999) and mountain goats (Mainguy *et al*. 2007). Compared to those species, a significant amount of MHC polymorphism has been retained through the population bottleneck that bison experienced in the late 19th century (Mikko *et al*. 1997). Nevertheless, the number of MHC alleles has doubtlessly been reduced to a small fraction of the alleles present before the bottlenecks.

Radwan *et al*. (2007) examined MHC genes in European bison and found that alleles conferring resistance to posthitis in males have been lost. Posthitis is a disease affecting the reproductive organs of bulls and poses a new threat to the survival of the species. European bison underwent an extreme bottleneck; the current population originated from only 12 founders.

Hybridization and genetic swamping

Crossbreeding with cattle and crossbreeding with plains bison (either of pure lineage or carrying some cattle heritage from past breeding experiments) are the primary forms of hybridization that potentially threaten the genetic integrity, fitness and evolutionary pathway of wood bison.

Presently, the most imminent hybridization threat is between the expanding Nahanni wood bison population and feral plains bison in British Columbia. Originating as a private herd that escaped into the wild, the Pink Mountain plains bison population occupies historic wood bison range in northern British Columbia. The growing commercial plains bison ranching industry in this province has also resulted in an increased number of escapees (Harper and Gates 2000). The genetic integrity of every wood bison herd existing today is already compromised by some plains bison introgression (Van Zyll de Jong 1986; Polziehn *et al*. 1996; Wilson and Strobeck 1999).

Where cattle ranches are located within wood bison range, hybridization has a low probability. The two species do not voluntarily interbreed on open range, and if forced matings do occur, fertility of the offspring is compromised and restoration of fecundity of hybrids in future generations requires backcrosses with either bison or cattle (Hedrick 2009; Boyd *et al*. 2010).

Introgression of cattle genes from “cattalo” experiments in the past remain in many privately owned and wild plains bison herds. Cattle genes in bison have some deleterious effects such as reduced body size and fitness (Hedrick 2010; Derr *et al*. 2012). At present, there are no privately owned herds of mixed lineage bison within the range of wood bison.

Predation and alternate prey

An active wolf poisoning program across much of the NWT was in place until the end of the 1960s. Bounties continued to be paid until 1974, but many aboriginal trappers held a traditional aversion to killing wolves (Look pers. comm. 1980). The Greater Wood Buffalo Ecosystem bison population had been fairly stable for several decades at about 14,000, until the wolf control program ended (Carbyn *et al*. 1993). After that, the Greater Wood Buffalo Ecosystem population began to decline rapidly in the presence of high wolf numbers, and bison were the primary prey (Van Camp and Calef 1987; Carbyn *et al*. 1993). More specifically, the decline was attributed to excessive predation on calves resulting in low recruitment. The bison population was depressed further by the 1974 drowning of 3,000 animals, which could conceivably have provided a short term glut of carrion to boost the wolf to prey ratio.

Following the drowning event, Wood Buffalo National Park bison failed to rebound and partially stabilized between 5,000-6,000 animals for the next eight years (Bradley and Wilmshurst 2005). Wolf numbers appeared to compensate downward for the smaller food base (Joly and Messier 2000), but the lag time for this was unknown and wolves continued to exert predation pressure during the decline.

Van Camp (1987) estimated that 64 to 76 wolves were preying upon approximately 754 bison of the Slave River Lowlands during the winter of 1976-77, and capitalizing on wounded animals, offal, and diseased carcasses left in the field by hunters. Despite an experimental wolf reduction carried out between 1977 and 1979 that eliminated most of the wolves in the Slave River Lowlands, juvenile bison recruitment did not improve and the Hook Lake and Grand Detour subpopulations of the Greater Wood Buffalo Ecosystem continued to decline to 444 and 107 respectively by March 1979 (Jalkotzy 1979).

The Wood Buffalo National Park bison continued to decline at a fairly steady rate of 8.5% from 5,600 at the beginning of the 1980s until 1991, when it was 3,310 animals. Recruitment dropped as low as three yearlings: 100 cows (Carbyn *et al*. 1993). Despite a total decline of 41% in bison numbers during this period, there was an increase in the wolf population of 39% from 110-130 to 150-180. After predator-prey studies in the Slave River Lowlands were completed, the Hook Lake subpopulation sunk to a new low of 183 bison in 1987 (Gates pers. comm. 1988 *in* Van Camp 1989). Coincident with the Hay Camp subpopulation decline to 300 in the mid-1980s, predation on that herd diminished (Carbyn *et al*. 1993), suggesting a threshold bison density affecting the wolf population.

Wolves do not attack large prey indiscriminately because of the risk of injury. As selective foragers, wolves must capitalize on vulnerable prey and be risk adverse (Smith *et al*. 2004; MacNulty 2002). In a wolf – bison system, bison calves are expected to be the preferred prey because they are smaller and usually easier to kill than adults. Since numbers of calves are limited and their prey biomass is low, bison calves alone are not enough to sustain robust wolf populations without a broader prey base.

Summer is the critical season for survival of wolves (Mech 1970). This is when any form of alternate prey becomes most important (e.g., Kuyt 1972; Stahler *et al*. 2006) as adult ungulates are in peak physical condition and at lowest vulnerability.

A wolf pack typically consists of the dominant breeding pair, sub-adult offspring and young-of-the-year. Larger pack size does not equate with greater hunting efficiency because the main killers are the dominant pair (Schmidt and Mech 1997). With the onset of the birthing season, the breeding pair must confine its hunting activities to a short radius from the denning site, and starvation is the primary source of mortality among pups (Mech 1970).

The areas east of the Slave River (Hook Lake subpopulation) and Wood Buffalo National Park south of the Peace River (most of the range of the Delta subpopulation) seemed to account for most of the decline and have the highest predation rates in the Greater Wood Buffalo Ecosystem (Van Camp 1987; Joly and Messier 2004b). This may be the result of higher summer survival rates of wolves due to the availability of alternate prey species unique to these two areas. Year round food studies of wolves carried out east of the Slave River (Van Camp 1987) and in Wood Buffalo National Park (Carbyn *et al.*1993) may provide some clues as to the presence of alternate prey species (the winter-only food study of Larter *et al.* (1994) is not comparable). These surveys (Carbyn *et al*. 1993; Van Camp 1987) found that muskrat ranked second (after moose) in terms of adjusted related biomass consumed. Remains of muskrat and other aquatic species were present much more frequently than moose in scats from the Peace – Athabasca Delta portion of the survey area. East of the Slave River, muskrat comprised the largest percentage of prey weight in the Taltson pack, and ranked second in the Hanging Ice and Hook Lake packs during the snow-free period of 1977 (Van Camp 1987). In contrast, the North Prairie pack had the greatest access to bison and alternate prey appeared to be unimportant. Of the four packs studied by Van Camp (1987) from 1975-78 in the Hook Lake bison range, only two consumed a substantial amount of bison during summer, and muskrat, hare and duck were more important than moose among all of the packs.

Despite the fact that muskrats achieve very high densities east of the Slave River and in the Peace – Athabasca delta, they occupy a different ecosystem than wolves in the habitat matrix. Muskrats only become available to wolves if one or both cross the terrestrial/aquatic boundary. Janzen (1986) first defined cross-boundary subsidies as a process whereby organisms that disperse from one patch into another impact resident organisms by providing increased food resources or opportunities for reproduction. Simulation modeling by Nevai and Van Gorder (2012) showed that depending on the amount of input from the subsidy, a numerical response of predators could cause the primary prey to decline.

The concept of non-ungulate prey as an important subsidy for wolves is not without precedent. In Denali National Park and Preserve, Alaska, Adams *et al*. (2010) found that Pacific salmon were a significant alternate food source for wolves residing in the area, and reached as high as 34% of their diets. Because salmon act as subsidies to these wolves, relatively high wolf to ungulate ratios resulted from numerical responses of wolves to salmon availability, and predation pressure on resident ungulates was elevated.

If muskrats provide a critical subsidy that improves summer wolf survival east of the Slave River and in the Peace – Athabasca Delta, the Hook Lake and Delta subpopulations may be inherently prone to higher predation than other herds.

Episodic catastrophes

Drowning

In cases where bison break through lake or river ice, they are generally unable to climb out (Carbyn *et al*. 1993). Before the Bennett Dam was completed in 1969, there had been several major drownings of bison in the Peace – Athabasca Delta due to natural flooding/drawdown events (Carbyn *et al*. 1993). Since then, the only recurrence was in 1974. Mortality of large herds of plains bison by falling through thin ice was summarised by Roe (1970). Gates *et al*. (1991) documented the 1989 accidental drowning of 177 bison through spring ice on Falaise Lake in the Mackenzie Bison Sanctuary. In winter 2008-09, thin ice likely caused the loss of 13 bison of the Nahanni population, and an additional 13 individuals drowned between 2004 and 2011 (Larter and Allaire 2013). Fourteen bison died in the ice on the Horn River in March 2011 and three more had fallen through the ice on that river in November 2012 (Armstrong pers. comm. 2015).

Boat and barge traffic also represents a potential threat to wood bison in the NWT. Wood bison, especially calves and mature males, which sit lower in the water than other age classes, are vulnerable to waves and wakes created by these vehicles (Larter *et al*. 2003; Larter and Allaire 2007).

Climatic anomalies

Adverse climatic conditions may be confined to a single season, or climatic oscillations such as the Pacific North American Pattern, North Pacific Oscillation, and Southern Oscillation Index (La Niña and El Niño) could have multi-year impacts on forage production and availability. Sedge growth is particularly sensitive to mean monthly temperature (Gorham 1974). In Yellowstone National Park, Meagher (1973) considered harsh winters to be the greatest source of mortality, and spring calf to adult ratios were negatively correlated with snow pack (Fuller *et al*. 2007). Van Camp and Calef (1987) alluded to the role of harsh weather when describing the disappearance of approximately 33% of the Hook Lake subpopulation during the winter of 1974-75.

Carbyn *et al*. (1993) tracked snow measurements from Fort Smith and Fort Chipewyan for the years 1965 to 1980, and compared them to the depth of snow that first becomes stressful to bison, the critical snow depth for calves, and the critical snow depth for adult males. From the data, lower calf production and yearling recruitment would be expected in the first half of the 1970s than in the second half, but negative impacts of severe winters would probably be offset by benign winters.

Because good wood bison habitat is closely associated with high water tables, excessive levels of precipitation may result in flooding of important feeding areas. This flooding may be particularly severe over the short term if it is extreme and widespread. Over the longer term, this damage may be partially offset by wet meadows invading areas that are normally drier. Above average rainfall temporarily removes landscape fire from the ecosystem and plant succession proceeds to the detriment of bison habitat. Prolonged flooding late into the summer renders forage resources unavailable, and if it lasts for several years in succession, plant mortality occurs.

Drought had been a major limiting factor historically for plains bison as grasses desiccated and drinking water disappeared. On the other hand, low precipitation in wood bison range is likely to facilitate conversion of high biomass wet meadow to low biomass dry meadow. In the Slave River Lowlands, the presence of sedge to reedgrass was 2:1 in wet meadows and 1:60 in dry meadows (Reynolds *et al*. 1978). Pringle (1987) found the quantity of forage produced annually in the Slave River Lowlands to be highly related to fluctuations in the water table. This may be offset by sedges invading habitats that are normally too wet for them to grow.

Other threats

Timber harvesting and associated infrastructure

With two new Forest Management Agreements now in place, timber harvesting is expected to increase in the range of the Mackenzie and Greater Wood Buffalo Ecosystem populations (ENR 2015b, c, and d). Land use permits have been issued for the first five years of timber harvesting in the Fort Providence and Fort Resolution areas (Mackenzie Valley Land and Water Board 2015a and b). The development of roads, access trails and ice crossings for timber harvesting may modify wood bison habitat and movements, hunter and predator access, and bison-vehicle collisions (ENR 2015b, c, and d). It remains unclear how significant these potential impacts will be on wood bison populations.

Habitat heterogeneity

Spatial irregularity on the landscape introduces a difference between the total prey population density and the proportion that is actually available to the predator (Gorini *et al*. 2012). Sinclair (1979) hypothesized that in heterogeneous environments where prey have opportunities to avoid encounters with predators, prey populations would fluctuate and become food limited. However, in more homogeneous environments where they are in closer association, predators could have a stronger impact on prey. Gates *et al*. (2005) reviewed the various ways that ungulates find refuge from predators during the critical time when calves were most vulnerable, and found that ungulate populations that employed this strategy outnumbered conspecific populations that did not seek refuge.

Carbyn *et al*. (1993) proposed the ‘habitat dispersion hypothesis’ to account for the decline of the bison in Wood Buffalo National Park, whereby this decline was unique to the Peace – Athabasca delta and did not occur north of the Peace River. Bison use forest patches for escape as an anti-predator strategy (Fuller 1960). Carbyn *et al*. (1993) suggested that bison have a greater predation risk in the large meadow complexes of the delta, compared to other areas north of the Peace River where forest and meadow habitats are more interspersed. The expansive open habitats of the delta lack escape cover, contain highly predictable bison concentrations for wolves, and provide fewer moose as alternate prey. Carbyn *et al*. (1998) stated that extensive foraging areas have been underutilized by bison, and Carbyn *et al*. (1993) raised the possibility that bison may not have been abundant in the Peace – Athabasca delta in historic times even if the forage base could support higher numbers.

During their study from 1997 to 2001, Joly and Messier (2004b) stated that the Nyarling River subpopulation never exceeded 230 bison and no wolf predation was observed. They suggested that moose were the main prey, and bison density was too low to maintain wolf densities high enough to be a significant source of bison mortality for this herd. Although wolf predation was highest in the Delta subpopulation (9-10%), they expected this rate to eventually drop as it did with the Hay Camp and Garden River subpopulations. Joly and Messier (2004b) rejected the 'habitat dispersion hypothesis' because their interpretation of population trends demonstrated that the 1976 to 1999 Hay Camp decline was indistinguishable from the 1981 to 1999 Delta decline. Consequently, the negative trend in the Peace–Athabasca delta was not unique within Wood Buffalo National Park. The interpretations differ primarily with regards to the validity of the Peace River as the boundary between the two main bison populations. North of the Peace River, Joly and Messier (2004b) recognized a zone of overlap between the Hay Camp and Delta subpopulations. They suggested that the Carbyn *et al*. (1993) demarcation based on the Peace River has not been adequately tested and may have obscured the dynamics of the Hay Camp subpopulation.

Disease vulnerability

During his disease survey in and around Wood Buffalo National Park between 1983 and 1985, Tessaro (1987) found that four out of five wolf-killed bison he examined exhibited extensive tuberculosis. Tessaro *et al*. (1990) proposed that advanced diseases predispose bison to predation, and that this should be taken into account when considering proportional mortality due to wolves. This was termed the 'disease-predation hypothesis' by Gates (1993). Until the 1970s, the Greater Wood Buffalo Ecosystem population grew in the presence of exotic diseases, but in the absence of substantial wolf predation (Joly and Messier 2004b). Decline of this population occurred in the presence of disease and predation from 1970 to 1999 (Van Camp and Calef 1987; Carbyn *et al*. 1993; Joly and Messier 2004b).

Joly and Messier (2004b) supported the 'disease–predation hypothesis', whereby the presence of bovine tuberculosis and bovine brucellosis would likely reduce productivity of the bison population by suppressing birth rate and survival, and as a consequence, bison densities would be relatively low and regulated by wolf predation. The 'disease–predation hypothesis' also predicts that in the absence of wolf predation, bison populations would grow to high density in the presence of exotic disease.

Stochastic population simulations by Joly and Messier (2004b) showed that growth of bison populations in the absence of exotic disease exceeded the maximum wolf predation rate at all densities. Disease-free bison populations, regardless of anthrax or drowning episodes, were highly likely to persist at high densities that would be regulated by food competition. In contrast, simulations predicted that a bison population with tuberculosis and brucellosis was likely to decline to low densities, regulated by wolf predation, particularly when drowning and anthrax were added to the model. Joly and Messier (2004b) also stated that the difference between the simulated growth of bison populations with and without tuberculosis and brucellosis likely underestimated the true impact of exotic disease on bison productivity. These simulations implied that an interaction between tuberculosis, brucellosis, and predation may account for the decline of bison abundance in Wood Buffalo National Park from 1970 to 1999. Joly and Messier (2004b) acknowledged that recent surveys in Wood Buffalo National Park showed substantial bison population growth, and interpreted this as indicating that the wolf population had declined, possibly because of disease or reduced prey availability. When heavy predation on the highly preferred calves results in scarcity, wolves need to rely on aged or other vulnerable adults as their primary prey. Low recruitment levels from 15 to 20 years ago may not have provided enough geriatric prey to maintain high wolf populations. As a result, calf predation is relaxed and recruitment may be increasing.

Bradley and Wilmshurst (2005) discounted the 'disease–predation hypothesis' on the grounds that all subpopulations did not decline, even though all were diseased. They disagreed with Joly and Messier (2004b) that the 1976 to 1999 Hay Camp decline was indistinguishable from the 1981 to 1999 Delta decline, because in concurrence with Carbyn *et al*. (1993), they assigned the overlap area north of the Peace River to the Hay Camp subpopulation. Their analysis indicated that the population decline was highest and juvenile survival was lowest in the Delta subpopulation, despite evidence that disease incidence was lower in the Delta subpopulation than in the rest of Wood Buffalo National Park. Bradley and Wilmshurst (2005) used the same model and a similar data set as Joly and Messier (2004b), but chose different juvenile survival rates. Joly and Messier (2004b) proposed a 20% difference in juvenile survival rates between diseased and healthy populations based on the differences in recruitment data between Wood Buffalo National Park and the non-diseased Mackenzie bison of the Mink Lake area. This difference was assumed to be equivalent to the loss from brucellosis-induced abortion. Bradley and Wilmshurst (2005) questioned that assumption because the effects of brucellosis-induced abortion at the population level had not yet been studied, and juveniles were the age class least susceptible to disease effects. They also stated that the Wood Buffalo National Park juvenile survival rate in recent years had increased to a level equivalent to the Mink Lake rate reported by Larter *et al*. (2000), and even if it had not, the reason would not necessarily be related to disease. More recently, Fuller *et al*. (2007) has studied abortion effects at the population level for the Yellowstone National Park bison and calculated negative impacts on birth rate and population growth rate. In this case, study results showed that *Brucella*-exposed three year old bison have lower pregnancy and birth rates than older individuals and suggested that the elimination of brucellosis could affect an increase of 29% in population growth rates (Fuller *et al*. 2007).

Bradley and Wilmshurst (2005) believed that population data collected after Joly and Messier's (2004b) study altered change points and weightings in the bison population trajectories in such a way that validated the original proposal by Carbyn *et al*. (1993) that the decline of the Delta subpopulation was unique. Bradley and Wilmshurst (2005) also claimed that the decline between the 1970s and the 1990s would have occurred regardless of the disease status of the Wood Buffalo National Park population. They suggested that mortality due to predation was not strongly exacerbated by disease, since the Delta subpopulation had the highest predation rate, as well as the lowest disease prevalence. Survival of juveniles was likely an important determining factor affecting changes in population size.

Tessaro *et al*. (1990) suggested that availability of substantial numbers of debilitated bison maintains larger numbers of wolves, which would intensify the problem of poor recruitment of juveniles into the bison population. If a substantial proportion of the adult bison segment is more vulnerable to predation because of debilitating disease, wolf populations will increase and this, in turn, would result in greater losses of calves because they are the most vulnerable to predation.

Age structure

Vucetich and Peterson (2004) suggested the reason why moose calf abundance on Isle Royale did not appear to be an important factor in wolf population growth rate was because the caloric value of a calf carcass is too low and the diet of wolves must be supplemented with adult moose. They found that the most important predictor of wolf population growth rate is the abundance of moose older than nine years of age. Also, they suggested that age dependent predation is more important than is generally recognized in wolf – ungulate systems.

As is typical for wolf – ungulate relationships (Mech and Peterson 2003), bison of all ages become more vulnerable with the onset of deep snow. Carbyn *et al*. (1993) noted that Wood Buffalo National Park wolf packs became larger in early winter as some of the inexperienced sub-adults returned, possibly to profit from the killing abilities of the dominant pair. Larger pack size does not result in more food/wolf/day (Schmidt and Mech 1997) and food consumption in Wood Buffalo National Park was estimated by Carbyn *et al*. (1993) to average 2.5 kg/day/wolf in early winter. Packs became smaller as winter progressed, probably because bison were at maximum vulnerability and this would be the most opportune time for the older sub-adults to test their independence. Most disperse permanently from their natal pack by three years of age (Schmidt and Mech 1997). Food consumption in Wood Buffalo National Park rose to an average of 4.3 kg/day/wolf by mid-winter, and reached 6.2 kg/day/wolf during the severe winter of 1978-1979 (Carbyn *et al*. 1993).

Winter radio-tracking data of several packs indicated that wolves selected calves and old bison greater than 11 years of age (Carbyn *et al*. 1993). Calves were always killed at a disproportionately higher rate (24%) than they occurred in the population (11%), except in 1978-1979 when it was suspected that fewer calves were available to wolves in the study area. Two- to five-year old bison seemed to be relatively immune to predation. Animals greater than 11 years of age were killed at a disproportionately higher rate (14-20.8%) than they occurred in the population (10.8%). Unlike the impact calf predation can have on recruitment into the herd, Fuller (1966:37) stated, “Very old animals are generally considered to be a biological surplus, and the loss of individuals in that class to predators or from any other cause is not usually detrimental to the herd welfare.” Whether the harvest of older animals bolsters the wolf population and thus increases harvest pressure on calves was considered by Vucetich and Peterson (2004) and is discussed below.

When examining reasons why the bison of Wood Buffalo National Park had stabilized by the 1940s, Fuller (1966:40) stated, “The growing population from 1890 to 1925 must have been essentially a young population. Undoubtedly, there were a few old animals in 1890 when the total numbers of wood buffalo were under 500, but there would practically be no increase in the proportion of aged animals for some 15 to 20 years, when the increasingly large calf crops had advanced through maturity and had reached old age."

The more than 6,000 plains bison imported during 1925-29 were also young animals, and Soper's (1941, 1942) 1932-34 faunal studies in Wood Buffalo National Park indicated that wolf predation was having little impact on bison. The geriatric cohorts arrived in the 1940s and continued to represent large age classes in a stable population until the end of the 1960s when wolf control ceased. If the Vucetich and Peterson (2004) proposal regarding age dependent predation has merit in this wolf - ungulate system, the wolf population released from control would grow because of an abundant supply of old bison. This would be compounded by brucellosis and tuberculosis, as prevalence for both diseases increases with age (Joly and Messier 2004a). Because calves are the preferred prey, the drop in recruitment occurring in the wake of the burgeoning wolf population would have been expected.

In the Mackenzie population, predation was not observed on calves until 1983 (Chowns and Graf 1987), and was much later for adult bison (Larter *et al*. 1994). Figure 13 (p. 141) shows the Mackenzie population kill ratio of calves to yearlings to adults, calculated from a 1989 to 1992 study period, to be quite different from Wood Buffalo National Park and Hook Lake kill ratios that were calculated from late 1970 study periods. Of the wolf-killed bison documented in the Mackenzie population by Larter *et al*. (1994), the calf to yearling to adult ratio was 26:5:10. Larter *et al*. (2000) stated that this bison population appeared to be regulated by food supply, despite considerable wolf predation on calves. The 17:3:28 kill ratio in Wood Buffalo National Park (Carbyn *et al*. 1993) was remarkably similar to the 16:2:28 Hook Lake kill ratio (Van Camp 1987). In contrast to the Mackenzie population of 1989-1992 when its age structure was dominated by younger animals, few juveniles were being recruited into the Wood Buffalo National Park and Hook Lake herds during the late 1970s, resulting in their age structures being dominated by older animals. Carbyn *et al*. (1993) believed that wolves maintained a strong search image for calves and the pressure on them would be relentless, as long as they remained available. Switching to adults only occurred when calf encounter rates dropped below a profitability threshold. Carbyn *et al*. (1993) suggested that wolf predation of adult bison in some years, in their study area, may have equalled recruitment, taking into account relative additive and compensatory levels. In the snow-free period, they observed that wolves in Wood Buffalo National Park killed calf bison opportunistically, and largely ignored adult bison as long as calves were available.

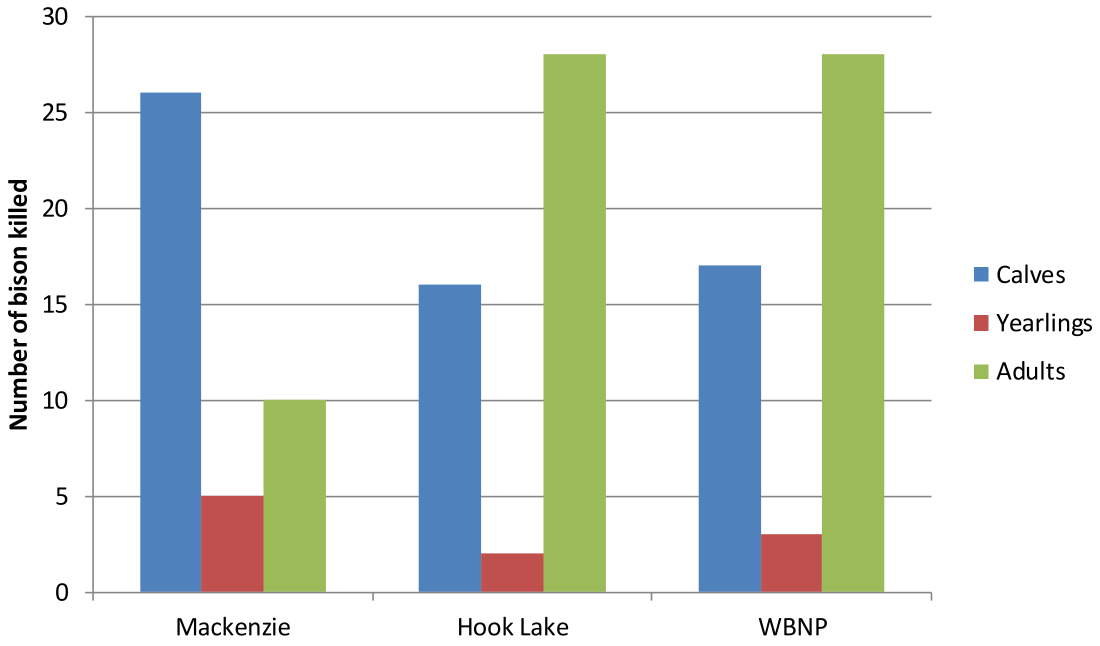

Figure 13. Predation and age class (data for Mackenzie population from Larter *et al*. (1994); data for Hook Lake drawn from Van Camp (1987); data from Wood Buffalo National Park (WBNP) drawn from Carbyn *et al*. (1993)).

Large scale anthrax outbreaks may interrupt the progression of an aging population structure of bison, as older animals are much more susceptible to the disease (Elkin *et al*. 2013). In African ruminants where susceptibility is also age-linked, Hugh-Jones and de Vos (2002) found that high proportions of young animals can be left in the wake of an epidemic. After a glut of carrion for a few weeks in the summer, the loss of vulnerable older age bison could adversely affect the wolf population.

POSITIVE INFLUENCES

Habitat conservation

In the late 1990s, the issue regarding agriculture in the Mills Lake – Horn River delta was finally resolved when Ducks Unlimited Canada bought out the leases. It is intended that this area will be transferred to the federal government upon establishment of the Edéhzhíe National Wildlife Area through the NWT Protected Areas Strategy (Canada Gazette 2013). Land use planning initiatives, if passed, could also have a positive influence on wood bison. For example, the possible future approval of the Dehcho Land Use Plan has the potential to complement wood bison management in the Dehcho region (Armer pers. comm. 2015).

From a continental perspective, the Wildlife Conservation Society set a vision for the ecological future of bison (Redford and Fern 2006). Also, the 'Vermejo Statement' has articulated a vision that the ecological recovery of North American bison will occur when large herds move freely across large landscapes (Sanderson *et al*. 2007).

Increasing knowledge necessary to preserve and manage genetic diversity

One of the most profound management decisions to be made was to follow the recommendation of Van Zyll de Jong *et al*. (1995) that all public herds of bison in northern Canada be considered as wood bison. Prior to that, the bison of the Greater Wood Buffalo Ecosystem were "allegedly worthless hybrids" (Geist 1991:284). When Wilson and Strobeck (1999) compared the founder effect among different herd populations, they observed that the Pink Mountain plains bison herd, established by error in northern British Columbia from 48 individuals, appeared to contain an adequate representation of genetic material from its parent population. Accordingly, a minimum standard based on science has now become established for starting new wood bison populations. To retain 99% of genetic variation, Wilson (2001) recommended an effective population size of 50, but because few males breed every year, a reasonable sex ratio would be 25% males and 75% females. For that reason, at least 67 animals is the new requirement for founding herds.

At least one migrant per generation has been a basic rule accepted by the conservation community to ensure adequate gene flow among isolated populations. The robustness of the rule has been tested by Wang (2004) and found to be generally valid.

McFarlane (Zittlau) *et al*. (2006) developed a simulation modeling approach to evaluate genetic management strategies and the relative effects of wood bison population size, number of populations, movement of animals between populations, and harvesting or culling regimens on genetic diversity. Their recommendations included conducting additional genetic salvage from diseased bison in and around Wood Buffalo National Park to ensure that diversity of the wood bison genome is well represented and conserved in disease-free populations, basing each salvage effort on a large number of founding individuals, using the most genetically important disease-free populations as the primary source for creating new disease-free populations, and managing individual wood bison herds above a minimum population size (i.e., census size > 400 individuals). They also recommended gene flow via movement of animals among all herds to reduce the rate at which diversity is lost, but giving population growth precedence over gene flow when populations are below carrying capacity.

Advances in reproductive technology are continuing to find ways of salvaging valuable genetic material from diseased populations. For example, better understanding of disease transmission will help in the preservation of germ plasm (Robison *et al*. 1998). There are preliminary developments in assisted reproductive technologies as a means of conserving genetic diversity from infected herds (e.g., Thundathil *et al*. 2007; Aurini *et al*. 2009).

Safeguarding genetic integrity

The federal (Canadian) *Species at Risk Act* (2002) includes any "subspecies, varieties or geographically or genetically distinct population" in its definition of wildlife species, and the *Species at Risk (NWT) Act* (2009) allows a distinct population (a geographically or biologically distinct population of a species or a distinct population identified by the Conference of Management Authorities) to be assessed. These measures affirm that taxonomic entities below the species level also need protection for conservation of biological diversity. Subsequently developed *Guidelines for Recognizing Designatable Units* approved by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in November 2011 clearly deem wood bison in northern Canada to be a discrete population that requires its own management strategy (COSEWIC 2012).

Such decisive actions recognize that wood bison and plains bison are on different evolutionary pathways that must not be impeded by undue human interference. Accordingly, territorial and provincial wood bison management plans have the justification to call for goals and objectives that conform to this position. For example, the *Management Plan for Wood Bison in British Columbia* (Harper *et al*. 1999) calls for prevention of interbreeding between reintroduced wood bison and free-ranging plains bison at Pink Mountain and game-farmed commercial bison, while the *NWT Wood Bison Management Strategy* (ENR 2010) calls for the prevention of hybridization of wood bison with plains bison, domestic bison and cattle. To accomplish this, management zones have been established for the Pink Mountain plains bison herd and bison ranching activities.

Managing exotic disease

Monitoring and removal of bison in the Bison Control Area between Wood Buffalo National Park and the Mackenzie River has continued since 1987 to reduce the risk of contact between infected and non-infected wild bison populations (ENR 2010). A risk assessment on the potential spread of tuberculosis and brucellosis from bison in and around Wood Buffalo National Park predicted that the introduction of infection to wild healthy bison herds would occur perhaps once every eight years for brucellosis and once every six years for tuberculosis (Animal, Plant and Food Risk Assessment Network [APFRAN] 1999). A movement corridor analysis recommended additional aerial surveillance of specific areas within the Bison Control Area based on the habits of bison (Gates *et al*. 2001a).

The Greater Wood Buffalo Ecosystem population persists with tuberculosis and brucellosis at population numbers that have never dropped below 2,200 animals (Joly and Messier 2004a). This is safely above the 1,000 figure considered for a bison population to be ecologically restored (Sanderson *et al*. 2007). The Greater Wood Buffalo Ecosystem population has at least 12 generations of co-evolution with the two exotic diseases.

Promoting natural resistance to bacterial infection in domestic cattle is an attractive alternative for disease control. When unvaccinated cattle were inoculated with *Brucella abortus* in a study by Templeton *et al*. (1990), 18% of the animals exhibited natural resistance to brucellosis. Westhusin *et al*. (2007) have reported the rescue of a genome providing natural disease resistance to brucellosis, tuberculosis, and *Salmonella* in cattle.

In their review of natural resistance to brucellosis, Adams and Schutta (2010) recognized that natural immunity to bacterial diseases has been known for centuries, but the genetic implications are only recently being understood. Given the rate of development of new genetic tools, and rigorously controlled phenotyping protocols for innate and adaptive resistance to bacterial diseases, it is anticipated that genetic selection as an approach to controlling infectious diseases, such as brucellosis in domestic livestock, will become increasingly feasible within the next decades. These developments provide hope that natural genetic selection among wild bison will produce similar results. If there is a process of natural selection in bison populations towards resistance to tuberculosis and brucellosis, then wolves ought to be a catalyst if they are exerting higher predation pressure against those bison weakened by disease.

Range expansion

Catastrophic events causing mass mortality are generally sudden, while climatic oscillations often follow multi-decadal trends before they shift. Both have localized effects on wood bison populations. The most effective protection against them is dilution of risk by population dispersal over wide areas. The Greater Wood Buffalo Ecosystem population has essentially reached its limits of distribution, but the Nahanni and Mackenzie populations are still undergoing range expansion, and as this proceeds, the risk of a significant proportion of the population falling victim to a local catastrophe or adverse climate diminishes.

Interagency cooperation

Using the definition of metapopulation as a group of populations among which actual or potential movements of animals can occur, and realizing that anthropogenic barriers primarily limit dispersal among wood bison populations, McFarlane (Zittlau) *et al*. (2006) believed that defining the wood bison metapopulation as all public herds of these animals is warranted. In the past, northern bison have been managed as isolated units, mainly because of conflicting federal, territorial and provincial government mandates. Now that the Greater Wood Buffalo Ecosystem population has been recognised as a distinct entity, subpopulations inside Wood Buffalo National Park are managed cooperatively with those subpopulations ranging outside of the park.

The Nahanni population extends across several jurisdictions and is managed in collaboration with the governments of Canada (Parks Canada, Nahanni National Park Preserve), the NWT, Yukon and British Columbia. All wood bison populations have co-management protocols between government and resource management boards (ENR 2010).

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Biography of Preparer

Tom Chowns received his Bachelor of Science degree, majoring in Wildlife Biology, from the University of Guelph in 1975. His first introduction to the status of wood bison in the NWT was from Dr. Nick Novakowski (Canadian Wildlife Service) who visited the university in 1974 as a guest speaker. Tom was employed by the Department of Environment and Natural Resources from 1975 to 2002, and since then, he has been an environmental consultant.

For most of his career, he was a field officer in Hay River where wood bison management was a prime responsibility. Field experience included assisting Regional Biologists and Bison Ecologists with studies of bison populations using ground and aerial census techniques, age and sex segregation surveys, radio telemetry, collection of biological samples, monitoring the Bison Control Area, prey selection among wolf populations, seasonal changes in forage selection, and habitat assessment using satellite imagery, ground truthing and GIS. As a nationally certified Wildland Fire Behaviour Specialist, he supervised the prescribed burning program for bison habitat improvement.

Tom was also very involved with the Fort Providence Integrated Resource Management Plan, the species management plan for wood bison, the Ten Year Prescribed Burn Plan for the Wood Bison range, the forest fire history of the Fort Providence land base, a study of the historic range of wood bison, ecosystem-based forest policy, departmental input into species at risk legislation, and the Protected Areas Strategy.

Presentations and technical papers were contributed to proceedings of the Interior West Fire Council, and North American Bison Symposium regarding prescribed burning in bison habitat. Writing also included internal manuscript reports on bison, and co-authoring the chapter entitled "Wood Bison at the Crossroads" in the publication "Buffalo".

Cooperative and advisory roles with other groups included Parks Canada and Alberta Environmental Protection regarding inter-jurisdictional bison issues, the Wood Bison Recovery Team, the U.S. Fish and Wildlife Service with their proposed reintroduction of wood bison into Alaska, World Wildlife Fund (WWF) and the Canadian Parks and Wilderness Society (CPAWS) regarding bison habitat protection. Tom is also a member of the IUCN/SSC Bison Specialist Group/North America, and the Bison Centre of Excellence.

Since becoming an environmental consultant, Tom has compiled reports entitled *State of the Knowledge of Woodland Caribou in Ontario* – 2003 for the Forestry Research Partnership (industry and government), and *Ecological Interactions among Caribou, Moose, and Wolves: Literature Review* for the National Council of Air and Stream Improvement (NCASI). He has also been an invited observer to a series of Northeast Region Caribou Task Team meetings attended by representatives of all stakeholders from Ontario. Tom authored the chapter "Review of Literature on Ungulate Movements" in *The Ecology of Bison Movements and Distribution In and Beyond Yellowstone National Park* submitted to Yellowstone National Park. He has been the primary author of wildlife sections in *Ecological Regions of the Northwest Territories* series of reports (Taiga Plains, Taiga Shield, Cordillera, Southern Arctic, and Northern Arctic), and conducted a literature review for distribution and abundance for all mammals and birds found in the NWT for the wildlife species range mapping project.

Status and Ranks

Region	Coarse filter (Ranks) To prioritize	Fine filter (Status) To provide advice	Legal listings (Status) To protect under species at risk legislation
Global	T2 – Imperiled (NatureServe 2015)	NT – Near Threatened (Gates and Aune 2008)	Appendix II (CITES 2006)
Canada	N2N3 – Vulnerable to Imperiled (NatureServe 2011)	Special Concern (COSEWIC 2013)	Threatened (SARA 2003)
Northwest Territories	**S1S2 – May be at Risk (NWT General Status Ranking Program 2016)**	**Threatened**	**To be determined**
Adjacent jurisdictions			
Alberta	S1 – Critically Imperiled (NatureServe 2015)	Endangered (Fish and Wildlife Division 2008)	
British Columbia	S2 – Imperiled (NatureServe 2015)		
Saskatchewan	SX – Presumed Extinct (NatureServe 2015)		
Yukon Territory	S2S3 – Vulnerable to Imperiled (NatureServe 2015)		

Information Sources

TRADITIONAL AND COMMUNITY KNOWLEDGE COMPONENT

Traditional and community knowledge contributors

From Berger 1975:

Larry McConnell

From Cluff *et al.* 2006:

Behchokǫ̀ (7), Detah (8), Gamèti (16), Whatì (13) - Included Francis Simpson, Peter Moosenose, Lloyd Bishop, Pierre Beaverho, William Chocolate, Daniel Chocolate, John DeQuitte, Sammy Arrowmaker, Charlie Pride, Joe Zoe, Eddie Chocolate, Jimmy Wagary, Joe Black, Pierre Tlokka, Isadore Zoe, Georgina Chocolate, Michel Paper, Eddie Sikyea, Isadore Tsetta, and Judy Charlo, among others.

From Ferguson 1989:

Ron Loonskin, Jim Thorn, Mike Thorn, Bob Head, James Christie, Art Look, Michael Macleod, Harvey Bulldog, Daniel Sonfrere, Roy Fabien, Frank Laviolette, David King, Henry Beaver, Raymond Beaver, Frank Laviolette, Ken Hudson, Chief Sayine, Harvey Denechoan, Sonny Rett, Archie Waquan, Matthew Lepine, Edward Lepine, Andrew Campbell, Pat Marcel, and others.

From Gunn 2009:

James Antoine

From Lotenberg 1996:

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Appendix A – Additional Information

APPENDIX A1 – SYSTEMATIC AND TAXONOMIC CLARIFICATIONS

Bovine relationships

All members of this group have diverged recently and a number of phylogenetic studies from molecular and morphological data have resulted in ambiguous relationships, particularly among bison and yak (*Bos grunniens*).

Classification of wood bison at the genus level is not without controversy. The concept of species is based on the premise that in order for an interbreeding group of individuals to maintain itself in nature, the unit must be reproductively isolated from its close relatives (Van Gelder 1977). The criteria for defining higher and lower taxonomic levels are much more subjective. There is debate about whether *Bison* is a valid genus or should be united with *Bos*, and whether the genus *Bos* should be further subdivided (e.g., Nijman *et al*. 2008). Much of the disagreement stems from how the concept of species is applied. Van Gelder (1977) maintains that if reproductive incompatibility is accepted as the upper limit to species differentiation, then it should at least be the lower limit in the definition of genus, and hybridization between different genera at a higher taxonomic level should not be achievable. There is widespread agreement that members of *Bos* and *Bison* should be partitioned as separate species because they do not produce fertile male and female hybrids, and do not interbreed in nature. Advocates of uniting *Bison* with *Bos* argue that *Bison* are able to produce viable offspring with several (if not all) species of *Bos* including cattle (*Bos taurus*), gayal (*B. frontalis*), and yak, thereby exceeding the lower limit in the definition of genus (Van Gelder 1977).

Some proponents (e.g., Van Zyll de Jong 1986; Corbet and Hill 1991) have suggested that because of morphological similarity between American bison and European bison and their capacity to interbreed, their taxonomic relationship should be at the subspecies level. Studies of the taxonomic position of American and European bison have not led to a definite conclusion (Prusak *et al*. 2004). Nucleotide sequencing of a mitochondrial cytochrome gene by Janecek *et al*. (1996) was indicative of the genus *Bison* being paraphyletic, with American bison being more closely related to species of *Bos* than to European bison. Amplified fragment length polymorphism (AFLP) fingerprinting by Buntjer *et al*. (2002) placed American and European bison in one of the three bovine clusters, and the technique could not assign a consistent placement for yak. Phylogeny of bovine species based on three mitochondrial DNA (mtDNA) sequences studied by Verkaar *et al*. (2004) showed a closer affinity of American bison to yak, whereas European bison were closer to cattle. In contrast, their Y chromosomal analysis supported closer association between American and European bison. As an explanation for this discrepancy, Verkaar *et al.* (2004) proposed 'transpatry', whereby the European bison could be the result of an ancient Eurasian cattle-like population that was changed by repeated introgression of genes from dominating bison bulls. Hypothetically, this hybridization eventually created a new species with bison-like appearances, autosomal genes and Y chromosomes, but with the original mtDNA from the maternal cattle-like ancestors. The idea would also explain the sudden paleontological appearance of the European bison without clearly identifiable ancestors. Verkaar *et al.* (2004) cited the likely role that transpatry played in the evolution of North American deer, Asian macaques, South American camelids, and Eurasian goats. With the advent of genetic analysis, hybridization between closely related species and subspecies has proven to be more common than previously supposed, and may actually have important effects on the dynamics of hybrid zones, speciation, and adaptive radiation (Grant *et al.* 2005). To account for uncertainty around phylogenetic reconstruction of the two species of bison and yak, MacEachern *et al.* (2009) considered double mutations and introgressive hybridization, but found more support for lineage sorting from an ancestral species with a large polymorphic population.

Bison evolution

Because the small isolated populations of *B. bison* (modern bison) are poor representatives of the dynamic ecosystems they were once part of, Cannon (2001) suggested that the long prehistoric baseline of conditions that bison endured can provide insights for future management decisions. The progression from the ancestral bovine progenitor to modern wood bison has been punctuated by a series of profound environmental events. In the Late Miocene epoch, ancestral bovines developed robust dentition for grazing fibrous, gritty grasses that were evolving together on the subcontinent of India. Climate changes led to the expansion of grasslands and bovine invasions of Africa, Asia and Europe (Agustí *et al.* 2001; Bibi 2007). Bovina (cattle, bison and yak) invaded cooler temperate habitats, splitting from Bubalina (African and Asian buffaloes), which invaded tropical regions. Climate changes in the Pliocene epoch also favoured grasslands, thus permitting the ancestral Bovina to become much more widely distributed (MacEachern *et al.* 2009).

The Pleistocene epoch followed from about 2.6 million to 11.7 thousand years before present, and was characterized by repeated glaciations. Ecological changes associated with the earliest severe glacial advance probably caused Bovina to split very rapidly into taurine cattle, Indochinese cattle, and bison/yak. *Bison sivalensis* (Lydeckker 1878), the earliest identifiable form of bison, probably originated in the Himalayan foothills of northern India (Flerov 1979).

Guthrie (1970) theorized on bison evolution and competition. Bison occupied the large bovid grazing niche in northern Eurasia. In the warmer south (including tropical regions) the grazing niche was occupied by wild cattle species such as auroch (*Bos primigenius*), zebu (*B. indicus*), banteng (*B. banteng*), kouprey (*B. sauveli*), gaur (*B. gaurus*) and buffalo genera, consisting of

Syncerus and *Bubalus*. *Bison priscus* Bojanus (1827) evolved as changing climatic conditions extended cool grasslands across northern Eurasia. When sea levels dropped during glaciations, the land bridge that emerged across the Bering Sea allowed *B. priscus* to enter North America. Although bison did not penetrate southern Eurasia because of competitive exclusion - Guthrie (1970) hypothesized that *Bison* and *Bos* acted as biotic barriers to each other due to having similar diets - there was no such limitation in North America. Bison underwent considerable range expansion and phylogenetic change in the New World that was unparalleled in the Old World.

The Ice Ages of the Pleistocene created unprecedented evolutionary turmoil in mammals, producing giant ungulates with enormous horns, antlers, ossicones and tusks (Geist 1971). According to Geist's (1971) 'dispersal theory', pioneering populations of *priscus* encountered a superabundance of high quality forage in the vacant habitat of Beringia, leading to high growth rate and rigorous social interactions. Strong selection for large body and horn size, especially on the dispersing fringe, did not subside until the habitat became saturated. The first waves of *priscus* across the land bridge were able to penetrate midcontinent North America during deglaciations and evolve into giant forms with massively spreading horns such as *B. latifrons* Harlan (1825) and *B. crassicornis* Richardson (1854). The return of the Ice Ages blocked gene flow between Beringia and the rest of North America.

McDonald (1981) described bison evolution as rapid morphological, behavioural and ecological adaptations to new environments, followed by relative stability, until the next environmental change displaced the old selection regime. Rapid evolution over compressed time periods suggests that all bison, living and extinct, were very closely related. Although many variants have been named as separate species, limited coexistence among extinct bison suggests that there may have been a continuum of evolution within a single species (Guthrie 1970).

From his morphometric study of bison, Van Zyll de Jong (1986:53) stated:

> *"An interesting observation that emerged from these analyses is that the variation within modern bison may be similar to that found within and between Holocene and late Pleistocene forms, as well as that between modern and earlier forms of bison. Viewed together in multivariate space they form one morphometric continuum, which is best regarded as representing one variable chronospecies."*

Hill *et al*. (2008:1753) summarized, "In other words, we are dealing with one animal, albeit one displaying morphological differences in time and space, which greatly simplifies things."

When Ice Ages advanced, lower sea levels exposed 1,600 kilometer-wide plains from the Bering and Chukchi seafloors between Asia and North America (Creager and McManus 1967). This formed a continuous unglaciated refugium (Beringia), too arid for ice to accumulate, that extended from eastern Siberia to most of Alaska, northern Yukon, and reached as far east as the southern Arctic coast of the NWT. According to Shapiro *et al*. (2004), the early cold periods of the last glaciation provided arid conditions most favourable for the expansion of grasslands in Beringia. Consequently, its bison population grew large and diverse, represented by three distinct genetic lineages (clades). Saiga antelope (*Saiga tatarica*), now restricted to Eurasia, were widespread in Beringia, and remains have been found as far east as the Baillie Islands on the southern Arctic coast of the NWT (Harington and Cinq-Mars 1995). Harington (1981) described saiga as an environmental indicator species of arid, level, low-lying steppe grassland, warm summers, and severe winters with thin snow cover. There are many theories to account for the unique character of these grasslands in Beringia, so different from the tundra vegetation of today (e.g., Zimov *et al*. 1995; Guthrie 2001; Walker *et al*. 2001; Hu *et al*. 2002; Williams *et al*. 2004; Swanson 2006; Kienast *et al*. 2008; Doughty *et al*. 2010). In his analysis of plant tissue samples taken from molars of fossil Beringian bison, Guthrie (2001) found that grasses were overwhelmingly represented, compared to sedges and other forages. A brief interval of warmer and wetter climate 37,000 years ago initiated a dramatic reduction of the bison population, as tree cover replaced much of the grassland (Drummond *et al*. 2005).

While full glacial periods expanded bison habitat in Beringia, moister conditions beyond the ice sheets in North America created an opposite effect. Most of the Great Plains became forested, restricting bison mainly to enclaves of savannah woodland in southern parts of the continent (McDonald 1981).

When the ice began rapidly retreating about 14,000 years ago, Beringian bison expanded eastward into the NWT, and a partially preserved *priscus* carcass was recently uncovered at Tsiigehtchic in the upper Mackenzie Delta (Zazula *et al*. 2009). Routes followed by people into North America were free of ice, and a severe population bottleneck in Beringian bison coincided with the arrival of humans (Drummond *et al*. 2005). Much of Beringia disappeared under rising seas and moister conditions in northern parts of the continent, resulting in the conversion of grassland habitats, which supported bison and the other grassland specialists such as mammoth, horse, camel and saiga, to forest habitats utilized by browsers such as moose (Guthrie 2001). In contrast, southern North America experienced drier climate patterns at this time that allowed grassland to replace forest as *B. antiquus* Leidy (1852) evolved from *B. latifrons*, and advanced across the Great Plains (McDonald 1981).

A western corridor emerged between Beringia and the rest of North America after the cordilleran and continental ice sheets separated, proglacial lakes subsided, and open vegetation became established on recently exposed substrates (MacDonald and McLeod 1996). This offered a window of opportunity for Beringian and southern bison populations to remix, before forest expansion into the corridor diminished their grazing habitats. Apparently, Beringian bison only accomplished a minor southern advance, and contributed no maternally inherited mitochondrial DNA (mtDNA) to modern bison (Shapiro *et al*. 2004; Douglas 2006). All three clades of Beringian bison eventually went extinct by little more than 1,730 years ago, leaving only bison from the single clade south of the ice sheet to repopulate the continent (Shapiro *et al*. 2004; Wilson *et al*. 2008).

Between the rapid recession of southern ice margins 13,000 to 11,000 years ago until the end of the Younger Dryas cold interval from 11,000 to 10,000 years ago (Dyke 2004; Muscheler *et al*. 2008), McDonald (1981) stated that *antiquus* underwent a rapid evolution to a smaller sized, highly variable subspecies that originated in the mid-latitude grasslands of North America. Human predation, extinction of large predators (American lions, tigers, sabre-toothed cats and short-faced bears), and extinction of competitors (mammoths, camels and horses) may have played a role in this bison size diminution, but Hill *et al*. (2008) attributed aridity-driven reductions on forage quality as the most likely cause.

Following the Pleistocene, the Holocene epoch commenced about 11,700 years ago and continues to this day. The 'Holocene Climatic Optimum' lasted from 9,000 to 5,000 years before present. Its warmer, drier conditions accelerated the spread of grasslands across the Great Plains, and at its height, the Grassland biome extended north of its present limit into what is now the boreal forest biome (Ritchie 1976; Vance *et al*. 1995). Near the end of this period, Wilson (1969) and McDonald (1981) suggested that the smaller modern American bison began differentiating from *occidentalis*. However, Wilson *et al*. (2008) identified a taxonomic inconsistency with *occidentalis* because the type specimen from Alaska represents a lineage now known to have become extinct. Consequently, bison resembling *occidentalis* from south of the ice sheet that survived to repopulate the continent required an appropriate name. Because it developed from *antiquus* and into modern bison over such a short time span, Wilson *et al*. (2008) described this bison of "*occidentalis* character" as a chronomorph (rapidly evolving organism) rather than a biologically discrete species.

Larger-sized bison were possibly extirpated by advancing hunting societies (Guthrie 1970), and like people everywhere, the first North Americans became most populous in environments rich in biodiversity (Meyer *et al*. 2011). The more recently evolved modern bison developed several adaptations to cope more effectively with human predation, such as higher reproduction and exploitation of less productive ecosystems (McDonald 1981; Isenberg 2000; Lott 2002).

McDonald (1981) selected 5,000 years before present as the separation date of *B. bison* from their ancestral stock on the basis that typical specimens older than this time resembled extinct phenotypes, while younger specimens strongly resembled modern bison. He also thought that the late Holocene Climatic Optimum and the early 'sub-boreal' period that followed improved the environmental conditions for range expansion and population increase for the newly evolved plains bison over the central and southern Great Plains.

The late Holocene Climatic Optimum (5,000 to 6,000 years ago) also led to forest expansion and peatland development in the boreal region of the northwestern part of the continent during the cooler, wetter ecological transition to the sub-boreal period (Zoltai and Tarnocai 1975; MacDonald 1987; Cwynar and Spear 1995; Hebda 1995; MacDonald 1995; Szeicz *et al*. 1995; Vance *et al*. 1995; Bigelow *et al*. 2003). This is where the unique lineage of wood bison originated (Wilson 1969; Van Zyll de Jong 1986), and McDonald (1981) surmised the time to be about 5,000 to 4,000 years before present, even though no samples were available to him for dating. Throughout the course of bison evolution, the habitat of these grazers has declined when forests expanded, but this time a distinctive graminoid niche was created by the emerging peatlands. Accumulation of incompletely decomposed plant material (peat) is triggered when climatic conditions allow annual precipitation to exceed evapotranspiration (Gignac and Vitt 1994). Fens are wetlands underlain by shallow peat, and their vegetation cover is dominated by sedges (Zoltai and Vitt 1990). Wood bison have adapted to foraging on sedges as their main source of food, becoming 'sedge meadow specialists'. This is a departure from other forms of bison that have largely been 'grassland specialists'. Even when Beringia supported bison, soils were underlain with ice-rich permafrost, but were generally not peaty or waterlogged and supported a rich variety of productive grasses (Guthrie 2001; Swanson 2006).

Based on morphometric comparisons to *occidentalis* and *occidentalis*-like bison, wood bison appear to be a more primitive form than plains bison (Skinner and Kaisen 1947; McDonald 1981; Van Zyll de Jong 1986). The fossil and ancient DNA record has yet to clarify whether wood bison evolved directly from its *occidentalis*-like ancestor, or from an early plains bison intermediary that remained in the northwest after the grasslands were usurped by boreal forest and peatland. McDonald (1981) suggested that they are not necessarily mutually exclusive, and there may have been regular gene flow from northern plains bison into wood bison populations. He also stated that wood bison are the largest bison in North America and historically, plains bison followed a north-south cline of decreasing body size. While wood bison continued to evolve physical adaptations to exploit the forest opening/woodland environment, southern plains bison were being subjected to different selective forces in the new short-grass prairies (Guthrie 1980; McDonald 1981; Isenberg 2000). The most recent body size diminutions up to 2,000 years ago balanced energy demands with environmental conditions, and were most pronounced in the populations south of 40 degrees latitude (Hill *et al*. 2008).

Bison remains in the NWT from Cape Bathurst, Harrowby Bay, Baillie Islands and Old Horton River on the southern Arctic mainland, and Minto Inlet on Victoria Island have been radiocarbon dated between 9,560 and 420 years before present (Gardner and DeGange 2003). Their lineages have not always been easy to determine because of the fragmentary nature of most skeletal remains, and some of the later specimens resemble modern bison. During this time period, significant vegetation change occurred in the Mackenzie River basin from an herb/shrub dominated landscape that became widely replaced by muskeg (MacDonald 1987). The Beringian lineages disappeared (Shapiro *et al*. 2004), and the range of wood bison has since contracted to its more recent historical proportions (Van Zyll de Jong 1986).

Bork *et al*. (1991) described the first step of the speciation process as the geographic isolation of populations, whereupon each population accumulates unique genetic differences. They suggested that prior to human intervention, wood and plains bison had at least reached this step in their evolutionary divergence. The geographic centre of wood bison abundance has been the boreal forest biome where wet meadows produce sedges, particularly awned sedge (*Carex atherodes*), as the most important food for these bison. True grasslands are restricted to very few sites in this biome (Schwarz and Wein 1997). In contrast, the geographic centre of plains bison abundance was the grassland biome that provided drought resistant short-grasses such as blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) as their most important food. Sedge fens are nearly absent in this biome (Zoltai and Vitt 1990). McDonald (1981) suggested that aboriginal hunting patterns may also have contributed to the separation of the two bison gene pools.

In his account of bison subspeciation, Van Zyll de Jong (1986) referred to a heavily forested transition zone between wood bison in the upper Peace River and plains bison of the prairies. He also considered the aspen parkland of eastern British Columba, Alberta and western Saskatchewan as a transition zone between wood and plains bison, and this ecotone between the boreal forest and grassland biomes is also the approximate southern limit of sedge fens (Zoltai 1975). Further east, no historical geographic separation between the two varieties of bison has been defined. Van Zyll de Jong (1986) was unable to acquire bison samples for comparative analysis from anywhere north of Saskatchewan's aspen parkland. In 1969, a herd of plains bison was established in the Prince Albert National Park area, located in the southern boreal region of Saskatchewan. As described by Fortin and Fortin (2009), these animals have adopted a behavioural and feeding ecology that is very similar to wood bison. As part of the Wood Bison Rehabilitation Program and the expectation that historical wood bison range extended into Manitoba, a herd was established in the Interlake District near Waterhen and Chitek Lake in 1981 (Reynolds 1987). However, Van Zyll de Jong (1986) scored the few skeletal samples available from the interlake and other boreal regions north of the Manitoba aspen parkland as plains bison.

APPENDIX A2 – WOOD BISON GENOTYPE

Classification of wood bison as a subspecies has been controversial ever since Rhoads (1897) described it. Skinner and Kaisen (1947) concluded that the number of wood bison specimens available for identifying the subspecies was too small to present a comprehensive understanding of the amount of variation possible. Based mainly on pelage characteristics, Krumbiegel and Sehm (1989) proposed two extant North American bison subspecies consisting of a northern plains bison, which included wood bison, and a southern plains bison. Geist (1991) cautioned that precision sampling of the small range of the natural variation remaining in today's remnant herds, and ignoring phenotypic plasticity, increase the risk of accepting taxonomic deviants and peculiarities as normal.

Bison that formerly occupied mountainous habitats may have constituted a third modern subspecies known as the mountain bison (Christman 1971; Meagher 1973). From skeletal analysis, northern cordilleran specimens have basically been classed as wood bison type, and southern counterparts as plains bison type (McDonald 1981; Van Zyll de Jong 1986; Stephenson *et al*. 2001), but there are inconsistencies (e.g., Skinner and Kaisen 1947; Peach 2002; Cannon 2007).

The International Code of Zoological Nomenclature (1999) accepts only one taxonomic rank below species, namely the rank of subspecies. Accepting the definition of Mayr (1969) that a subspecies inhabits a geographic subdivision of the range of the species and differs taxonomically from other populations of the species, Van Zyll de Jong (1986) concluded from his multivariate morphometric analysis of skeletal and external character data that there was a geographic and phenotypic discontinuity sufficient to distinguish wood bison as a subspecies.

Geist (1971) pointed out that ungulate taxonomy has usually been based on physical structures that have social significance to the animals (skull proportions, horn core diameter, skin glands, hair colour and pattern, etc.), without considering habitat adaptations. Geist (1991) came to the conclusion that wood bison is not a valid subspecies, but is actually an ecotype whose adaptation to a particular set of environmental conditions is more distinctive than its lineage or morphology. He theorized that some physical differences between wood and plains bison may be due to local ecology rather than heredity, but Van Zyll de Jong *et al*. (1995) demonstrated that external characteristics of bison are genetically based. The concept of ecotypes has gained acceptance in classifying caribou (*Rangifer tarandus*) primarily by their behavioural adaptations to different environments, as taxonomy is uncertain at the subspecies level and the genetic relationships among the various clades became particularly tangled after deglaciation (COSEWIC 2002). The caribou example recognizes that fundamentally distinct groups of animals may be following new evolutionary pathways, regardless of ancestry.

The arrival of firearms led to excessive human predation and reduced the plains bison population from millions, or even tens of millions in the mid-1860s (Shaw 1995), to a few hundred by the late 1880s (Hornaday 1889). During approximately the same period, wood bison dropped from thousands to a few hundred (Ogilvie 1893). After the wood bison population in Wood Buffalo National Park had risen to 1,500-2,000 animals (Seibert 1925), the subspecies distinction issue was further complicated during the period of 1925 to 1928, when more than 6,000 plains bison from Buffalo National Park near Wainwright, Alberta were released into Wood Buffalo National Park, and hybridized immediately with the indigenous wood bison (Raup 1933). As recovering herds of wood bison and plains bison were derived from several lineages, neither subspecies is a well-defined taxon (Polziehn *et al*. 1996). Wood bison and plains bison exhibit many differences in morphological, molecular and genetic characters, but the debate has centred on the degree of distinctiveness.

There had been speculation that small groups of pure wood bison existed in the northwestern part of Wood Buffalo National Park, too remote to mix with descendants of Wainwright plains bison (Raup 1933; Soper 1941; Fuller 1951). During an aerial survey by Novakowski (1957), bison were found in the upper Nyarling River area, which appeared to be far removed from the main herds of Wood Buffalo National Park. In 1959, specimens were procured from this area for comparison to the wood bison type, and field investigations were carried out in the Fort Providence area to evaluate the feasibility of bison reintroduction (Novakowski 1959). Based on large size, dark pelage and most skull measurements falling within the wood bison parameters developed by Skinner and Kaisen (1947), Banfield and Novakowski (1960) concluded that the specimens collected represented an isolated population of the wood bison subspecies, and that any contact with hybrid animals would have been minimal.

Novakowski (1963a) reported on the subsequent rescue. Although the question of genetic purity was not completely clarified, animals were captured from the Nyarling River area as breeding stock for establishing new herds of wood bison able to avoid hybridization and debilitating cattle diseases. The presence of tuberculosis and brucellosis in some of the captured animals indicated that isolation was not as complete as anticipated, but it was hoped that the purity of the subspecies was not obviated. After diseased animals were removed, 18 were reintroduced in 1963 to the newly created Mackenzie Bison Sanctuary, near Fort Providence (Novakowski 1963b). As the Mackenzie Bison Sanctuary population expanded beyond the boundaries of the preserve, protection was extended and the herd became more appropriately known as the Mackenzie population.

In 1965, an additional 23 bison from Nyarling River were transported to Elk Island National Park when anthrax outbreaks in bison along the Slave River were perceived as a threat to the survival of the Nyarling River subpopulation (Novakowski and Stevens 1965). The Isolation Area in Elk Island National Park, south of the Yellowhead Highway, was set aside to hold representatives of this population in semi-captivity, specifically for good bison recovery (Babbage 1969). Plains bison roam separately in the portion of Elk Island National Park north of the Yellowhead Highway.

Many factors seem to have prevented genetic swamping by the plains genotype, perhaps including lower fitness by hybrids (Armstrong pers. comm. 2015), and studies have shown wood bison characteristics of northern populations to be more intact than expected. Geist and Karsten (1977) documented physical differences between plains and wood bison held in Elk Island National Park. McDonald (1981) found the skeletal morphometrics of post-1929 Wood Buffalo National Park bison to be closer to wood bison, and suggested that evolutionary selection for adaptive traits in this environment (such as larger size) is ongoing. After weighing all the phenotypic evidence, Van Zyll de Jong *et al*. (1995) classed all bison in the NWT as wood bison, including those in and around Wood Buffalo National Park.

While there appears to be little or no variation between wood bison and plains bison by blood characteristics (Peden and Kraay 1979) or at the chromosomal level (Ying and Peden 1977; Cronin and Cockett 1993; Stormont 1993), more polymorphism has been revealed in mtDNA. Of the 12 mtDNA haplotypes Polziehn *et al*. (1996) identified among three wood bison and six plains bison populations, one is universal and three are widespread. This raises the possibility that prior to the elimination of bison in the sympatric ranges of the late 1800s, some gene flow had occurred between adjacent plains and wood bison populations. From sampling in Wood Buffalo National Park, the Mackenzie Bison Sanctuary (Mackenzie population), and the Elk Island National Park Isolation Area, Polziehn *et al*. (1996) found four haplotypes to be unique to these wood bison, indicators that they shared a common gene pool. It is not known whether these haplotypes were limited to wood bison, or if they were present in lower frequencies in plains bison herds. Any evidence of a cline would have been lost during the severe depopulation in the late 1800s. Five haplotypes are shared between the two subspecies. These may have been present in the original population of wood bison or introduced along with the plains bison from Wainwright. Unfortunately, the magnitude of population reduction likely removed many more haplotypes, both shared and unique. Genetic distances measured by Polziehn *et al*. (1996) indicated that bison from Wood Buffalo National Park, the Mackenzie Bison Sanctuary and the Elk Island National Park Isolation Area are more related to each other than to the plains populations sampled.

Douglas *et al*. (2011) sequenced complete mtDNA genomes from 43 bison and bison-cattle hybrids, including two wood bison from the Elk Island National Park Isolation Area. Two of the seventeen bison haplotypes discovered were unique to these two wood bison, but they did not form a clade separate from the plains bison haplotypes.

Whereas mtDNA is maternally inherited, nuclear DNA is passed on from both parents. Bork *et al*. (1991) studied the genetic relationship of wood and plains bison based on restriction fragment length polymorphism from nuclear DNA. Results were indicative of a recent divergence similar to geographically isolated populations of other species such as red deer (*Cervus elaphus*).

DNA microsatellites, highly polymorphic nuclear markers that are more sensitive in detection of genetic variation, were used by Wilson and Strobeck (1999) to test genetic diversity and heterogeneity among several bison populations. Their analysis of 11 microsatellite loci revealed some evidence for the existence of subpopulations in Wood Buffalo National Park; however, very small genetic distances between them suggest that nuclear material from the introduced plains bison has diffused throughout the Park. They also determined that genetic distances between sampled populations of wood and plains bison are generally larger between than within the two subspecies. In addition, genetic distances between wood bison populations are low, relative to other bison populations.

Could some distinguishing morphological traits of wood bison be unrelated to DNA? Epigenetics is a relatively new field of biology referring to modifications of the genome that do not involve a change in the underlying DNA sequence of the organism (Richards *et al*. 2010). Instead, non-genetic factors such as environmental variation cause the organism's genes to express themselves differently, and these changes may contribute to phenotypic variation passed down for multiple generations. Llamas *et al*. (2012) tested cytosine methylation in ancient DNA as a means to study the role of epigenetics in rapid adaptation to climate and environmental change, without the requirement for DNA sequence alterations. They demonstrated that steppe bison (*Bison priscus*) exhibited high morphological diversity, but low mtDNA heterogeneity. If epigenetics is responsible for these morphological changes, the loci where the epigenetic changes occurred will need to be identified.

One of the original intents of salvaging bison in the Nyarling River area was to rescue indigenous wood bison from genetic swamping by plains bison introduced to Wood Buffalo National Park (Reynolds 1979). With a numerical imbalance exceeding 3:1 in favour of plains bison, why do studies show such a considerable representation of wood bison characteristics? There were probably many contributing factors. Graham (1924) believed that about 500 wood bison were scattered in small herds across a northern range of Wood Buffalo National Park that did not mix with the southern population. His summary of the planned release of Wainwright plains bison stipulated that in the first year all animals were to be yearlings, at a ratio of one male to five females. Later shipments would contain two year olds and three year olds, and no males of any age. Graham (1924:189) stated, "…the bison transferred from Wainwright will be placed on one or two selected locations in the southern range of Wood Buffalo Park, where they will meet and come under protection and leadership of adult wild bison in those areas." Officially, 47 bison died enroute and the remaining 6,673, comprising 4,826 yearlings, 1,515 two year olds and 332 three year olds were delivered to their destination (Kitto 1930). However, testimony from persons involved with the unloading indicates that many bison died between the landing and the nearest meadow (Fuller 2002).

The fact that plains bison males generally do not breed until they are at least five years of age (McHugh 1958; Lott 2002), and so few were shipped, indicates that wood bison bulls could have been the primary sires of the first cohorts from the female plains bison and early hybrid generations (Van Zyll de Jong 1986). Also, because successful competition among male bison for mates is related to age, size, and prior reproductive success (Komers *et al*. 1994b; Wilson *et al*. 2002), the younger, smaller, inexperienced male plains bison from Wainwright would be at a breeding disadvantage. Y chromosomal analysis would be required to evaluate paternally inherited markers. If the northern and southern ranges in Wood Buffalo National Park were partially separate, pure wood bison from the reservoir in the north that entered the hybrid zone and backcrossed with hybrids, would have further diluted the plains genes. Some of the less fit plains regions of the genome may have been selected against, resulting in a decline in their frequency over time from the hybrid zone. Van Camp (1989) and Carbyn *et al*. (1993) discussed several other setbacks the plains bison had in contributing to the gene pool, including local oral history reports of mortality in the thousands among the new arrivals.

APPENDIX A3 – SEARCH EFFORT

<u>1897 to 1910</u>

After wood bison had reached the brink of extinction and the *Unorganized Territories Game Preservation Act* was passed in 1894 to protect them, officers of the North West Mounted Police were appointed as ex-officio game guardians. Until 1897, the police had been restricted in the north to outposts on the Athabasca River. With the gold rush into the Klondike, the police commissioner decided to establish winter patrols along the major waterways as far north as Fort Resolution on Great Slave Lake (Herschmer 1898). As the first officer to be sent to Fort Smith and Fort Resolution, Inspector Jarvis (Jarvis 1897) was instructed to locate the remaining wood bison, determine exact numbers and find out whether the 1894 game act was effective. Jarvis found that all wood bison were west of the Slave River between the Peace River to within 20 miles (32 km) of Fort Resolution, no more than 300 existed, and most of the residents in this area were unaware of the protective legislation. Jarvis also heard that a few bison may still have been surviving in the upper Liard River, but there were no reports of these animals after 1897 (Soper 1941).

During his travels in 1901 to Fort Chipewyan, Fort Smith and Fort Resolution as Treaty 8 Commissioner, Macrae (1901) interviewed a large number of native people who had returned from the bison range. He concluded that wood bison existed in three separate herds: Salt River south to Peace River, east and west of Salt River, and Salt River north to Great Slave Lake.

Jarvis (1907) continued exploration of the areas around the Grand Detour, Nyarling and Salt rivers with naturalists Preble and Seton, who published their discoveries pertaining to wood bison (Preble 1908; Seton 1911). After the 1907 patrol, Jarvis believed that sporadic law enforcement was insufficient to prevent poaching of bison. He recommended that a Dominion game sanctuary and resident game guardians were better solutions. The next year, the Royal North West Mounted Police Commissioner established permanent detachments at Fort Vermilion, Fort Chipewyan and Fort Smith, and forwarded the game sanctuary recommendation to Ottawa (Perry 1909).

To enforce the prohibition of bison hunting, it was imperative that all police officers who followed Jarvis become familiar with the distribution of the remnant herds. Police Superintendent Routledge penetrated bison range seldom visited, nearly 75 miles (120 km) west of the Salt River settlement (Routledge 1908). When Sergeant McLeod (McLeod 1909, 1911) travelled from Fort Vermilion on the Peace River to the mouth of Hay River on the south shore of Great Slave Lake, he did not observe any sign of bison or feed for them, neither in 1909, nor by a different route in 1911. He learned from aboriginal informants that the western edge of bison occurrence was 35-40 miles (56-64 km) east of Buffalo Lake. In 1910, Corporal Mellor and Constable Johnson explored the area west of Little Buffalo River to Sulphur Point on Great Slave Lake, then to the shores of Buffalo Lake, and found no bison. From a summary of this patrol and other police searches, Mellor (1910) outlined the approximate limits of bison distribution as bounded westerly by the Caribou Mountains, southerly by the Peace River, easterly by the Slave River, and northerly by a line from the Caribou Mountains 50 miles (80km) south of Buffalo Lake to Point Ennuyeuse on the Slave River.

In 1909, Harry Radford (Radford 1911) was sent by the American Bison Society for a two year study of the present and former range of wood bison. He confirmed that the subspecies had disappeared from all parts of their original range, particularly in the past 15 years, except for the area west of the Slave River. Radford believed that police protection had stemmed the decline, and 325-335 wood bison were widely scattered in small roving bands.

1911 to 1922

When the Royal North West Mounted Police were relieved of their special supervision of wood bison in 1911, the responsibility was transferred to Game Guardians, under the direction of the Forestry Branch. All searches for wood bison were carried out on the ground with dog teams in winter, and by canoe and horseback during the rest of the year. George Mulloy and Peter McCallum were the first to monitor the bison range as newly appointed Game Guardians. Their investigations mainly covered the area north of the upper Little Buffalo River, and they concluded that two separate herds remained (Mulloy 1912). A herd that once ranged from Salt River north to Great Slave Lake had evidently disappeared and this was confirmed by Camsell (1917). During a comprehensive faunal reconnaissance of the Great Slave Lake region in 1914, Harper (1932) accompanied McCallum on patrol and documented the state of the knowledge of wood bison. McCallum believed that the population had grown to about 500 animals, and the larger northern herd was separated from the southern herd by jack pine forest 20-30 miles (32-48 km) in width.

As a prelude to a Dominion reserve for wood bison, Seibert (1923) and Kitto (1924) carried out comprehensive surveys of bison distribution from 1920 to 1922. Their work determined the boundaries for the creation of Wood Buffalo Dominion Park in 1922 (or Wood Buffalo National Park as it was later renamed in 1930). Seibert's investigations were mainly focused in the NWT portion of the range and he mapped distribution and habitat. The area occupied by bison to the northeast, east and south was well known and here the park was bounded by the Nyarling, Little Buffalo, Slave and Peace rivers, excluding the settlement environs of Salt River, Fort Smith and Fort Fitzgerald. In the western and northwestern areas where Kitto and Seibert were less informed, park boundaries were fixed by straight lines conservatively beyond the known range.

1923 to 1930

After the *National Parks Act* was passed in 1930, a warden service replaced the Game Guardians with cabins, roads, trails and telephone lines constructed throughout the park for improved bison monitoring efforts (Kitto 1930). When about 400 Wainwright bison were observed crossing the Peace River southward to the Peace – Athabasca Delta in 1925-26, the park boundaries were enlarged to accommodate this range expansion (Seton 1927).

From 1928 to 1930, Raup (1933) travelled extensively in his evaluation of bison range conditions in Wood Buffalo National Park from topographical, soil and vegetation perspectives. He also collated early history, local knowledge of long term residents and observations of park wardens regarding bison habits and their geographical distribution. The remains of old connecting bison trails gave Raup reason to believe that the separation between the northern and southern herds occurred only after their maximum population decline, otherwise no real barriers to movement existed. Because bison numbers were steadily increasing, he believed that interchange between the two herds would recommence soon, if not already. Raup observed that bison were returning to the Salt Plains where they were formerly abundant. With information collected about the early history and their habitat requirements, he predicted range expansion to the south and west of the lower Peace River, the base of the Caribou Mountain plateau, and the upper Hay River, but limited by agricultural development in areas beyond the Park. He also anticipated range expansion across the Little Buffalo and Slave rivers as far east as the Precambrian shield.

1931 to 1946

In an attempt to overcome difficulties of estimating the bison population from the ground, the first aerial bison survey in Wood Buffalo National Park was in 1931, with the cooperation of the Royal Canadian Air Force. All bison were to be photographed from orderly flight lines over the winter range, and a Park Warden was present for a direct visual count. Reports from the wardens described the outcome as unsatisfactory, mainly because of the problem with forest cover (Soper 1941).

Unconvinced about the feasibility of aerial surveys after his own attempt in 1932, Soper (1941) investigated the numbers and distribution of bison in Wood Buffalo National Park from the ground during the period of 1932-34. His efforts involved a systematic evaluation of pasturage within 72 square mile (186.5 km^2) quadrats of land, and the degree of use by bison. Even at low density, he found that bison made their presence very obvious in the form of trails, trees that are rubbed or horned, and willows browsed and thrashed into odd shapes. Soper (1941) calculated a population of 12,000 bison, but conceded that neither aerial nor ground surveys alone were capable of providing a very creditable approximation. He believed that the population occupied about 8,200 miles^2 (21,240 km^2) in eastern and central portions of the park, whereas 9,100 miles^2 (23,570 km^2) in western and northern areas were substantially uninhabited by bison. Although there was plenty of habitat available for expansion, he considered the section of the park north of the Caribou Mountain plateau to be unsuitable for bison. Soper also noted a few restless herds that occasionally left the park, including a group of about 40 animals that temporarily crossed to the east side of the Slave River during the winter of 1933-34. This was an indication that bison were starting to reuse the Slave River Lowlands (at least as far east as the Slave River), but this was not part of Soper's study area.

1947 to 1961

Aerial surveys were restarted by Oldham (1947) and have been used exclusively for population estimates ever since. Due to their large size, dark colouration, and preference for open habitat, bison are easily spotted from the air against a white snowy background. Feeding craters in snow often signal to the observer that further searching will reveal their presence. In 1949, Fuller (1950) improved upon Oldham's strip transect techniques by surveying later in the winter, employing two observers, covering a narrower strip, and maintaining unidirectional flight lines. In his review of the problems encountered by earlier census attempts, Fuller believed that Soper's 1934 (1941) ground estimate of 12,000 was too high, and Oldham's 1947 aerial estimate of 7,482 was too low. By 1949, Fuller thought that the ranges in and around Wood Buffalo Park contained at least 12,000 bison. Since the time of Soper's work, Fuller determined that the bison population had expanded east of the Slave River (which he did not survey), to the eastern base of the Caribou Mountain plateau, and further into areas around the lower Peace River to encompass a region that resembles the current Greater Wood Buffalo Ecosystem's area of occupation. Fuller also stated that the population trend was as important as absolute numbers, and if survey methods were standardized, trends may be tracked. Fuller (1951) resurveyed the bison range two years later to reconfirm his 1949 results.

Novakowski (1957) duplicated Fuller's methodology in 1957, and estimated a bison population of 12,000-14,000. He also discovered about 200 bison at the headwaters of the Nyarling River, and subsequent flights showed these animals to be quite isolated from all other herds. The Nyarling subpopulation was studied in detail with the intention of using it for establishing disease-free herds of pure wood bison (Novakowski 1959). As bison in the Slave River Lowlands were becoming more important, Novakowski (1961) estimated that 1,300 occurred between the Little Buffalo and Taltson rivers.

1962 to 1971

Starting in 1962, six anthrax outbreaks had killed over 1,000 bison in the Greater Wood Buffalo Ecosystem by 1971 (Choquette *et al*. 1972). Most search efforts were directed towards locating infected carcasses for disposal, and rounding-up herds for vaccination. As a result, comprehensive bison censuses in Wood Buffalo National Park were deferred.

Following the salvage of wood bison from the Nyarling River area, the Mackenzie bison population was established on August 14, 1963 (Novakowski 1963b). James Bourque was appointed to monitor the herd for the first few years while they remained in the vicinity of Falaise Lake. The aerial surveys in 1968 and 1969 that located 42 and 56 bison respectively indicated that animals had started to occupy Dieppe and Calais lakes (Gates and Larter 1990).

Williams (1966) was the first to survey the Slave River Lowlands herds east and west of the river as separate entities. Results from strip transects of partial coverage estimated 302 bison for the Grand Detour subpopulation and 1,430 for the Hook Lake subpopulation. The mandate for wildlife management outside of Wood Buffalo National Park was transferred to the new

Government of the Northwest Territories when it was created in 1967. Consequently, surveys of the Grand Detour subpopulation whose animals moved in and out of the park were not being coordinated between the federal and territorial agencies. When Hall (1968) flew transects of partial coverage, he estimated 249 in the Grand Detour area and 1,232 for the Hook Lake subpopulation. Rippin (1971 *in* Van Camp and Calef 1987) carried out the first strip transect total coverage survey in the Slave River Lowlands. He estimated 336 bison for the Grand Detour subpopulation, and his 1,700 estimate (Rippin 1971 *in* Nishi 2010) east of the Slave River is the highest ever recorded for the Hook Lake subpopulation.

1972 to 1986

The beginning of this time period marked the onset of a long term decline of the Greater Wood Buffalo Ecosystem population. From the initial anthrax outbreak until 1974, surveys in Wood Buffalo National Park were limited to the high bison concentrations of the Hay Camp and Delta subpopulations, mainly to assist with the placement of vaccination corrals (Tempany and Cooper 1975). In 1975, coverage was extended to the Nyarling and Grand Detour ranges, but survey effort in those areas varied between years (Bradley and Wilmshurst 2005). Surveys in the Slave River Lowlands followed the same flight lines as established by Rippin in 1971 for the next several years (Van Camp and Calef 1987), which would have limited search effort in peripheral areas. Calef (1976) indicated that bison were distributed across most of the Slave River Lowlands from the delta to the Alberta border, but that they concentrated on the large prairies from mid-May to mid-July. He also stated that movements could be erratic and during the particularly severe weather of 1974-75, most of the animals wintered further south than usual.

Growth of the Mackenzie population was documented by total count surveys carried out every year. The procedure was to search 100% of the marl lake beds occupied by bison and the major trails connecting them. Less than three hours of flight time was sufficient to account for virtually the entire population. Bison were beginning to occupy Boulogne Lake (Gates and Larter 1990) and Calais Lake (Jacobson 1974). After bison started invading the Mink Lake area in 1980, the extended search effort doubled the survey flight time. The number of bison observed became the minimum estimate for the population, with no accompanying estimate of precision.

The Nahanni population was established in 1980 when 28 wood bison from Elk Island National Park were released (Reynolds 1982). The population was monitored by surveys that tracked the total count and expanding distribution (Larter and Allaire 2007).

1987 to 2001

In 1987, a bison-free management zone (Bison Control Area) was established south of the Mackenzie River and north of the Mackenzie Highway, between Mills Lake and Hay River, to prevent the Greater Wood Buffalo Ecosystem bison from infecting the Mackenzie and Nahanni populations with tuberculosis and brucellosis. In 1990, the control area was greatly expanded to the Alberta border, between Trout River and Wood Buffalo National Park (Gates and Gray 1992). Since then, an area of 39,623 km^2 has been searched several times per year, by ground and by air, for the purpose of removing bison (Greig and Cox 2012). Geographic information system (GIS) software and global positioning system (GPS) technology became available for aerial survey navigation.

The Mackenzie population was expanding its range to Mills and Beaver Lake on the Mackenzie River, Lonely Bay and Frank Channel on Great Slave Lake, and the base of the Horn Plateau. In addition to systematic surveys in 1989, 1992, 1996, 1998, and 2000, targeted searches to monitor these movements were documented by field officers in the Wildlife Sightings appendices of their Monthly Reports (Chowns pers. comm. 2012). As the Mackenzie population became too large and dispersed to rely solely on total counts, the study area was stratified into high, medium and low density units (Gates *et al*. 1991). The high density stratum consisted of the main meadows where bison concentrated and these areas were still covered by total counts. Systematic parallel transects covered medium and low density strata between areas of high density. Since the first Mackenzie bison anthrax outbreak in 1993 (Gates *et al*. 1995), regular, widespread searches have been carried out in the summer season for carcass detection and disposal (Dragon and Elkin 2001; ENR 2010).

Prior to the establishment of permanent transects in the high-density areas of Wood Buffalo National Park in 1991, search effort changed almost every year (Bradley and Wilmshurst 2005). Lower density areas that were covered by reconnaissance flights depended on available funding. Fifty survey hours were flown annually.

The Hook Lake subpopulation had declined to such low numbers that the 1987, 1994, 1996 and 2000 minimum population estimates were based solely on total counts (Ellsworth pers. comm. 2012).

Aerial surveys of the primary bison range in the Nahanni Butte and Netla and Kotaneelee River areas, the Liard River Valley and its islands from Flett River to Fort Liard and the cutblocks in the La Biche River area of northeastern British Columbia were carried out in 1995, 1996, and 1997 to generate a minimum population estimate (Larter and Allaire 2007). However, these were not systematic aerial surveys of the population that could be replicated.

<u>2002 to present</u>

GPS and tracking with onboard laptop computers were advances in technology that aided in the prevention of double counting. Attempts described below have been made to remedy the problem of inconsistent survey effort that has been recognised in the historical datasets of all three NWT wood bison populations.

A biological program for the Dehcho Region was established in 2002, which included more regular monitoring of the growing Nahanni bison population (Larter and Allaire 2007). In 2003, they added all information from local residents and the Governments of British Columbia and Yukon Territory on bison distribution to the knowledge base for compilation of a map of the winter range of the Nahanni bison population. For the 2004 aerial survey, 1,288 km of parallel strip-transect lines were flown at 4 km intervals over the Nahanni bison winter range in the NWT, British Columbia and the Yukon (Larter *et al*. 2007). A similar survey of nearly 20 hours was carried out in 2011, except that the transect lines were increased to 2,155 km at 3.5 km apart (Larter and Allaire 2013). Because most of the Nahanni winter range is forested, with major river drainages, mountains and deep valleys bisecting it, seven bison were equipped with satellite collars to determine a sightability correction factor, and improve the delineation of the search area. The population was estimated at 431 (± 213, 95% CI). This had a lower coefficient of variation than the 2004 estimate, partially because transect lines were lengthened according to expanding the bison range, animals were more evenly distributed, and fewer transects were used where no bison were observed in 2004. Following the survey, collared animals were located beyond the 2011 survey area boundaries, which indicated continuing range expansion.

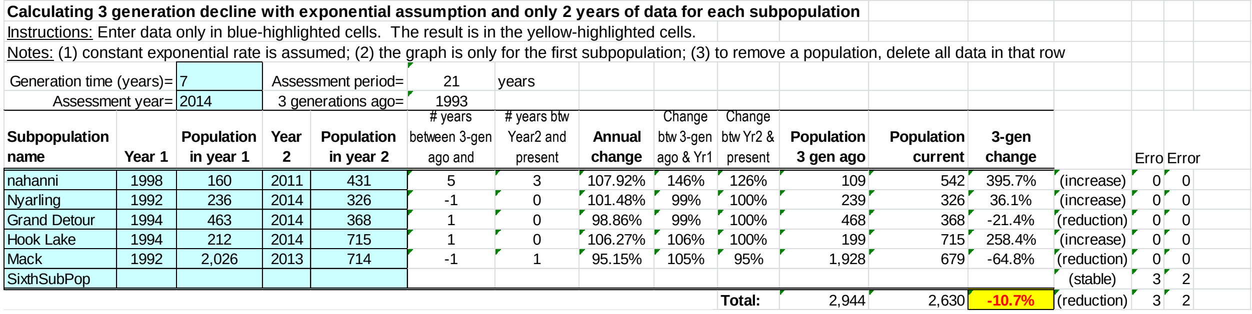
In 2002, permanent transects were established in the lower density areas of Wood Buffalo National Park, resulting in an annual effort exceeding 100 hours. To enable comparisons with 1990s level of effort, the increase in survey effort was compensated by buffering the flight lines (Bradley and Wilmshurst 2005). The 2009 bison survey was classified into four strata consisting of total count, strip transect, combined total count/strip transect, and reconnaissance of areas that are expected to contain few or no bison (Vassal and Kindopp 2010).

The 2009 Slave River Lowlands survey of the Hook Lake and Grand Detour subpopulations used over 23 hours of flying time, and was coordinated with Wood Buffalo National Park's bison survey. A total of 1,162 bison were observed on and off transects, giving a population estimate of 1,790 bison (SE 323), which is nearly triple the previous estimate of 600 in 2000 (Armstrong 2011). The ranges of the Hook Lake and Grand Detour subpopulations are fairly well defined within the Slave River Lowlands. Searches rarely cross the Taltson River. Although bison have occasionally been reported on the Precambrian Shield, east of the Taltson (Ogilvie 1979), it contains little potential habitat (Armstrong pers. comm. 2012).

The Mackenzie population surveys were increasing above 75 hours of flying time. From a total of 1,252 bison observed on and off transects in 2008, the population estimate was 1,555 bison (SE 146), about 22% less than the 2000 estimate of 1,998 ± 163 bison (Armstrong 2010). When the next estimate in 2012 was reanalysed with 2013 data the estimate was 1,531 (SE 257). The Mackenzie population was resurveyed in 2013 because of an anthrax outbreak in summer 2012, producing an estimate of 714 (SE 156) (Armstrong 2013b). Armstrong (2013b) used distance sampling, a survey technique particularly useful for estimating wildlife abundance in forested areas that collects data on the distances of the animals from randomly placed lines (Buckland *et al*. 2001). Potential areas of expansion for these animals include historical range around the Horn Plateau, and as far north as Lac La Martre (Richardson 1851), and these areas are occasionally searched (Armstrong pers. comm. 2012). Reports from the Taiga Shield east of the North Arm of Great Slave Lake are mainly from highway travelers and this area contains some habitat, mainly near the lake (Armstrong pers. comm. 2013).

APPENDIX A4 – TRENDS AND FLUCTUATIONS

Methodology for calculating IUCN Criterion A, exponential assumption, two data point calculator is as follows (Fig. 14, below).



Calculating 3 generation decline with exponential assumption and only 2 years of data for each subpopulation

Instructions: Enter data only in blue-highlighted cells. The result is in the yellow-highlighted cells.

Notes: (1) constant exponential rate is assumed; (2) the graph is only for the first subpopulation; (3) to remove a population, delete all data in that row

Generation time (years)= 7 | Assessment period= 21 years

Assessment year= 2014 | 3 generations ago= 1993

Subpopulation name	**Year 1**	**Population in year 1**	**Year 2**	**Population in year 2**	# years between 3-gen ago and	# years btw Year2 and present	**Annual change**	Change btw 3-gen ago & Yr1	Change btw Yr2 & present	**Population 3 gen ago**	**Population current**	**3-gen change**		Erro	Error
nahanni	1998	160	2011	431	5	3	107.92%	146%	126%	109	542	395.7%	(increase)	0	0
Nyarling	1992	236	2014	326	-1	0	101.48%	99%	100%	239	326	36.1%	(increase)	0	0
Grand Detour	1994	463	2014	368	1	0	98.86%	99%	100%	468	368	-21.4%	(reduction)	0	0
Hook Lake	1994	212	2014	715	1	0	106.27%	106%	100%	199	715	258.4%	(increase)	0	0
Mack	1992	2,026	2013	714	-1	1	95.15%	105%	95%	1,928	679	-64.8%	(reduction)	0	0
SixthSubPop													(stable)	3	2
									Total:	2,944	2,630	**-10.7%**	(reduction)	3	2

Figure 14. Methodology for calculating IUCN Criterion A, exponential assumption, two data point calculator.

With respect to the estimate of population trends for all NWT wood bison (*Trends and fluctuations*, p. 99), the data in Table 6 (below) was used to try to assess the number of wood bison in all populations, and how that has changed over different generations. Survey estimates over a five generation period (1980-2014) were collected for all populations/subpopulations; these are the black values in the table. For years where estimates weren't available, an estimate was derived by calculating the annual growth rate between successive population estimates and projecting that forward. These estimates are shown in red font on the table. For example, the Nahanni population size was estimated as 403 in 2004 and 431 in 2011. The estimated annual change was an addition of four animals per year, as shown in Table 6 (below). With population estimates for all populations/subpopulations and all years, the annual summed total of bison was used to provide a population dynamic of all bison, in all populations, over a period of five generations. This permitted the examination of overall NWT bison populations trends, broken down by generation.

Table 6. Abundance since 1980 with rate of growth estimates included for non-census years (red text).

			Greater Wood Buffalo Ecosystem			
	Nahanni	Mackenzie	Nyarling	Grand Detour	Hook Lake	**Total**
1980	28[8]	645	0	240	386	**1299**
1981	14	668	22	231	361	**1296**
1982	15	712	35	215	339	**1316**
1983	16	980	48	198	316	**1558**
1984	17	1165	35	144	283	**1644**
1985	19	1349	12	58	250	**1688**
1986	20	1534	79	32	216	**1881**
1987	25	1718	145	6	183	**2077**
1988	38	2075	5	71	192	**2381**

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[8] Initial reintroduction of 28 bison to Nahanni area.

1989	40[9]	2431	36	118	201	**2826**
1990	45	2296	112	56	210	**2719**
1991	50	2161	144	3	219	**2577**
1992	55	2026	236	4	228	**2549**
1993	58	1984	216	234	220	**2712**
1994	61	1942	196	463	212	**2874**
1995	64	1899	174	356	360	**2853**
1996	78	1857	173	288	508	**2904**
1997	107	1883	49	282	452	**2773**
1998	160[10]	1908	229	148	396	**2841**
1999	201	1953	184	95	339	**2772**
2000	241	1998	200	235	283	**2957**
2001	282	1943	217	308	352	**3102**
2002	322	1887	233	380	421	**3243**
2003	363	1832	652	453	489	**3789**
2004	403	1776	585	525	558	**3847**
2005	407	1721	518	598	627	**3871**
2006	411	1666	618	670	696	**4061**
2007	415	1610	717	743	764	**4249**
2008	419	1555	647	815	833	**4269**
2009	423	1549	576	888	902	**4338**
2010	427	1543	526	784	865	**4133**
2011	431	1537	476	680	827	**3926**
2012	435	1531	426	576	790	**3721**
2013	439	714	376	472	752	**2703**
2014	443	306	326	368	715	**2096**

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[9] 12 bison introduced into Nahanni population.

[10] 59 bison introduced to Nahanni population.

APPENDIX A5 – ERUPTIVE OSCILLATION

Riney (1964) and Caughley (1970) described a four stage eruptive oscillation in ungulate populations that occurs when there is a great discrepancy between how many animals the environment can support and the numbers actually present. This scenario usually unfolds after a population has been significantly reduced, or has been introduced, and predators may be present. Ford (1931) suggested that natural selection is relaxed during population increases, allowing inferior genotypes to survive. When conditions deteriorate, inferior individuals are eliminated through increased natural selection causing the population to decline.

Since the turn of the last century, all wood bison populations appear to have undergone eruptive oscillations that are somewhat analogous to the Riney (1964) and Caughley (1970) predictions (e.g., Larter 1994). Although there are many information gaps, the most intensively documented population dynamics have been for the herds within Wood Buffalo National Park, plus the Hook Lake and Mackenzie herds.

Stage One: Mortality is low, the population begins to grow, and then the growth becomes exponential. Towards the end of this stage, preferred forage plants in critical parts of the habitat begin to decline.

In response to the looming threat of extinction of wood bison, the *Unorganized Territories Game Preservation Act* was passed in 1894, but was not enforced or well-advertised in the north until North West Police patrols began in 1897 (Jarvis 1897). Soper (1941) suggested that the limit of population decline was 1896-1900, and may have ebbed as low as 250 animals. After the police became active in the bison range, the bison population began rebounding (Macrae 1901; Seton 1911; Radford 1911; Harper 1932). By the time Wood Buffalo Dominion Park was created in 1922, the population had climbed to 1,500-2,000 animals (Seibert 1925). Between 1925 and 1929, the population was bolstered with the addition of over 6,000 plains bison and may have reached 10,000-12,000 by 1934 (Soper 1941), but early methods of estimating populations were very crude.

After disappearing from the Slave River Lowlands east of the Slave River by 1880 (Radford 1911), bison reinvaded the Hook Lake area in the late 1930s or early 1940s from Wood Buffalo National Park (Fuller 1950). Unfortunately, initial population growth of the newcomers in this pristine habitat was never documented.

From 18 founders in 1963 (Novakowski 1963b), Calef (1976) estimated the Mackenzie population exponential growth rate at 24% until 1975. In these early years, Calef (1984) observed relatively high reproduction and little or no evidence of mortality in any age class of the Mackenzie population. The exponential rate appeared to peak in the early 1970s at 26-27% (Gates and Larter 1990; Larter *et al*. 2000). Previously, such an exceptional growth rate had only been observed in captive populations (Van Vuren and Bray 1986). By the mid-1970s, the growth rate started to decelerate (Gates and Larter 1990). Beginning in 1980, there was a major range expansion from the Mackenzie Bison Sanctuary into the Mink Lake area to the northwest, and increasing bison density may have been a factor (Gates and Larter 1990). Although almost all Mackenzie Bison Sanctuary foraging activities were in *C. atherodes*-dominated meadows, bison in the Mink Lake area seemed to be utilizing a wider variety of plant species.

Larter and Allaire (2007) outlined the history and status of the Nahanni Population. In 1980, 28 wood bison from the Elk Island National Park Isolation Area were released into the Nahanni Butte area. Supplemental releases carried out in 1989 and 1998 with 12 and 59 individuals respectively, augmented the population. There was an average annual growth rate of approximately 19%, producing an estimate of 403 bison in 2004. Range expansion is still progressing into British Columbia and the Yukon. The Nahanni population appears to have stabilized at about 400 animals.

Stage Two: Vegetation trends continue to decline. Although the population exceeds its carrying capacity, reproduction is still high because of the large proportion of young age groups in the population. Even if the mortality rate of younger animals begins to increase, the total population continues to rise. The physical condition of the animals starts to decline, especially in critical periods of the year.

Fuller (1961, 1966) believed that there would be almost no increase in the proportion of aged animals for the first 15 to 20 years after the wood bison population started to grow. Also, as increasingly large calf crops advanced through maturity, net annual increment would grow. By the late 1940s and early 1950s, bison may have reached 12,500-15,000 animals (Fuller 1950). Even with slaughters of up to 1,000 bison per year, carried out for meat and disease control, as well as predation and accidents, recruitment possibly still equalled 8-10% (Fuller 1961).

Until the mid-1960s, bison occupying the area between the Little Buffalo River and the Taltson River (Grand Detour and Hook Lake range) were originally counted as a single unit in the Slave River Lowlands (e.g., Fuller 1950; Novakowski 1961). Ever since Williams (1966) counted over one thousand animals east of the Slave River, the Hook Lake herd has been considered a separate subpopulation. By 1968, the Hook Lake subpopulation was at approximately 1,232 bison, and reached a maximum estimate of 1,700 by 1971 (Rippin 1971 *in* Nishi 2010).

Between 1975 and 1987, the rate of growth of the Mackenzie population declined from 26.7% to 10.3% per annum (Gates and Larter 1990). Although wolves prefer moose, they capitalize on rising bison populations and could have reduced the Mackenzie bison population growth rate (Joly 2001). This population reached its maximum estimated abundance in 1989 at 2,431 animals (Gates *et al*. 1991; Larter *et al*. 2000). Throughout the range they appeared to be increasing their breadth of diet. The first evidence of wolf predation on bison was three calves in 1983 (Chowns and Graf 1987). For the next decade, the frequency of wolf-killed calves seemed to be increasing, and some wolf-killed adults were being discovered.

Stage Three: Large scale die-offs occur, especially when some element of the habitat becomes critical. The most heavily used parts of the range start to show signs of recovery.

Fuller (1961, 1966) predicted that when the large cohorts of the early years reached old age, the population would experience a lower reproductive rate and a higher mortality. From approximately 13,000 bison in 1971, the bison of the Greater Wood Buffalo Ecosystem declined steeply to less than half of that number by 1976 (Carbyn *et al.*1998; Calef 1976). In the Slave River Lowlands, the combined numbers of the Hook Lake and Grand Detour subpopulations dropped 35% from about 1,904 in March of 1974 to 1,245 after the severe winter of 1974-75 (Van Camp and Calef 1987). Any apparent trends within the Greater Wood Buffalo Ecosystem population must be treated with caution because of the fluidity of bison movements. When Carbyn *et al.* (1998), analysed the census data from 1971 to 1998, they concluded that the entire decline in Wood Buffalo National Park could be accounted for south of the Peace River. A mass drowning of 3,000 animals in the Peace–Athabasca Delta in 1974 was the largest single die-off ever recorded in the Park. According to Bradley and Wilmshurst (2005), all Wood Buffalo National Park subpopulations were probably stable or growing by 1992, except the Delta subpopulation. Recruitment was above five yearlings per 100 cows and increasing. The total Wood Buffalo National Park population number had bottomed out at 2,200 in 1999 (Joly and Messier 2004a). Carbyn *et al.* (1998) believed that a great deterioration of habitat has been occurring since the delta started drying out in recent decades.

After peaking at about 2,431 bison in March 1989, the Mackenzie population suffered a mass drowning of 177 bison two months later. Two major anthrax outbreaks and continuing range expansion, all effectively lowering population density, may currently be forestalling any large-scale die-offs that would be related to critical elements in the habitat. The 2012 anthrax mortality of over 440 animals in combination with predation and collisions reduced the Mackenzie population to approximately 714 animals (Armstrong 2013b).

Stage Four: The population attains a more stable adjustment with the carrying capacity. Amplitudes of oscillations are determined by a variety of environmental factors, until another large discrepancy emerges between how many animals the environment can support and the numbers actually present.

For Wood Buffalo National Park bison, Vassal and Kindopp (2010) documented a population increase from 1999 to 2005, and a levelling off in numbers between about 4,000 to 5,000 animals through to 2009. Two of the Greater Wood Buffalo Ecosystem subpopulations occurring within the NWT (Nyarling River and Grand Detour) have shown some stability from the 1970s to the 1990s, and since then they have been gradually increasing (Vassal and Kindopp 2010). Any period of stability in the Hook Lake subpopulation is difficult to determine because of information gaps from 1980 to 1987, and 1987 to 1994.

APPENDIX A6 – ANTHRAX

The first diagnosis of anthrax in wood bison was from the Slave River Lowlands on July 28, 1962 (Novakowski *et al*. 1963), although ten years earlier, two wardens experienced a cutaneous infection after they handled a bison carcass in Wood Buffalo National Park (Hugh-Jones and de Vos 2002). The first documented case of anthrax in the Mackenzie population was in July 1993 (Gates *et al*. 1995). Outbreaks of varying proportions have arisen periodically in the Greater Wood Buffalo Ecosystem and Mackenzie populations, and many years may elapse between epidemics of high mortality (Elkin *et al*. 2013; Table 7, p. 234). It had been widely speculated that anthrax was brought to North America along with European cattle, and carried north to wood bison range in recent times by some vector such as migratory birds (Broughton 1987), but Ferguson and Lavoilette (1992) documented historical accounts from the 1800s of wood bison die-offs that resembled anthrax outbreaks. Findings by Kenefic *et al*. (2009) indicate that anthrax actually spread into central North America from Beringia after the ice-free corridor emerged, and remained associated with the range of bison, possibly due to the herding behaviour of this host. Anthrax spores are able to remain viable for decades if they are buried in the soil (Turnbull 1996). Even though historical range north of the Mackenzie River had been devoid of bison from the late 1800s until the 1963 reintroduction, retrospective blood serum analysis of anthrax antibodies showed that Mackenzie bison had been exposed to this pathogen at least as far back as the 1980s (Turnbull *et al*. 2001).

Although poorly understood, transmission pathways for anthrax include ingestion and inhalation from the environment (Elkin *et al*. 2013). After the spores germinate into the vegetative form of the bacterium inside its host, the disease may be peracute (very severe and short duration) or subacute and nonlethal, but the natural prevalence of infection, exposure and resistance in animal populations is not well known (Bagamian *et al*. 2013). When anthrax is peracute, replication in the bloodstream and release of toxins cause septicaemia and often rapid death (Novakowski *et al*. 1963; Dragon and Rennie 1995; Gates *et al*. 2001b). The organism is destroyed by putrefaction inside intact carcasses, but upon release by scavengers, warm temperatures, oxygen and dessication stimulate the bacteria to develop into highly resistant spores that contaminate the surrounding environment; however, viability and virulence may be reduced by acidity or microbial competition (Minett 1950; Choquette and Broughton 1981; Titball and Manchee 1987; Hugh-Jones and de Vos 2002). Hugh-Jones and de Vos (2002) suggested that a wildlife population may suffer high initial losses of its most susceptible animals, and then the losses become self-limiting as more survivors respond with protective immunity. Determining how bison ingest or inhale enough spores to trigger new epidemics and spread the disease has been problematic (Elkin *et al*. 2013).

Anthrax has generally been considered an extremely lethal pathogen, possibly because the subacute form of the disease often goes undetected (Bagamian *et al*. 2013). In sero-epidemiological studies of the Mackenzie and Greater Wood Buffalo Ecosystem bison populations, Turnbull *et al*. (2001) found high antibody titres to the anthrax toxin after and between epidemics, suggesting that a significant proportion of animals survive outbreaks and develop a protective immune response. They also found evidence of maternal antibodies being passed on to young calves through the colostrum.

Table 7. Number of wood bison carcasses found during documented anthrax outbreaks in the Slave River Lowlands, Wood Buffalo National Park (WBNP) and Mackenzie population, 1962-2015 (Elkin *et al*. 2013; New 2014; Elkin pers. comm. 2016). Research on antibodies suggests that there have been additional anthrax cases when outbreaks in these populations have gone undetected (Elkin *et al*. 2013).

Year	Slave River Lowlands	WBNP	Mackenzie Bison Range	Total
1962	281	-	-	281
1963	257	47	-	304
1964	303	60	-	363
1967	-	120	-	120
1968	-	1	-	1
1971	33	-	-	33
1978	39	47	-	86
1991	-	32	-	32
1993	-	-	172	172
2000	-	106	-	106
2001	12	91	-	103
2006	26	3	-	29
2007	-	64	-	64
2010	46	7	9	62
2012	-	-	451	451
2013	-	1	-	1
2015	-	58	-	58