COSEWIC
Assessment and Status Report

on the

Plains Bison
Bison bison bison

in Canada

THREATENED
2004

COSEWIC
COMMITTEE ON THE STATUS OF
ENDANGERED WILDLIFE
IN CANADA

COSEPAC
COMITÉ SUR LA SITUATION
DES ESPÈCES EN PÉRIL
AU CANADA

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COSEWIC
Assessment Summary

Assessment Summary – May 2004

Common name
Plains bison

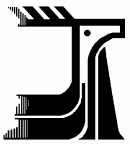
Scientific name
Bison bison bison

Status
Threatened

Reason for designation
There are currently about 700 mature bison of this subspecies in three free-ranging herds and about 250 semi-captive mature bison in Elk Island National Park. The largest free-ranging herd, in the Pink Mountain area of BC, is outside the historical range of this subspecies. The population in Prince Albert National Park is increasing by about 10% a year. The greatest problem facing these bison in Canada is the lack of habitat, due to conversion to agriculture and urbanization. Additional threats include domestic cattle disease and the risk of genetic pollution from escaped ranched bison, including some that may carry cattle genes. The total number of free-ranging and semi-captive mature bison of this subspecies is just under 1000, and there are fewer than five populations.

Occurrence
British Columbia, Alberta, Saskatchewan, Manitoba

Status history
Designated Threatened in May 2004. Assessment based on a new status report.



COSEWIC
Executive Summary

Plains Bison
Bison bison bison

Species information

Plains bison, *Bison bison bison* Linnaeus 1758, are one of two subspecies of *Bison bison*, along with *Bison bison athabascae* Rhoads 1897, the wood bison.

Distribution

Plains bison were once widespread across North America, but now only occur in fragmented populations throughout their historic range. Wild populations occur in British Columbia and Saskatchewan. Alberta, Saskatchewan, and Manitoba contain semi-wild or captive herds.

Habitat

The Canadian range of plains bison once extended over the prairies, including grasslands, shrublands and some woodland areas. However, plains bison will only exist in regions containing suitable grasslands and meadows. Much of the original plains bison habitat has changed drastically during the last century due to agricultural conversion and urbanization. A large amount of the current Canadian bison range is under government protection, and no changes are expected in habitat availability. Although little remains of the original traditional prairie habitat for plains bison, some reintroduction opportunities do exist.

Biology

Plains bison are polygynous mammals. They are gregarious and herd size and structure vary throughout the year. Males establish a fluid dominance hierarchy, where dominance rankings often change within a breeding season, and many males breed each year. Bison are well adapted to exist in native grasslands and meadow regions. They primarily consume sedges and grasses.

Population sizes and trends

The Canadian population of plains bison includes 670-740 mature animals in three free-ranging herds and 250-270 mature animals in one semi-wild herd. An additional

63-83 mature bison occur in four small, captive populations. All populations, except for Pink Mountain, are stable or increasing in size. Elk Island National Park, the semi-wild herd, is either the direct or indirect source for all plains bison herds in Canada.

Limiting factors and threats

The largest impediment to plains bison conservation is a lack of habitat. Most of its original range has been lost to agriculture and urban development. There are, however, a few areas where reintroductions may still be possible. A number of plains bison populations in the United States have hybridized with cattle. To date, Elk Island National Park and Pink Mountain, the only Canadian plains bison surveyed for cattle genes, have shown no evidence of hybridization. Only three free-ranging herds of plains bison are subject to natural selective factors. Two of these populations are small, with 100 and 320 bison. Most Canadian plains bison populations were founded with between 10 and 50 individuals from Elk Island National Park, raising concerns as to their levels of genetic diversity. Efforts to conserve plains bison in Canada are hampered by the lack of a consensus for protection between provincial and federal legislation. Hybridization with wood bison may also be a threat to the conservation of plains bison in Canada. Game ranching poses a threat to plains bison; there is a risk of hybridization between wild plains bison populations and ranched herds of wood and plains bison when ranched animals escape. At present, no Canadian plains bison population is infected with any disease that jeopardizes its existence. However, domestic cattle can act as disease reservoirs for bison, and their proximity could put the health of some bison herds at risk.

Special significance of the species

Millions of plains bison once roamed the prairies of North America, where they were the dominant herbivore. As such, they greatly affected the Great Plains ecosystem. The histories of plains bison and Aboriginal Peoples in North America are inextricably linked.

Existing protection or other status designations

Bison have a global heritage status rank of G4, meaning they are globally common but rare in parts of their range. The General Status of Species in Canada classifies bison as Sensitive. In British Columbia and Manitoba, plains bison are listed as Vulnerable. In Saskatchewan, plains bison are listed as At Risk. In Alberta, plains bison are considered extirpated from provincial land. Plains bison are classified as domestic animals in Alberta and Manitoba. The Pink Mountain herd in British Columbia is on land that is not protected by a government agency, but is protected from unregulated hunting under the B.C. Wildlife Act.

COSEWIC HISTORY

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. On June 5, 2003, the *Species at Risk Act* (SARA) was proclaimed. SARA establishes COSEWIC as an advisory body ensuring that species will continue to be assessed under a rigorous and independent scientific process.

COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assesses the national status of wild species, subspecies, varieties, or other designatable units that are considered to be at risk in Canada. Designations are made on native species and include the following taxonomic groups: mammals, birds, reptiles, amphibians, fishes, arthropods, molluscs, vascular plants, mosses, and lichens.

COSEWIC MEMBERSHIP

COSEWIC comprises members from each provincial and territorial government wildlife agency, four federal organizations (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biosystematic Partnership, chaired by the Canadian Museum of Nature), three nonjurisdictional members and the co-chairs of the species specialist and the Aboriginal Traditional Knowledge subcommittees. The committee meets to consider status reports on candidate species.

DEFINITIONS
(after May 2004)

Species	Any indigenous species, subspecies, variety, or geographically or genetically distinct population of wild fauna and flora.
Extinct (X)	A species that no longer exists.
Extirpated (XT)	A species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A species facing imminent extirpation or extinction.
Threatened (T)	A species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats.
Not at Risk (NAR)**	A species that has been evaluated and found to be not at risk.
Data Deficient (DD)***	A species for which there is insufficient scientific information to support status designation.

* Formerly described as “Vulnerable” from 1990 to 1999, or “Rare” prior to 1990.

** Formerly described as “Not In Any Category”, or “No Designation Required.”

*** Formerly described as “Indeterminate” from 1994 to 1999 or “ISIBD” (insufficient scientific information on which to base a designation) prior to 1994.

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Canada

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SPECIES INFORMATION

Name and classification

Scientific name:	*Bison bison bison* Linnaeus 1758
Common name:	plains bison
French name:	bison des prairies
Other subspecies:	wood bison (*B. b. athabascae* Rhoads 1897)
Other common names:	American bison, prairie bison, bison, buffalo

Plains bison are one of two extant subspecies of *Bison bison*, the other being wood bison. The validity of bison subspecific designations is a controversial issue due to its implications for the genetic diversity of North American bison, and their consequent management. An overview of the taxonomy is described in Appendix 1.

Description

Bison bison is the largest land mammal in North America. Adult males typically range in body mass from 600 to 860 kg, with a mean of around 700 kg (Halloran 1961; Reynolds et al. 2003). Shoulder height of an adult male ranges from 167 to 280 cm, while the total length is 304 cm to 380 cm (Reynolds et al. 1982). Bison have a large head, with a broad snout and black horns on the sides (Figure 1A). The forequarters are heavier than the hindquarters. Plains bison are distinguishable from wood bison by five key morphological features (Figure 1). Plains bison have a distinctively lower and more centrally located shoulder hump, which is due to the shorter neural spines of their cervical and thoracic vertebrae (van Zyll de Jong 1986), lighter, woollier pelage, and a longer beard that is almost nonexistent in wood bison. Other, subtler differences include shorter tails and thicker head hair on plains bison (Geist and Karsten 1977; van Zyll de Jong 1986). Females are smaller than males and their horns are more curved and slender. Calves are generally reddish-orange in colour for the first 3 months, after which they become darker (Meagher 1978). Plains bison are primarily grazers and historically occurred in biomes containing extensive grassland and meadow systems.

DISTRIBUTION

Global range

The original plains bison range extended from the Rocky Mountains to present day Washington, DC and from mid-Alberta and Saskatchewan to northern Mexico (Figure 2). Plains bison only occur in grass- and sedge-land habitats, and in Canada their primary range ends at the boundary between grassland and forest (Reynolds *et al*. 1982). Seton (1929) estimated that 60 million bison existed across the plains before the arrival of European settlers (Shaw 1995). McHugh (1972) estimated that only 30 million bison could have been supported by the carrying capacity of the land at the time (Shaw 1995). These estimates at best represent the theoretical maximum for the range (Shaw 1995). Factors such as predation and hunting were not incorporated into the estimates. The continental pre-contact bison population was likely below 30 million (Lott 2002).

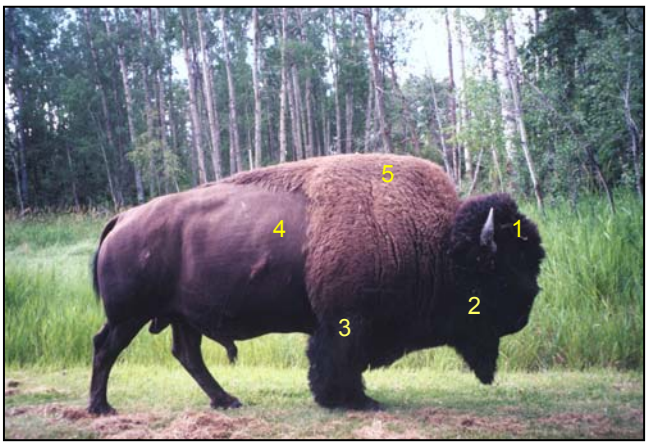

Figure 1A. Plains bison at Elk Island National Park.

Male Plains Bison

1. Thick, woolly hair covers horn
2. Longer beard and throat mane
3. Well-developed chaps
4. Distinct woolly cape, usually lighter
5. Lower, more central hump

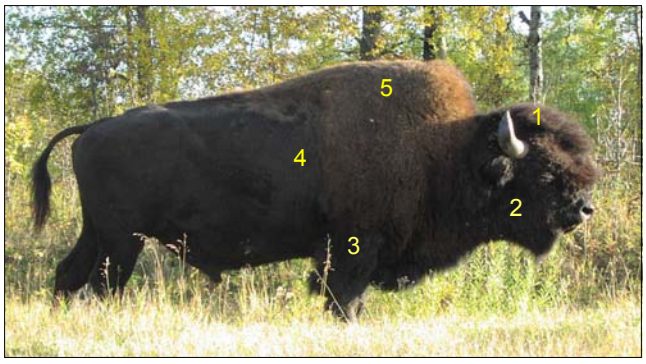

Figure 1B. Wood bison at Elk Island National Park.

Male Wood Bison

1. Horn clear, hair shorter
2. Shorter beard and throat mane
3. Reduced chaps
4. No clear cape, usually darker
5. Larger hump, forward of leg axis

The current range of plains bison is severely restricted in comparison to their original distribution (Figure 3). "Original distribution" is represented by oral and traditional accounts of Aboriginal Peoples, combined with written records and paleontological evidence (Gates et al. 2001). Bison occur as a native taxon in British Columbia, Saskatchewan and Manitoba (2002; NatureServe Explorer). The existing wild plains bison population in Alberta occurs on federal lands and plains bison are considered to be extinct on property under provincial jurisdiction (G. Court, pers. com., 2002). Plains bison occur in isolated units throughout their historic range as wild, free-ranging populations, as public display herds, or in privately owned game farms. There are approximately 600,000 to 720,000 plains bison in North America (Reynolds *et al*. 2003). However, over 95% of the total population is maintained for commercial production (Boyd 2003). In 2001, there were about 1900 bison ranches in Canada (Statistics Canada 2001a). Currently, four wild or semi-wild herds occur in Canada (Figure 3). In the United States, 42 conservation plains bison herds exist in several states, fewer than ten are wild and free-ranging (Boyd 2003).

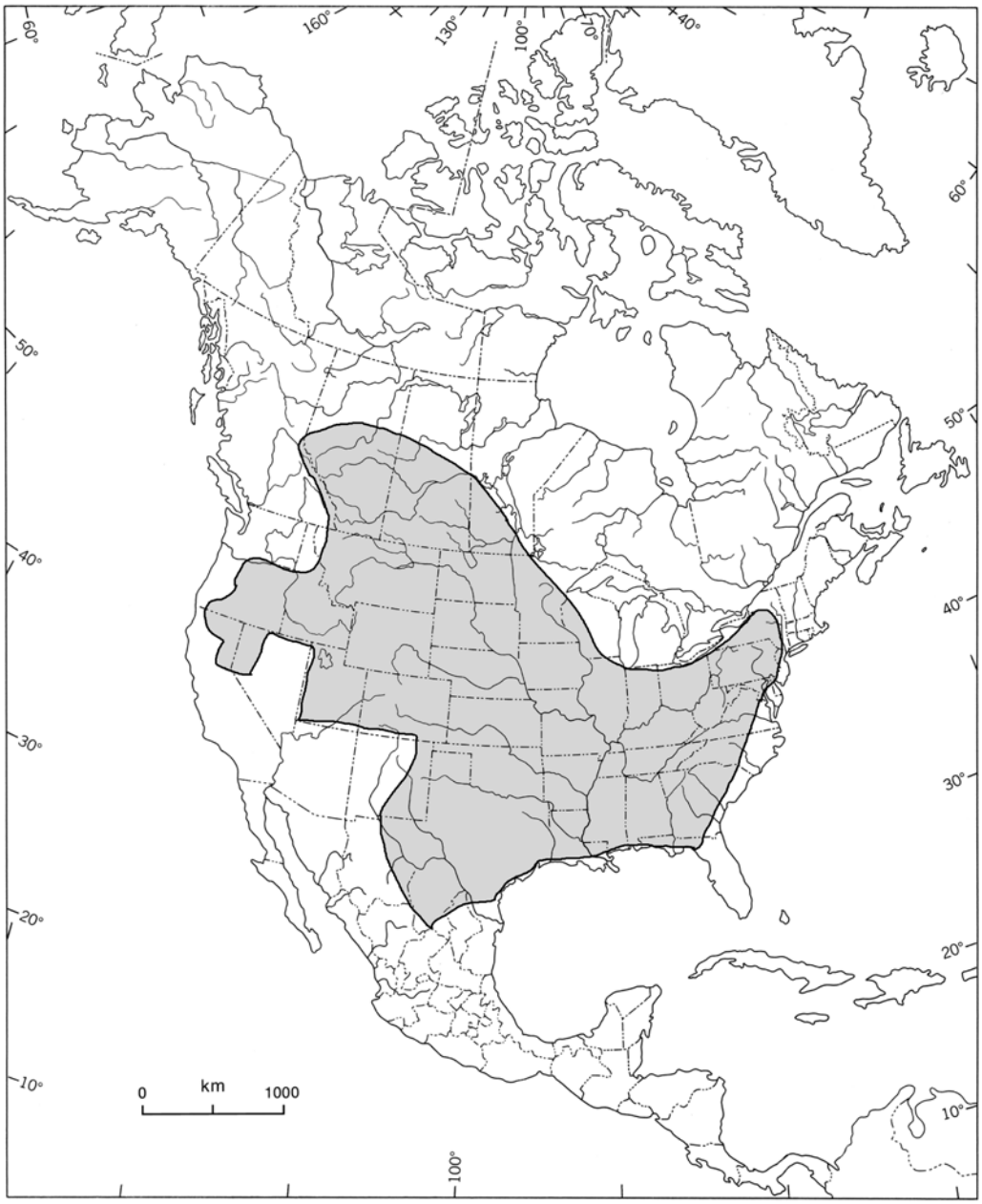

Figure 2. Original distribution of plains bison in North America (modified from van Zyll de Jong 1986).

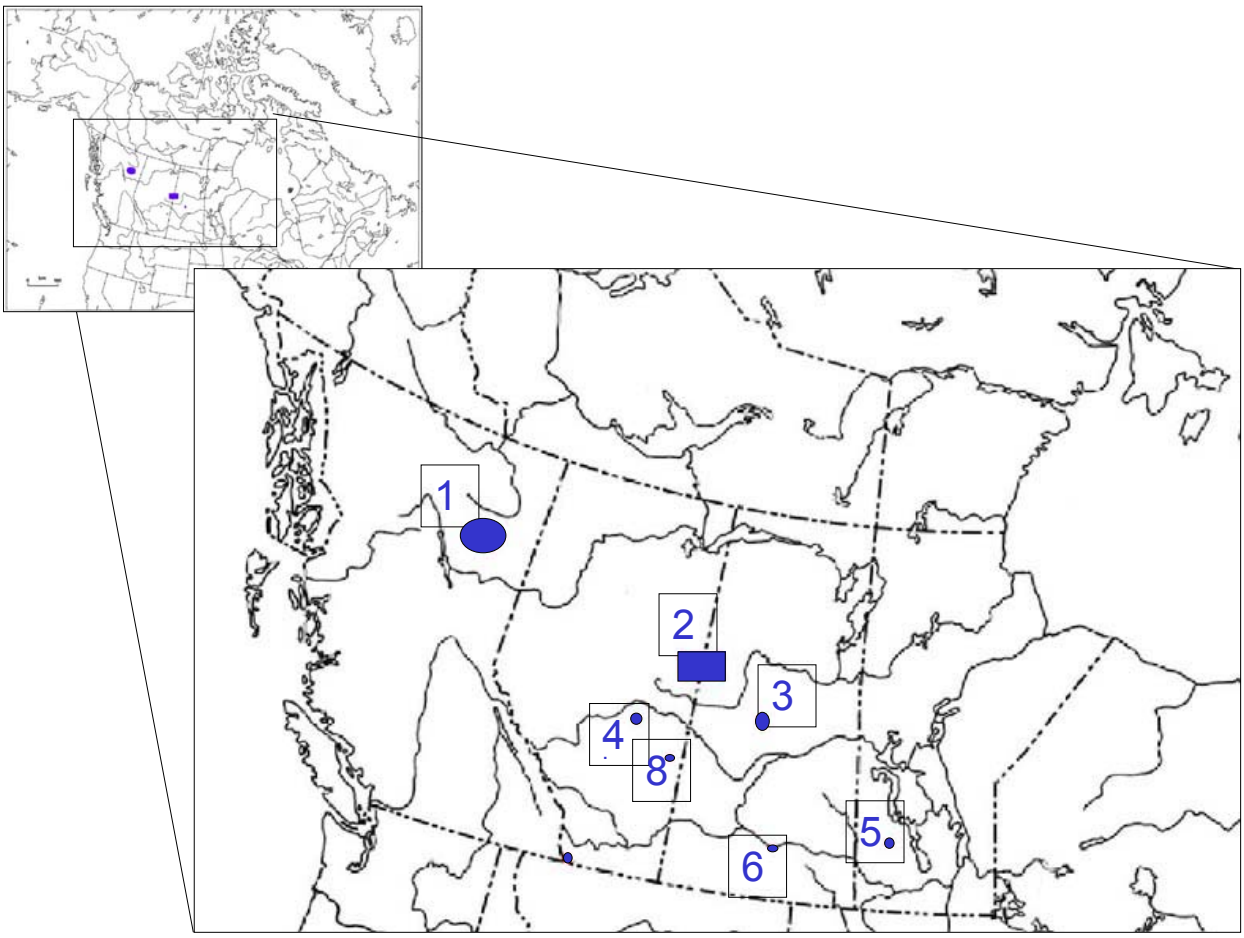

Figure 3. Current locations of the publicly owned plains bison Canadian populations. (1) Pink Mountain[a], (2) Cold Lake/Primrose Air Weapons Range[a], (3) Prince Albert National Park[a], (4) Elk Island National Park[b], (5) Riding Mountain National Park[c], (6) Buffalo Pound Provincial Park[c], (7) Waterton Lakes National Park[c], (8) Bud Cotton Buffalo Paddock[c].
[a]wild
[b]semi-wild
[c]captive

Canadian range

The original distribution of plains bison in Canada likely included the area from the Rocky Mountains, and possibly even west of the Continental Divide, trailing off through southern Manitoba, and from mid-Alberta and Saskatchewan to the Canada-U.S.A. border. Their range extended across grasslands, shrublands, montane meadows, and some wooded areas. By 1888, only an estimated eight animals remained in Canada.

Currently in Canada, there are between 670 and 740 mature plains bison in three free-ranging herds, and 250 to 270 mature plains bison in one semi-wild herd (Figure 3). The semi-wild herd is fenced and occasionally supplementally fed, but it is managed in a way that mirrors natural conditions as closely as possible. The four public display

herds are small, intensively managed and do not fluctuate in size. These herds are not considered by COSEWIC for status assessment. The Canadian range of plains bison is around 2750-3000 km^2, it is highly fragmented and there are no corridors between herds.

British Columbia

Plains bison historically occurred in eastern British Columbia, south of the Peace River and west into the Rocky Mountains. The extent of this range is unclear. van Zyll de Jong (1986) found bison remains in the Peace River region that were intergrades between *B. b. bison* and *B. b. athabascae*. Consequently, he proposed that the Peace River area was the boundary between wood and plains bison range (van Zyll de Jong 1986). Cowan and Guiguet (1965) only discovered a single specimen of *B. b. bison* remains west of the Canadian Rockies. Archaeological and cultural evidence suggests that plains bison occurred in the Rocky Mountain trench (Wikeem and Ross 2002). However, the discovered remains may be the result of plains bison killed and subsequently transported from the east side of the Rocky Mountains (Kay *et al*. 1999).

During the late 1960s, a small herd of bison was frequently seen near the British Columbia-Alberta border, near Clear Hills. Bison were also reported near the Buckinghorse River and in the Kotcho Lake area in the late 1970s and early 1980s, respectively (B.C. Ministry of Environment 1991; Harper *et al*. 2000). These animals could have been wood bison, which have been introduced near northern British Columbia since 1980 (Gates *et al.* 2001). Currently, the Pink Mountain herd, established in 1971, is the only plains bison herd occurring in that area.

The Pink Mountain herd occurs in the Pink Mountain – Sikanni Chief River area, 180 km northwest of Fort St. John (B.C. Ministry of Environment 1991). Its current range is approximately 1500 km^2 (D. Fraser, pers. com., 2003) and the habitat is primarily sedge meadows and grassland (B.C. Ministry of Environment 1991). Since its establishment, the Pink Mountain herd has increased in range and size, although it seems to have stabilized during the last few years. The 2003 survey indicates that the herd consists of 876 animals. It is maintained at this approximate level through harvesting (Table 1; D. Fraser, pers. com., 2003). This population exists in original wood bison habitat (Reynolds 1991).

Alberta

Historically, plains bison ranged throughout central and southern Alberta. However, wild plains bison were extirpated in the 1880s. A plains bison population was re-established on federal land in 1907, forming the Elk Island National Park population. This population is the only semi-wild herd in Canada and is the founding herd for all Canadian plains bison conservation herds. The fenced range of 136 km^2 lies 50 km east of Edmonton. The herd currently contains about 500 plains bison and has been stable since the mid-70s due to management for this size (Olson 2002; Cool 2003).

Table 1. Population size, model estimate, amount of harvesting, and range for the Pink Mountain plains bison population, 1975-present. Courtesy the BC Ministry of Water, Land and Air Protection, 2003.

Year	Population Count	Population Estimate	Harvested Males	Harvested Females	Harvested Juveniles	Total	Number Permits	Annual Range (km^2)
1975	50	50						60
1976	70	69.1						450
1977	95	95.6						750
1978	130	132.1						
1979	175	182.7						
1980		201.8						
1981		222.9						
1982		246.2						
1983		272.0						
1984		300.4						
1985		331.9						
1986		366.6						
1987		404.0						
1988		447.4						
1989		494.2						
1990		545.9						
1991		603.0						
1992	648	666.1	43	0	0	43	50	
1993		692.9						
1994		765.4						
1995		845.4						
1996		933.9	92	11	0	103	200	
1997		928.7	93.5	42	6.5	142	260	
1998		883.8	95	73	13	181	260	
1999		795.3	22	27	3	52	144	
2000		826.6	34	35	5	74	120	1500
2001		839.1	45	52	5	102	120	
2002		824.9	12	23	2	37	120	
2003	876	874.2					120	

The Waterton Lakes National Park herd is carefully managed at 20 bison (Boyd 2003). The Bud Cotton Buffalo Paddock is located immediately south of Wainwright, Alberta. The herd was established in 1980 from four individuals (Bud Cotton Buffalo Paddock 2001). The current herd size is 16 (Boyd 2003).

Saskatchewan

Plains bison historically existed throughout the Prince Albert National Park region until they were extirpated in the late 1800s. Consequently, the current Prince Albert National Park plains bison herd is the only free-ranging herd that occurs within the original range of plains bison in Canada and is protected by a national park (Parks Canada 2001a). The 3,875 km^2 park is located approximately 200 km north of Saskatoon in central Saskatchewan. The herd range is about 750 km^2, with 700 km^2 in

the southwest corner of the park, along with a 50 km^2 area outside of park boundaries (D. Frandsen, pers.com., 2003). The boundary between the historical range of plains bison and wood bison falls within the park (D. Bergeson, pers. com., 2002). Previous to the establishment of a free-ranging herd, the park maintained a public display herd of bison. In 1995, management shifted to focus on the maintenance of the free-ranging plains bison herd that had established itself within the park. The free-ranging population was originally founded from at least ten bison that had moved south into the park after a 1969 re-introduction effort in the Thunder Hills region in north-central Saskatchewan, about 60 km north of Prince Albert National Park, near Neyakamew Lake (D. Frandsen, pers. com., 2002). Small groups of bison travel between the park and adjacent private lands (D. Frandsen, pers.com., 2003).

The Cold Lake/Primrose Air Weapons Range, which straddles the Alberta-Saskatchewan border, also maintains a free-ranging herd of plains bison. The bison reside on the Saskatchewan side of the Air Weapons Range (D. Frandsen, pers.com., 2003; D. Brakele, pers. com., 2004). However, during the late 1980s, evidence of bison may have been observed within the Alberta range (H. Reynolds, pers. com., 2004). The herd was established in 1969 with bison from Elk Island National Park. The transplants were originally intended to repopulate the Thunder Hills region in north-central Saskatchewan. However, the animals did not remain in that area. Some of them travelled south to Big River Community Pasture where they were captured and transplanted to Vermette Lake near the Cold Lake/Primose Air Weapons Range shortly thereafter (D. Frandsen, pers. com., 2002). This population likely exists on the northern periphery of original plains bison range.

The Air Weapons Range encompasses an area of over 12,000 km^2, but bison do not occur across the entire Range. Little is known about the size of the range occupied by this population. However, based on the size of the current plains bison population, we can extrapolate from herd range sizes of the Pink Mountain herd at various times (Table 1) that the current range of the Cold Lake/Primrose Air Weapons Range population occurs across an area of approximately 500-750 km^2.

One captive display herd, at Buffalo Pound Provincial Park, is located in southwest Saskatchewan, about 30 km northeast of Moose Jaw. The herd was established in 1972 and is maintained at 33 bison (Boyd 2003).

Other Canadian Provinces

The original range of plains bison extended across southern Manitoba. However, their range was limited to patches of grassland and meadow habitat (Reynolds *et al*. 1982; Boyd 2003). The densities of plains bison across these regions were low. Currently, plains bison do not occur as wild populations east of Saskatchewan. A captive display herd is maintained within Riding Mountain National Park, Manitoba, within the historical range of plains bison (D. Bergeson, pers. com., 2002). It was founded by 20 bison from Elk Island National Park in 1945-46 and is currently stable at 33 bison (D. Bergeson, pers. com., 2002).

Commercial Captive Herds

Bison game farms have increased during recent years. The 1996 census (Statistics Canada 2001b) reported 45,437 farmed bison on 745 ranches in Canada. Almost 86% of commercial bison production occurred in the western provinces, with 57 farms in British Columbia, 334 in Alberta, 175 in Saskatchewan and 73 in Manitoba (Statistics Canada 2001b). Ontario and Quebec hold 46 and 56 farms, respectively. Only four farms were located in the Atlantic Provinces. In the 2001 census, Statistics Canada reported 145,094 bison on 1,887 farms in Canada (Statistics Canada 2001a). Agriculture and Agri-Food Canada (2002) estimated that the bison population would increase to 200,000 on 1,900 farms in 2002 and that continued growth of this industry is expected.

HABITAT

Habitat requirements

The Canadian range of plains bison includes prairies, foothills, and montane meadows that are composed of grasslands, shrublands and even some woodland areas, which bison use for protection from the climate and predators (Reynolds *et al*. 2003; D. Frandsen, pers. com., 2002). In the southern Canadian Rocky Mountains, bison historically used the prairies during the summer and the montane valleys, foothills and aspen parklands in the winter (Kay and White 2001). Plains bison prefer open grassland or meadow habitats (Reynolds *et al*. 1982).

Plains bison are habitat generalists. They are primarily grazers and secondarily browsers (Reynolds *et al*. 1982). Their habitat is primarily selected by nutritional requirements, forage availability, snow depth, burn history and predator avoidance (Shaw and Carter 1990; Larter and Gates 1991). Seasonal shifts in habitat are often directed by forage availability, whereas shifts within a habitat are often directed by plant phenology. Bison prefer new growth herbage to old growth, although due to their large mouth, bison eat both old and new grasses because they are unable to select individual stems (Lott 2002). Bison also exhibit an affinity to prairie dog colonies. This is likely due to the spatial vegetation pattern containing numerous potential wallow areas within the colony and a high concentration of graminoids located on the periphery of the colonies (Coppock *et al*. 1983).

Bison diets are selected primarily to minimize foraging time (Bergman *et al*. 2001). Bison are less selective grazers than other ungulates in similar conditions (Reynolds *et al*. 1982). Bison are better adapted than other ungulates to digest poor quality rangeland forage. They are also better adapted than cattle to digest short grass prairie vegetation (Peden *et al*. 1974). This is likely due to their large size; digestion is slow and food remains in the rumen longer, resulting in a more efficient use of the microflora within their digestive tract (see Nutrition and Interspecific Interactions section).

Plains bison almost exclusively consume grasses and sedges. Forbs can also be important in some areas (Reynolds *et al*. 2003), as can browse in riparian willow communities (Waggoner and Hinkes 1986). Bison exhibit some seasonal variation in forage selection. Generally, during the summer the fibre content of their diet increases while the nitrogen content decreases. The reverse occurs during the winter. At Elk Island National Park grasses are primarily consumed during the summer and sedges during the winter (Holsworth 1960). In Prince Albert National Park, sedges and grasses make up 80-100% of their diet (Fortin *et al*. 2002). Sedges, particularly slough sedge, are the most important forage in all seasons, as they make up 59% and 73% of the winter and summer diets, respectively. Grasses are the second most important forage, ranging from 17% of the fall diet to 35% of the spring diet. In the Peace River Country, bison have been reported to consume willow and new aspen growth during the spring (Rutley *et al*. 1997). In Aspen Parklands, bison select upland meadows for summer grazing (Hudson and Frank 1987). Mixed-grass prairies contain cool season (known as C3 or CAM plants) and warm season (C4 plants) perennial forages. During the summer, bison select warm season grasses and during the spring and fall, bison select cool season grasses (Reynolds *et al*. 1982). The native short-, tall-, and mixed-grass prairies that were the plains bison's main source of forage have largely disappeared, and some areas of bison range have been reconstituted from agricultural land. Feed rations supplied to some of the managed populations also do not reflect the plant species historically eaten by plains bison. Current managed populations may have different diets than their free-ranging ancestors (Buehler 1997).

Bison play an important role in maintaining their habitat in a productive state. Bison tend not to overgraze preferred areas. They wander more often than other ungulates during grazing and therefore cause less damage to their range (VanVuren 1982; Reynolds *et al*. 2003). They also eat drier forage and spend less time in wetlands and riparian zones than other ungulates, resulting in less impact on those ecosystems (Reynolds *et al*. 2003). Bison affect soil nutrients through grazing, nutrient (especially nitrogen) cycling, physical disturbance and seed dispersal. The long hair on a bison's front quarters is particularly effective for aiding seed dispersal.

Bison home range size is affected by range productivity, forage distribution, social interactions, age and sex (Larter and Gates 1994). Home ranges tend to be larger if less forage is available, if forage is more widely dispersed on the range, if social groups are larger, and for subordinate individuals. Peripheral male bison often maintain a larger home range in order to access sufficient forage and mates during the rut. Larter and Gates (1994) suggest that access to mates has the greatest impact on home range size for adult males. Several reports of typical home range sizes for individual female bison exist. Van Vuren (1983) estimated a range size of 32-82 km^2, while Lott and Minta (1983) estimated a range size of 27-71 km^2. A minimum density threshold of 0.5-0.8 bison per km^2 was suggested for wild wood bison by Gates and Larter (1990), beyond which bison will disperse. Home range sizes have not been examined for plains bison in wild herds.

Trends

Most of the range inhabited by bison in Canada is protected by at least some government regulations and therefore, no changes in range have occurred for most of the current populations since their establishment. The range of the Pink Mountain herd has increased by 1000 km^2 since 1991 (D. Fraser, pers. com., 2003). In contrast, the bison habitat on the Cold Lake/Primrose Air Weapons Range is not managed for bison conservation and significant oil and gas development is occurring on the range. If development expands, the plains bison habitat may be impacted. Under current management circumstances, no future changes are expected in habitat availability for the plains bison populations. For wild herds, overgrazing is not a concern for bison habitat, as bison will not overgraze if given the opportunity to move to a different area. Furthermore, managed herds are maintained at their optimum size for the carrying capacity of the range. The primary threat to unoccupied and future potential bison habitat is direct loss through resource and industry development.

Once widespread across Canadian prairies, the current range of plains bison in Canada has been reduced to less than 3000 km^2. Human settlement and increased agricultural development during the past century have fragmented the landscape so considerably that only patches of suitable plains bison habitat remain (Reynolds 1991). However, there are some areas that still contain plains bison habitat where reintroductions are being considered. These are:

Banff National Park

A reintroduction effort is being considered by Banff National Park to re-establish the complex ecosystem dynamics from prehistoric and historic times (Kay and White 2001).

Waterton Lakes National Park

Waterton Lakes National Park currently manages a small, captive bison herd, and it has been proposed that it should be augmented in an effort to maintain the ecological integrity of this region (Canadian Endangered Species Conservation Council 2001).

Grasslands National Park

The reintroduction of a free-ranging bison herd into southwest Saskatchewan has been proposed as part of the Grasslands National Park management plan (Parks Canada 2001b). The park will eventually have a range of 906.4 km^2, a little over half of which has been acquired to date in seven discrete parcels. Seasonally variable surface water is available from the spring-run off, but most creek beds and lakes dry up during the summer. However, Frenchman River and Rock Creek rarely stop flowing. The program is currently under development.

Other suitable plains bison habitat includes:

- Great Sand Hills in west central Saskatchewan. The habitat is not currently protected.
- Pasquia Hills and Wildcat Hill Provincial Wilderness Park in east central Saskatchewan.
- The southeastern region of Alberta contains native prairie that could provide suitable habitat for plains bison. Although a large portion (43%) of the native grasslands has remained intact despite agricultural development throughout the province, these lands have been predominantly managed for cattle grazing for more than a century (C. Gates, pers. com., 2003). Consequently, reintroduction of bison into this area would be difficult based on the amount of suitable range that is available (G. Court, pers. com., 2002).
- Land managed by Aboriginal Peoples. For example, the Blood tribe in Alberta have expressed a desire to obtain plains bison from Elk Island National Park (N. Cool, pers. com., 2002).
- Suffield National Wildlife Area (454 km^2) and the Department of National Defence Canadian Forces Base Suffield (2690 km^2) in southeast Alberta (Environment Canada 2003; H. Reynolds, pers. com., 2003). Suffield is one of the largest blocks of unplowed grassland in the Canadian Prairies (Environment Canada 2003).
- Prairie Farm Rehabilitation Association (PFRA) community pastures (H. Reynolds, pers. com., 2003). These sections of crown land are managed for multiple uses including livestock grazing, and animal and plant biodiversity (Agriculture and Agri-Food Canada 2003). The PFRA currently manages 9290 km^2 of land in dozens of holdings scattered throughout southern Saskatchewan and southeastern Alberta (Agriculture and Agri-Food Canada 2003).

Protection/ownership

Three of the wild or semi-wild Canadian bison herds reside on federal lands and their ranges are therefore protected by either the National Parks Act (Elk Island National Park, and Prince Albert National Park), which prohibits hunting within the park, or the Department of National Defence (Cold Lake/Primrose Air Weapons Range), which prohibits trespassing on the range. However, Cold Lake First Nations peoples are permitted access to the Cold Lake/Primrose Air Weapons Range for hunting, trapping or fishing. The Cold Lake/Primrose Air Weapons Range is not managed for bison conservation and oil and gas resource development is currently occurring on the range. Bison that wander from either the park boundaries or the military range are not protected from hunting. Federal or provincial laws do not currently protect the Pink Mountain herd range, but the bison are afforded protection under the B.C. Wildlife Act (B.C. Ministry of Water, Land and Air Protection 1996). This herd occurs within the Muskwa-Kechika Management Area, for which a wildlife management plan has been drafted. Of the four captive display herds, two ranges occur on National Parks (Riding

Mountain and Waterton Lakes). The ranges of the display herds at the Bud Cotton Buffalo Paddock and Buffalo Pound Provincial Park are protected by the fact that the herds are contained within a fenced paddock and occur on provincial crown land. The Saskatchewan Wildlife Act (1998) also protects the Buffalo Pound Provincial Park herd.

BIOLOGY

Reproduction

Plains bison are polygynous and the reproductive success of males is related to status in a dominance hierarchy. Females are seasonally polyestrus; the first estrus occurs in late summer and subsequent estrus events take place until late fall if pregnancy has not occurred. A typical cycle consists of brief estrus periods of six to 12 hours in duration, cycling for about 21 days (Dorn 1995). The gestation period is usually slightly longer than nine months, but can range from 262 days (Towne 1999) to 300 days (Banfield 1974; Haugen 1974; Dorn 1995).

The prime reproductive age for bison cows is three to 16 years (Fuller 1961; Halloran 1968; Shaw and Carter 1989; Olson 2002; Wilson *et al*. 2002b). Cows often produce their first calf at three years (McHugh 1958; Fuller 1961; Shaw and Carter 1989; Green and Rothstein 1991). However, conception can also occur earlier, with first calving at two years. There is considerable variation in age of first conception both within and among herds (Fuller 1966; Haugen 1974; Halloran 1968; Shaw and Carter 1989). For example, Fuller (1966) reported that in Wood Buffalo National Park, 5% of yearlings conceive, while higher rates of yearling conception were reported for some American herds managed at lower densities and given supplemental food (Haugen 1974; Halloran 1968; Shaw and Carter 1989).

The calving season usually lasts three to four weeks, between April and June (Soper 1941; Egerton 1962; Banfield 1974; Rutberg 1984; Green and Rothstein 1993a). An average birthing season of 23 days was reported at the National Bison Range in Montana (Rutberg 1984) and 54 days at Wind Cave National Park (Green and Rothstein 1993a). The peak calving period in Elk Island National Park occurs from May until June, although calves have been born throughout August, and even as late as November as herd size has increased (Reynolds *et al*. 2003). Similarly, high population densities led to a prolonged calving season in Waterton Lakes and Yellowstone National Parks (Egerton 1962; Meagher 1973). Egerton (1962) reported that bison herds in northerly regions calve about two weeks later than those in more southerly regions. Nonetheless, if nutrition is sufficient for conception and parturition, calving can occur year round (Soper 1941; McHugh 1958; Banfield 1974). Female bison may synchronize parturition with other cows in response to climatic and habitat variations (Rutberg 1984; Berger 1992; Green and Rothstein 1993a).

Reproductive success varies between populations and is influenced by factors such as climate (Van Vuren and Bray 1986; Verme and Doepker 1988) and nutrition

(Verme 1969; Van Vuren and Bray 1986; Lott and Galland 1987; White *et al*. 1989; Wolfe *et al*. 1999). Calving rates can range from 35-100% (McHugh 1958; Meagher 1973; Lott 1979; Lott and Galland 1987; Kirkpatrick *et al*. 1993). Bison herds in harsher environments have lower reproductive success (Lott and Galland 1985). In confined herds, where nutrition is usually better than in wild herds, an average birth rate of 79% has been reported (Van Vuren and Bray 1986). In Elk Island National Park, an average pregnancy rate of 75% was estimated from 1999 to 2002 (Olson 2002).

Pregnancy rates may also be affected by stress and prior reproductive success. Some researchers have suggested that bison follow a two- or three-year calving pattern due to the nutritional costs of producing calves (Soper 1941; Meagher 1973; Kirkpatrick *et al*. 1993). This is supported by evidence that older cows may be more likely to reproduce in alternate years (Green and Rothstein 1991). Furthermore, if lactation is extended, perhaps due to shifts in environmental factors, ovulation could be delayed (Kirkpatrick *et al*. 1996). Fuller (1961) reported that lactating cows typically breed later than non-lactating cows. Conversely, Komers *et al*. (1994a) found that lactating females were more likely to ovulate than non-lactating females. Other studies report no evidence for either calving pattern (Lott and Galland 1985; Shaw and Carter 1989; Green and Rothstein 1991; Wilson *et al*. 2002b). Population density, age and past reproductive success may affect the timing of conception, and subsequently affect offspring fecundity in their adult years. Older females have a higher proportion of late calves (Green and Berger 1990; Green and Rothstein 1991; Reynolds *et al*. 2003). Twinning in plains bison is extremely rare (McHugh 1958; Fuller 1961; Reynolds *et al*. 2003).

The rut occurs between June and October, peaking in early August (Shaw and Carter 1989). Population density, habitat, climate, and photoperiod can influence breeding periods (Egerton 1962; Reynolds *et al*. 2003). Plains bison exhibit a longer rutting period than wood bison in Wood Buffalo National Park, lasting from early July until late September (Soper 1941; Fuller 1960; Banfield 1974).

Bison males establish a linear dominance hierarchy (Wolff 1998). Between 50 and 73% of males mate each year (Lott 1981; Wolff 1998). Male reproductive success is strongly correlated with social rank (Lott 1979). However, male rank changes often during the rut, as bulls tire from aggressive interactions (Lott 1981). Lott (1979) found that most dyads had dominant-subordinate role reversals at least once during a three-week study period. Males usually leave the cow herd for a time during the rut, presumably to recover body condition, and may return to the herd later (Komers *et al*. 1992; Wolff 1998). The absence of dominant bulls may allow lower-ranked males to breed. A linear regression of current reproductive success as a function of prior reproductive success and body mass was significant at Elk Island National Park, but its ability to explain variability in reproductive success was weak (Wilson *et al*. 2002b). Other studies have found no significant relationship between body mass and reproductive success (Lott 1979; Wolff 1998). Males generally do not breed pool until age six, despite being reproductively successful when no older males are present (Fuller 1961; Meagher 1973; Lott 1981; Rothstein and Griswold 1991; Wilson *et al*.

2002a). The effort expended toward reproduction increases with age from six to 12 years, with a peak occurring between eight and eleven years (Maher and Byers 1987). After 12 years of age, bulls still spend energy on reproduction, but less effort is directed toward aggression, as the number of wins begins to decline (Maher and Byers 1987). Consequently, reproductive effort is much more variable beyond 12 years of age. Other studies report no relationship between social standing, fighting ability or reproductive success and age (Lott 1979; Wolff 1998; Wilson *et al*. 2002b).

The sex ratios at birth in bison populations are slightly male-biased, ranging from 51% to 62% males (Rush 1932; Halloran 1968; Haugen 1974; Fuller 1966; Rutberg 1986a) with an average of around 54% males. The long-term sex ratio at birth in Elk Island National Park is 51% males (Olson 2002). Sex ratios of mature individuals are often slightly lower, ranging from 47% to 51% males (Halloran 1968; Rutberg 1986a). The adult sex ratio of a bison herd is typically female-biased due to the high mortality rates of young males (Van Vuren and Bray 1986).

Spring calf percentages have been reported to be around 20% (Meagher 1973; Fuller 1966). Calf-cow ratios can be highly variable, depending on disease and predation levels, and population age structure (Carbyn 1998). As calculated from Olson (2002), the calf-cow ratio of plains bison at Elk Island National Park has been 0.70-0.90 over the last 20 years. Calf-cow ratios as low as 0.12 have been reported in Wood Buffalo National Park where predation is prevalent and disease may affect calf survival (Carbyn and Trottier 1987).

Survival

Wild plains bison have an average lifespan of about 15 years (Fuller 1966; Reynolds *et al*. 1982). However, in captive or semi-wild populations, they are capable of living beyond 20 years (Meagher 1973; Berger and Peacock 1988; Olson 2002), and can even continue breeding beyond 30 years (Dary 1989; Dorn 1995). Plains bison at Elk Island National Park have an average lifespan of 16 years. In 2001 the oldest known-aged bull was 19 years and the oldest known-aged female was 26 years (Olson 2002).

Survival rates for adult males and females are similar in unharvested populations. Since hunting is typically male-biased, harvested populations will have increased adult male mortality. Male mortality is greater than female mortality among young bison. Calf survival rates are highly variable. In late spring, immediately after the calving season, calves make up about 20-25% of the population in Wood Buffalo National Park. However, calf mortality is estimated to be around 50% (Fuller 1962), so by early winter, calves will make up only 5-8% of the population (Fuller 1966). This wood bison population is subject to wolf predation, and brucellosis and tuberculosis are prevalent. The calf survival rate in Yellowstone National Park is approximately 18-20% (Meagher 1973). Calf survival in confined populations that are free of predators and disease can be over 90% (Van Vuren and Bray 1986). Adult survival is around 97%.

MacEwan (1995) suggested that the primary threats to bison survival can be ranked from most to least severe as: weak ice, hunting, fires, predators, disease, bogs and blizzards. Weak ice can be a risk to bison as they travel across rivers or swamps. Over-hunting was the primary cause of the near-extinction of bison in the late 1800s. Today, hunting is practiced to some extent on the three free-ranging populations, with varying degrees of regulation. In drought years, fires can be common on grasslands, chasing bison away from their range. However, some studies have shown that bison prefer burned habitat, as it possesses an abundance of new growth (Campbell and Hinkes 1983; Shaw and Carter 1990; Coppedge and Shaw 1998). Wolves also present a significant risk for bison, particularly in respect to calf survival. In eastern British Columbia, bison made up 10.3% of the prey items in the wolf diet (Weaver and Haas 1998). In a study of predation on wood bison, the majority of the wolf diet consisted of bison (Larter *et al*. 1994). Grizzly bears were once thought to be a major threat to bison. Currently, grizzly bears are known to prey on plains bison in Pink Mountain, the only location in Canada where their current ranges overlap (H. Schwantje, pers. com., 2004). Bison formed a significant portion of the bear diet in the form of kills and scavenged animals, particularly after hibernation (Meagher 1978). Before the introduction of domestic cattle to North America, it was thought that bison were relatively free of disease (Soper 1941). However, since that time a number of diseases have been introduced to bison populations from domestic cattle herds either directly or indirectly, including tuberculosis, brucellosis and bovine viral diarrhea (Lothian 1981; Dragon *et al*. 1999; W. Olson, pers. com., 2003).

Physiology

Females reach adult size at about four years of age but continue to grow until age five or six (Banfield 1974). Male bison continue to grow until eight to ten years (Banfield 1974). Kelsall *et al*. (1978) reported that males are, on average, 9.1% heavier than females of equal chest girth. Bulls generally range from 600 to 860 kg (Halloran 1961), with an average mass of 739 $\pm$ 10.0 kg (Banfield 1974). The average adult bull had a body mass of 732 kg at Elk Island National Park in 2001, with the heaviest bull weighing 877 kg (Olson 2002). Alternatively, cows range from 350-550 kg (Halloran 1961), with an average mass of only 440 $\pm$ 2.1 kg (Banfield 1974). At Elk Island National Park, the long-term mass of cows from 1962 to 2000 was 425 kg (Olson 2002). Bison weight is dependent on age, sex, population density, nutrition, weather, reproductive effort, birth date and inbreeding (Rutberg 1983; Lott and Galland 1987; Berger and Peacock 1988; Green and Rothstein 1991; Komers *et al*. 1994b). Calves weigh approximately 15-25 kg at birth (Halloran 1961). The December mean calf weight between 1962 and 2001 at Elk Island National Park was 164 kg for males and 152 kg for females (Olson 2002). The 2001 male calves had a mean mass of 169 kg, the largest since bovine viral diarrhea (BVD) was introduced to the herd (Olson 2002). Since that time, there have been several late-born calves that weigh less than 136 kg.

Energy metabolism in bison varies with season (Reynolds *et al*. 2003). In winter, bison decrease their metabolism in response to reduced forage intake and colder temperatures (Rutley and Hudson 2000). Bison produce 40% less heat in the winter,

when food intake is reduced, than in the spring when consumption increases (Galbraith *et al*. 1998). Metabolizable energy intake ranged from 146 ± 22kJ $W^{-0.75}$/day in December to 478 ± 45kJ $W^{-0.75}$/day in June in a study of yearling bison (Rutley and Hudson 2000). Correspondingly, bison also reduce their activity levels during winter. Data on metabolic rates suggest that they are particularly well suited for cold temperature, but perhaps not as well suited for warmer temperatures. Christopherson *et al*. (1978) measured metabolic rates of 748 kJ/kg metabolic body mass per day in yearling bison at 10°C, but 584 kJ/kg metabolic body mass per day at –30°C, which suggests that the upper critical temperature of bison is below 10°C. Furthermore, bison become cold tolerant around six months of age, which is much sooner than in other ungulates (Christopherson *et al*. 1978). Their ability to tolerate cold is in large part due to the insulating characteristics of their pelage. Bison have almost ten times as many hair follicles per cm^2 than cattle (Lott 2002).

Bison are well adapted for feeding on short-grass prairies. Their incisors are broad, allowing for a large amount of short grass to be taken into the mouth at one time (Geist 1996). Molars and premolars are large, which is perhaps an adaptation to the wear caused by chewing dusty, rough grasses (Geist 1996). Large snowfalls do not usually reduce a bison's ability to graze, given their feeding methods. Unlike most ungulates that paw through snow to reach forage, bison move their cheeks, muzzles and beards in a sweeping motion known as the head-swing technique to reach the forage underneath (Pauls 1995; Guthrie 1980).

Movements/dispersal

Historically, plains bison exhibited migratory movements between seasonal ranges. Migrations could either be elevational, as they were in the Rocky Mountains (Van Vuren 1983), or directional, as they were in the open prairies. In the southern Rocky Mountains, bison spend summers at higher altitudes and winters at lower altitudes (Van Vuren 1983). Open prairies are preferred for summer months due to the insect relief that the wind provides (Meagher 1973). In contrast, White *et al*. (2001) report that bison in the Canadian Rocky Mountains spent summers in the foothills and valleys, while winters were spent at higher elevations. Directional migrations typically involve an annual southward movement of a few hundred kilometres in the fall. Daily distances travelled are highly variable (Carbyn 1997; Reynolds *et al*. 2003). Forage and water availability, climate, insect densities and shelter can all influence annual migrations (Meagher 1989). Meagher (1973) reported that bison exhibit strong fidelity to their winter range. Others doubt that bison participated in regular migrations along specific paths in historical times. Instead, bison movements were likely irregular, with extensive mixing between herds.

Nutrition and interspecific interactions

Specific data on nutrient requirements are not available for bison (Reynolds *et al*. 2003). Most information regarding energy, protein, vitamin and mineral requirements have been based on cattle studies. However, bison have more efficient digestive

systems than cattle (see below), and it is reasonable to assume that nutrient requirements differ also.

Plains bison are ruminants and primarily consume grasses and sedges. However, bison are habitat generalists and are capable of shifting their diet when forage availability shifts (Larter and Gates 1991). Bison are more efficient than cattle and other ungulates at processing high fibre, low protein diets (Peden *et al*. 1974; Hawley *et al*. 1981; Hawley 1987). This may be due to their efficiency at nitrogen cycling (Reynolds *et al*. 1982). Since nitrogen is commonly limited in the bison rumen, they will recycle urea to increase microbial fermentation, resulting in improved digestion. Moreover, the size of their rumen slows the rate of turnover, thereby increasing the opportunity for microorganisms to more efficiently break down the forage. As microbial digestion is slow, bison spend much of their time resting and ruminating.

Due to their foraging habits, bison rarely compete for food with other ungulates. Primary plains bison habitat may overlap with elk, white-tailed deer, pronghorn, bighorn sheep and livestock, but not with moose, caribou or mule deer. However, among those ungulates that may share habitat in certain regions, few of those species have overlapping diets with plains bison. In Elk Island National Park, plains bison winter diets differ significantly from elk, with bison ingesting a much higher proportion of sedges, and a much lower proportion of browse (Telfer and Cairns 1986). Elk may select similar forage as bison in Aspen Parkland regions, but their cropping rates are lower (Hudson and Frank 1987). Bighorn sheep rarely occur on similar range as bison and the two species do not have overlapping diets, thereby minimizing potential competition (Singer and Norland 1994). Pronghorn have similar diets to bison, but as they are much more selective foragers, competition between these species is likely low. Pronghorns prefer browse and forbs and normally consume little grass (Lott 2002). Consequently, interspecific competition for food is probably not a limiting factor of plains bison population growth.

In Canada, there is currently no overlap of wild plains bison with prairie dogs (D. Fraser, pers. com., 2003). However, there is a historic relationship between the two species. The edges of prairie dog colonies provide efficient grazing areas for bison. These sites have high densities of young, high-quality graminoid vegetation. Bison like to graze in the newer areas (< 8 years) of the colony that possess the superior vegetation, and use the older areas (>26 years) for wallows (Coppock *et al*. 1983). Although it is unclear if prairie dogs benefit from this relationship, it is suspected that bison reduce predation on the colony, provide fertilizer (Coppock and Detling 1986), and trample the vegetation to an optimal height for prairie dogs, which was especially important in tall-grass prairies (Shaw 1998; Lott 2002).

Behaviour/adaptability

Within a bison herd, significant social structure can be identified. For most of the year, bison herds are separated into maternal groups and bull groups. Maternal groups form the majority of the herd and are composed of 20-50 cows and young bison (McHugh 1958). Group size is unstable and depends largely on forage and space

availability (Fuller 1960; Shackleton 1968; Van Vuren 1983). Several reports suggest the existence of stable subgroups of related animals, within larger aggregations of bison (Seton 1929; Soper 1941; Fuller 1960). However, others report that bison groups are quite fluid, and the relationships between individuals are random (Lott and Minta 1983; Van Vuren 1983). Adult males rarely interact with the cow groups outside the rut. Bulls often occur in loose associations, but are predominantly solitary for most of the year.

Both male and female bison exhibit a linear dominance hierarchy within the herd (Rutberg 1983; Green and Rothstein 1993b). Male dominance is correlated with age and body size, while female dominance is correlated only with age (Rutberg 1983). The most aggressive bulls are about four years old (McHugh 1958; Fuller 1960; Lott 1974). In contrast to bulls, female dominance is established early and ranks are not subsequently challenged. Earlier-born female calves tend to be dominant (Green and Rothstein 1993b). Higher dominance often corresponds to increased growth as juveniles and increased reproductive success. Older cows are dominant to younger cows (Rutberg 1986b).

During the rut, adult bulls join the maternal groups, resulting in a notable increase in herd size and activity level. Breeding herd sizes can be up to a few hundred animals (McHugh 1958; Lott 1974). Typical male mating behaviours include fighting, wallowing, horning, vocalizing, sexual investigation, tending cows, and mounting cows (Reynolds *et al*. 2003). Cows become restless and excitable, and frequently wander away from the herd (McHugh 1958). Males guard females until they are ready to copulate, and leave after remaining with the cow for a short period of time, presumably to guard against sperm competition (Lott 1981). Cows may dash through the herd shortly before they are ready to copulate (Lott 1979, 1981; Wolff 1998). This attracts the attention of a number of bulls that challenge the tending male.

Cows maintain very close associations with their calves for the first week after parturition. Although calves stay with their mothers during their first summer, the bond is gradually reduced after the first month (Van Vuren 1983). However, young mothers maintain more frequent contact with their calves beyond the first month than older mothers (Green 1993). Some cows will remain with calves during the following summer as well, but this reduces the reproductive potential of the cow (Green and Rothstein 1993b). Calves will usually stand within an hour of their birth (Egerton 1962; Mahan 1978; Reynolds *et al*. 2003). The duration of nursing varies between locations from seven to eight months (McHugh 1958), nine to 12 months (Mahan 1978), or even up to 24 months (Green *et al*. 1993). Barren cows nurse longer than pregnant mothers (Green *et al*. 1993). During their first few nursings, young cows may produce less milk than older cows (Green 1986).

As a predator avoidance tactic, plains bison generally calve near other members of the herd (Lott 1991). Cows protect their calves from other bison by keeping themselves between the calf and the herd (Egerton 1962; Mahan 1978). Typically, calves are protected by maternal defense, but the herd also acts to defend calves, by positioning them toward the front of the herd when being pursued (Carbyn and Trottier 1987).

POPULATION SIZES AND TRENDS

A history of the plains bison populations after 1870

Wild plains bison had declined by 1888 to what was estimated by Hornaday to be eight animals in Canada and 85 in North America (Coder 1975). Plains bison likely disappeared from Canada within a year or two of this date (Roe 1970). The numbers were based on reports from hunters, and may not have been accurate. However, there is little doubt that bison were in danger of going extinct. By the late 1800s, small bands of bison were scattered throughout their former range, and sometimes ended up mixed among domestic cattle herds. All but one plains bison population in existence today was founded exclusively from animals either bought from or donated by private citizens. The exception is the herd in Yellowstone National Park, in Wyoming and Montana, USA, which is a mixture of previously privately owned animals and an indigenous herd. The private herds that contained the ancestral bison of today's public herds were started from a small number of animals, captured from a few locations. Five herds played a key role in the establishment of the current North American plains bison populations, and four of these supplied the founding animals of the Canadian populations. The history of the four founding herds for Canadian plains bison, discussed below, reveals that most of the populations experienced numerous bottlenecks which likely resulted in a decline in the genetic diversity of the subspecies. The close proximity of bison and cattle during this time may also raise concerns about the genetic purity of today's herds.

Charles Goodnight, one of the private ranchers that provided bison for Canadian public herds, established his herd from one male and one female bison he captured in Texas in 1878. He later added three calves from two different ranches in the same area, whose histories are unknown, and captured two more calves from the wild. However, as two of his calves died before reaching reproductive age, his herd was founded from five individuals (Coder 1975).

The Alloway/McKay herd originated in 1873 from one male and two female calves captured southwest of Battleford, in what is now Saskatchewan (Lothian 1981). Another male and two female calves, obtained between Regina and Moose Jaw, Saskatchewan, were added to this herd the following year. However, one of the male calves died. By 1879, this herd had increased to 13 bison, and three cattle/bison hybrids. Samuel Bedson's herd was founded with the purchase of either eight (Coder 1975; Dary 1989) or all 13 (Lothian 1981; Novakowski 1989) of the bison in the Alloway/McKay herd. Bedson also captured three calves from what is thought to be the Stony Mountain, Manitoba region. Lord Strathcona also obtained animals from the Alloway/McKay lineage. He either purchased the five bison remaining from the Alloway/McKay herd after Bedson's purchase in 1879 (Coder 1975), or received either seven (Garretson 1938) or 27 (Lothian 1981) from Bedson in 1887.

Between 1886 and 1889, Buffalo Jones captured a number of calves in the Texas panhandle, of which 56 survived (Coder 1975). He then purchased about 100 animals

from Bedson, but lost around 25% of these during transit (Garretson 1938; Coder 1975; Lothian 1981; Novakowski 1989). He also obtained ten animals from ranches in Kansas and Nebraska, but nothing else is known about these animals (Coder 1975). Jones sold eight bison to Corbin in 1888 (Jennings and Hebbring 1983), and between ten and 12 of the Bedson bison to Corbin in 1892 (Ogilvie 1979; Novakowski 1989).

The last, and most important, private herd with regard to the conservation of plains bison in Canada was started by a member of the Pend d'Oreille named Walking Coyote. Around 1872, he obtained seven or eight calves about 300 km south of the Alberta – Montana border. Four died before reaching maturity, leaving two males and two females (Garretson 1938; Coder 1975). Ten or 12 animals were purchased from Walking Coyote by Pablo and Allard in 1883 (Garretson 1938; Coder 1975). In 1893, 26 bison purchased from Jones (after he obtained them from Bedson) were added to the Pablo/Allard herd (Coder 1975).

Canada's national parks began their role as sanctuaries for endangered species in 1897, when one male and two female bison arrived in Banff National Park from the Goodnight herd (Lothian 1981). At this time, plains bison had likely been extirpated from the wild in Canada. Lord Strathcona donated 13 more animals the following year (Lothian 1981; Novakowski 1989). Banff National Park exchanged two bulls with Corbin in 1904 (Lothian 1981). A second Canadian publicly owned population was founded in 1907, after the purchase of the entire Pablo/Allard herd by the Canadian government (Lothian 1981). At the time, this was considered to be a considerable accomplishment, as this was the largest herd of plains bison in existence. In 1907, 410 bison from the Pablo/Allard herd were shipped to Elk Island National Park (Lothian 1981; Novakowski 1989). These animals were joined by a few others shipped to the area from Banff National Park (Blyth and Hudson 1987). At the same time, 32 Pablo/Allard bison were shipped back to Banff from Elk Island National Park (Blyth and Hudson 1987). In 1909, 325 animals were shipped from Elk Island National Park to Buffalo National Park, near Wainwright, Alberta (Lothian 1981; Novakowski 1989). Most researchers believe that 48 animals were left as the founders for Elk Island National Park, but this number may have been as high as 71 (Blyth and Hudson 1987). Between 1909 and 1914, 306 more bison were shipped to Buffalo National Park from Pablo/Allard, and 87 from Banff National Park. In an attempt to increase the diversity of the Buffalo National Park herd, 30 bison were also added from the Corbin herd (Lothian 1981; Novakowski 1989).

The Buffalo National Park population rapidly increased in size. In 1923 and 1924, over 2000 animals were culled (Novakowski 1989). At this time, it was discovered that almost 75% of the population was infected with tuberculosis (Lothian 1981). The public criticism to the slaughter was such that it was decided to ship 6673 young animals, which at the time were thought to be less likely to be infected with tuberculosis, to Wood Buffalo National Park. This led to a hybridization event between plains bison and the last remaining herd of wood bison (see Appendix 1:The Hybridization of Wood and Plains Bison). Due to the high prevalence of tuberculosis in Buffalo National Park, it was decided that the region should be depopulated of wild ungulates, and in 1939, the last 2918 bison were killed (Lothian 1981).

After the large shipments of animals from Banff National Park to Buffalo National Park, the former population was managed at a relatively low level, and periodically received animals from Elk Island National Park. In 1980, the last eleven plains bison from Banff were removed so that this area could instead be used for a wood bison display herd (Novakowski 1989). All of the Canadian publicly owned plains bison are descendants of the 48 or 71 bison remaining in Elk Island National Park in 1909.

Current population sizes and trends

The Canadian population of plains bison consists of a total of 920-1010 mature animals in four populations of wild or semi-wild plains bison, and 63-83 mature animals in four small, captive populations for public display (Table 2).

Table 2. Sizes of each publicly owned plains bison herd in Canada in 2003, including mature and immature animals.

	Population	Size	Mature Individuals	Trend	Range (km^2)
Semi-wild	Elk Island National Park, Alberta	500	250-270	stable	136
Wild	Pink Mountain, British Columbia	900	450	stable	1500
	Prince Albert National Park, Saskatchewan	320	175-220	increasing	750
	Cold Lake/Primrose Air Weapons Range, Saskatchewan	70-100	45-70	stable - increasing	500 – 750[a]
Captive	Riding Mountain National Park, Manitoba	33	21-33	stable	
	Waterton Lakes National Park, Alberta	26	13-15	stable	
	Buffalo Pound Provincial Park, Saskatchewan	35	21-25	stable	
	Bud Cotton Buffalo Paddock, CFB Wainwright, Alberta	16	8-10	stable	

[a]estimated from the range of the Pink Mountain herd when it was a similar population size

Elk Island National Park

The Elk Island population is the main source of bison for the other plains bison conservation herds in Canada. The herd is semi-wild because, while it is fenced and has no natural predators, it is managed as a wild population as closely as possible. The herd range is 194 km^2. The EINP herd increased exponentially until the 1920s when the park initiated regular culling. The population reached its peak at 2,479 in 1936 (Blyth and Hudson 1987). After 1970, live sales and donations were implemented instead of annual culls.

The population at Elk Island National Park is currently being reduced, in an attempt to alleviate grazing pressure from bison and other ungulates (EINP 1999). In the fall of 2001, the plains bison numbered 419, with a density of 4.1 bison per km^2 (Olson 2002). The population size estimate was based on the number of handled and free-roaming bison estimated from November 2000, the calf crop estimate, palpation pregnancy checks, and recent mortalities. Ninety-six bison were removed early in 2002, bringing the population to 323 (Cool 2003). The population is expected to reach a size of around 500 animals by the fall of 2003 (Cool 2003). Annual removal of bison will continue so that the population is maintained at its current target level of 420-500 (Cool 2003). The optimal population size is currently being re-evaluated (Cool 2003). The population has been managed approximately at these levels since the mid-70s (Olson 2002).

Pink Mountain

The Pink Mountain plains bison herd in British Columbia occurs in the Pink Mountain – Sikanni Chief River area (B.C. Ministry of Environment 1991). The current range is approximately 1500 km^2 (D. Fraser, pers. com., 2003) and the habitat is primarily sedge meadows and grassland (B.C. Ministry of Environment 1991). The herd was established in 1971 from 48 bison, which escaped from the upper Halfway River area into crown land after being privately purchased by Lynn Ross from an Elk Island surplus bison sale (Reynolds 1991). The court declared the free-ranging bison to be the property of the province after several years, and in 1982 the bison were listed as "big game" and "wildlife" under the British Columbia Wildlife Act (B.C. Ministry of Water, Land and Air Protection 1996). In 1991, the Pink Mountain plains bison herd became fully managed as a public resource.

Until recently, the Pink Mountain herd appears to have grown at a rate of about 10% per year (Table 1). It peaked in the 1990s at approximately 900 bison (D. Fraser, pers. com., 2003). Controlled hunting by local residents, as well as recreational and commercial harvesting, is permitted. The optimum population size for this bison herd is estimated to be between 1000 and 3000 animals (B.C. Ministry of Environment 1991).

Prince Albert National Park

The Prince Albert National Park herd is the only free-ranging herd that occurs within the original range of the species. These animals are protected as long as they remain within the national park boundaries (Parks Canada 2001a). The range of the herd covers approximately 700 km^2 within the park and 50 km^2 outside of park boundaries. The presumed boundary between the historical range of plains bison and wood bison falls within Prince Albert National Park (D. Bergeson, pers. com., 2002).

The Prince Albert National Park free-ranging plains bison herd was established unintentionally from bison that travelled to and settled in the southwest region of the park, where the herd currently resides. These bison came from a herd of 50 that was used in a 1969 reintroduction effort to repopulate the Thunder Hills region, the upland area north of Prince Albert National Park, with wild plains bison. The goal was to re-

establish plains bison on parts of their former range and to eventually provide an additional food resource for the local First Nations bands. The Saskatchewan Department of Natural Resources obtained 36 females and 14 males, all four years of age or younger, from Elk Island National Park and released them at Two Forks River about 60 km north of Prince Albert National Park, near Neyakamew Lake (D. Frandsen, pers. com., 2002). Although it is estimated that approximately 15 calves were born into the population in the spring of 1969, the reintroduction was unsuccessful in the Thunder Hills region. Some of the bison travelled south toward Prince Albert National Park and, although several settled within the park boundaries, many had to be removed from the area due to complaints from local ranchers and farmers (D. Bergeson, pers. com., 2003). About 11-17 bison settled in the Big River Community Pasture and were transplanted to the Vermette Lake area north of the Cold Lake/Primrose Air Weapons Range (D. Frandsen, pers. com., 2003). Those that were not used to establish the Prince Albert National Park free-ranging herd, nor transplanted to the Cold Lake/Primrose Air Weapons Range on the Saskatchewan-Alberta border, were shot by hunters or destroyed (D. Frandsen, pers. com., 2003).

The exact founding number of bison in Prince Albert National Park is unknown. In 1969, it was estimated that between 16 and 22 bison were within the park. However, no more than four individuals were seen together at any time for about five years. Consequently, it is unknown if the other individuals died or if they were missed during the counts. It should be noted that bison counts were performed at different locations in the park, and other signs of the presence of bison were spread across the park (D. Frandsen, pers.com., 2003). Therefore, it is likely that the population was larger than observed at any one time (D. Frandsen, pers.com., 2003). Due to the significant coniferous forest cover in the park, up to 50% of individuals can be missed even using systematic transect helicopter surveys under good conditions (D. Frandsen, pers. com., 2002). Ground and aerial counts were not consistent until 1978, so they may not have been accurate until that time. As no bison were reported outside the park, where observations would have been evident, it is possible that the original 16-22 bison never left the park and contributed to the founding population.

Prince Albert National Park maintained an educational display herd from 1936-1995. In 1995, the park refocused its management goals toward the maintenance of the wild bison herd, and they sold or donated the 20 existing captive plains bison.

In 2002, the Prince Albert National Park population consisted of 320 bison (D. Frandsen, pers. com., 2002), including 269 adults and juveniles and 51 calves. This count was obtained from an opportunistic aerial survey on July 9, 2002 and therefore, some individuals may have been missed. The population has been increasing at approximately 10-14% per year for the last 20 years (D. Frandsen, pers.com., 2002). Predation does not appear to significantly affect the population, despite the relatively high density of wolves and black bears within this system.

Some plains bison have spent time outside of the park boundaries and travel between crown and private lands. A cattle gate was recently installed at the bridge

across the Sturgeon River, which has reduced the number of bison leaving the park (D. Frandsen, pers. com., 2003). Generally, fewer than 10 bison per year have been observed outside of the park (D. Frandsen, pers. com., 2003). Bison residing outside the park are occasionally shot to reduce the number of bison on private lands. Once outside the park, bison are no longer protected from aboriginal hunting. First Nations are permitted to hunt on crown land, as well as on private land if permission is granted and a regular hunting season exists (D. Frandsen, pers. com., 2003).

Cold Lake/Primrose Air Weapons Range

This free-ranging herd resides most often on the Saskatchewan side of the Cold Lake/Primrose Air Weapons Range that straddles the border between Alberta and Saskatchewan, although the herd does sometimes leave the Range. Evidence of bison was observed on the Alberta side of the range during the late 1980s (H. Reynolds, pers. com., 2004). However, bison have never been observed on the Alberta side of the range, either by Canadian Forces pilots or the oil and gas industry (D. Brakele, pers. com., 2004). The herd was established in 1969 from 11-17 of the 50 plains bison that were intended to repopulate the Thunder Hills region, north of Prince Albert National Park in Saskatchewan (D. Frandsen, pers. com., 2002). In 1969, the Saskatchewan Department of Natural Resources obtained 50 plains bison from Elk Island National Park to re-establish a bison population in north-central Saskatchewan. Several bison ended up near the Big River Community Pasture, about 30 km northeast of Prince Albert National Park, where 11-17 individuals (at least ten adults and one calf) were corralled and transported to Vermette Lake north of the Primrose Lake Air Weapons Range (D. Frandsen, pers. com., 2002; Boyd 2003). An additional six bison were reported north of the Big River Community Pasture and may also have been included in the transplant to Vermette Lake (D. Frandsen, pers. com., 2002). The six additional bison possibly account for the discrepancy between the reported 11 or 17 founding individuals (D. Frandsen, pers. com., 2002).

The current population is estimated to be approximately 70-100 animals, but may be increasing in size and range (B. Opekoque, pers. com., 2003). Very little information is available about this herd, and the accuracy of the size estimate is unknown. Bison hunting is permitted by the Cold Lake First Nations, whose access to the Range is regulated to prevent interference with military operations (C. Gates, pers. com., 2003).

Old-Man-On-His-Back Nature Conservancy of Canada Project

In 1996, the Nature Conservancy of Canada (NCC) acquired the Old-Man-on-His-Back Prairie and Heritage Conservation Area (OMB, NCC 2002). The 53 km^2 ranch is a flagship prairie grassland habitat, located in southwest Saskatchewan. Fifty calves and yearlings were introduced to the prairie preserve from Elk Island National Park on December 12, 2003 (Nature Conservancy of Canada 2004). The bison will be held in various parts of the preserve throughout the year. The grazing capacity of this preserve is estimated to be 250 adult bison.

There are four educational display herds in Canada. These are small, carefully managed herds that range inside a fenced paddock. They are maintained for historical and educational purposes and no attempt is made to manage them as wild populations, which limits their contribution to plains bison conservation in Canada.

Riding Mountain National Park

The Riding Mountain National Park plains bison population occurs within the historical range of plains bison, as determined from the various bison artifacts discovered in the area (D. Bergeson, pers. com., 2002). The habitat is primarily fescue grasslands with numerous interspersed sedge meadows.

The current Riding Mountain bison herd was established with 20 animals from Elk Island National Park in 1945-46. The population structure of the founding herd is unknown (D. Bergeson, pers. com., 2002). The herd grew to about 60 individuals, at which point regular culling was undertaken to maintain the herd below that size.

The Riding Mountain herd currently consists of 33 bison (D. Bergeson, pers. com., 2002), and is carefully managed between 25-50 animals of an average age of between four and seven. Bulls were sometimes traded with the Prince Albert National Park captive herd or imported from Elk Island National Park (S. Frey, pers. com., 2003).

Waterton Lakes National Park

Waterton Lakes National Park in southern Alberta maintains a 200 ha bison paddock near the Pincher Creek entrance to the park (R. Watt, pers. com., 2002). The herd was established in 1952, with bison obtained from Elk Island National Park, to honour the bison that once roamed freely in the area. The breeding stock is still periodically supplemented with plains bison from Elk Island National Park (R. Watt, pers. com., 2002). The current population is stable with 26 animals. The herd is managed to maintain between 12 and 24 individuals (R. Watt, pers. com., 2002). Surplus bison are sold at public auctions every two or three years. There are tentative plans to expand the herd size and range and to manage the increased herd as a semi-free-ranging population (R. Watt, pers. com., 2002).

Buffalo Pound Provincial Park

Buffalo Pound Provincial Park is in southwest Saskatchewan, northeast of Moose Jaw. The park was named after the many buffalo pounding sites found in the area (Saskatchewan Environment 2003). Indigenous people used these topographical features as corrals to capture plains bison. The display herd was established in 1972 with eight cows and four bulls from Elk Island National Park (T. Minter, pers. com., 2003). Between 1988 and 2000, ten additional bison introductions have occurred, ranging in size from one to three bulls (T. Minter, pers. com., 2003). All but one of the introduced bison came from private ranches (Kevin Wilkinson, Ron Sebastian, Sawki Ranch and Tatonka Ranch; T. Minter, pers. com., 2003), making the contribution of this

population to plains bison conservation minimal (see Limiting Factors and Threats – Game Ranching section). In 1988, one bison bull was introduced from Prince Albert National Park. The current population is stable at 35 bison, consisting of three bulls and 32 cows (T. Minter, pers. com., 2003).

Bud Cotton Buffalo Paddock, Canadian Forces Base Wainwright

Canadian Forces Base (CFB) Wainwright is located just south of Wainwright, Alberta. In 1980, a portion of Buffalo National Park was re-dedicated to bison. The new herd was founded with four young bison (Bud Cotton Buffalo Paddock 2001), and the current size of this herd is 16 animals (Boyd 2003).

LIMITING FACTORS AND THREATS

Lack of habitat

Before European settlement, millions of bison inhabited the Great Plains. Their available habitat has drastically declined in the last 150 years. Large quantities of prairie habitat have been lost to agriculture and urban development, and for the most part, large, unbroken areas of original prairie do not exist (Reynolds 1991). Since the establishment of Elk Island National Park, and subsequently Buffalo National Park between 1907 and 1910, the number of plains bison on public lands in their original range has not significantly changed, mainly due to the lack of available habitat and the loss of Buffalo National Park. For the most part, free-ranging bison are incompatible with agriculture and urban development (Reynolds 1991; D. Bergeson, pers. com., 2002). Currently, while Prince Albert National Park falls within the original range of plains bison, none of the wild plains bison populations in Canada exist on what was their typical and traditional prairie habitat (H. Reynolds, pers. com., 2003). Though rare, opportunities for the reintroduction of plains bison into native prairie habitat do exist.

Hybridization with cattle

Most of the bison herds existing today were founded with animals donated or sold by ranchers. Ranchers that found bison scattered among their cattle during roundups sometimes encouraged bison and cattle to interbreed (Garretson 1938; Rorabacher 1970; Polziehn 1993). In an examination of plains bison haplotypes, Polziehn *et al*. (1995) discovered that eleven of 30 bison from Custer State Park, South Dakota, possessed domestic cattle mitochondrial DNA. Their analyses suggested that the proportion of cattle nuclear DNA in the population would be 0.0083. Cattle mitochondrial DNA was not detected in eight other populations, including the plains and wood bison populations at Elk Island National Park, and the wood bison populations in the Mackenzie Bison Sanctuary, and Wood Buffalo National Park. As the bison at Custer State Park were not exposed to cattle, the hybridization likely took place before this park was founded in 1914 (Polziehn *et al*. 1995). A follow-up study by Ward *et al*. (1999) found cattle mitochondrial DNA present in four other publicly owned plains bison

populations: Antelope Island State Park, Utah; Finney Game Refuge, Kansas; Maxwell Game Refuge, Kansas; and the National Bison Range, Montana. Of these, Polziehn *et al*. (1995) only examined the National Bison Range population. National Bison Range and Antelope Island State Park introduced bison from the Maxwell State Game Refuge and this is likely why cattle mitochondrial DNA is present in these populations. The four free-ranging Canadian populations were also re-examined (Ward *et al*. 1999). No evidence of domestic cattle Y-chromosome introgression was found, suggesting that the hybridization of bison and cattle was mainly through the mating of domestic cows and bison bulls (Ward *et al*. 2001). This may be due to the unwillingness of domestic bulls to mate with bison, or the low fertility of male hybrids between cattle and bison (Rorabacher 1970; Polziehn *et al*. 1995; Ward *et al*. 2001). An examination of seven nuclear microsatellite loci in which the allele sizes for cattle were known revealed no evidence for hybridization at these loci in eleven bison populations, including the plains bison populations at Elk Island National Park and Pink Mountain (Wilson and Strobeck 1999). It should be noted, however, that this study was also unable to detect hybridization at the nuclear level in the Custer State Park population.

Due to the length of time that has passed since the hybridization of cattle and bison in the aforementioned areas, all animals within the populations where mitochondrial DNA was discovered likely contain some cattle nuclear genetic material, and consequently all must be considered hybrids. Interspecific hybridization likely caused a loss of some of the original plains bison genetic diversity present in these populations, as well as a decline in their genetic integrity (Rhymer and Simberloff 1996; Ward *et al*. 1999). While the introgression of cattle genetic material probably has little effect on the survivability of the bison, populations that do not contain bison x cattle hybrids should be a higher priority. Currently, 68% of the conservation bison populations in North America have not been tested for introgression with cattle, 14% appear to contain hybrid animals, and 18% have not tested positive for introgression with cattle (Boyd 2003). No animals from populations whose hybrid status is unknown or questionable should be moved to populations presumed pure. Several individuals knowledgeable in the field of bison conservation believe that this is a concern for the long-term survivability of this subspecies (P. Fargey, pers. com., 2002; T. Jung, pers. com., 2002; H. Reynolds, pers. com., 2002).

Hybridization with wood bison

Northern British Columbia is not only the location of the Pink Mountain plains bison herd, but also the home of the Nordquist wood bison population of 60 animals (Mitchell and Gates 2002). The Nahanni wood bison population ranges through the Liard River drainage in the Northwest Territories and northern British Columbia. As well, the Hay-Zama wood bison population in northwest Alberta occasionally moves into the Hay River drainage area in northeast British Columbia (Harper *et al*. 2000). While the distance between these populations has always been hundreds of kilometers, there is still the possibility that the Pink Mountain plains bison population will mix with one of the wood bison populations, resulting in the introgression of wood bison genetic material into the genome of the Pink Mountain plains bison. In order to combat this possibility, the Management Plan for Wood Bison in British Columbia calls for directed native

sustenance harvesting to prevent eastern movements of the Pink Mountain plains bison population (Harper *et al*. 2000). While this has been effective to date, the potential hybridization of wood and plains bison in this region has been identified as a concern (D. Fraser, pers. com., 2003).

Genetic health

A loss of genetic diversity can have extreme negative effects on a population's ability to exist through even short periods of time, for two reasons: a reduction in genetic variation can increase the effects of inbreeding in a population, and it will also decrease the population's ability to adapt to different selection pressures, otherwise known as its evolutionary potential. Rare or endangered populations often suffer from a lack of genetic diversity (see for e.g. Packer *et al*. 1991; Hoelzel *et al*. 1993; Roelke *et al*. 1993). This is usually attributed to a decrease in population size, or a population bottleneck, followed by a period of inbreeding as a result of the population's small size. The negative effects of inbreeding include high mortality, reduced competitive ability, greater susceptibility to disease, lower fecundity, and more frequent developmental defects (see for e.g. Wright 1977; Allendorf and Leary 1986; Ralls *et al*. 1988; Hedrick and Kalinowski 2000). Levels of genetic variation appear to be inversely correlated with rates of extinction in natural populations when environmental, ecological and demographic differences are controlled (Saccheri *et al*. 1998).

There seems to be little evidence for inbreeding depression in most of the larger bison herds (Gates 1993; Shaw 1993). No correlation was found between reproductive success and heterozygosity (a potential indicator of inbreeding) in wood bison (Wilson *et al*. 2002b). Conversely, the reproductive performance of European bison (*Bison bonasus*) declined as the level of inbreeding increased (Olech 1987). Low genetic diversity has been suggested to affect growth and mating success in one population of bison (Berger and Cunningham 1994). A study of laboratory populations of *Drosophila* showed that inbreeding effects could take over 50 generations to become manifested (Bijlmsa *et al*. 2000). This suggests that genetically depauperate populations in the wild that do not currently seem to be affected by inbreeding will not necessarily be free of these effects over the long term (Bijlmsa *et al*. 2000).

Due to the population bottleneck experienced by plains bison in the last 150 years (from a high of about 30 million to a low of fewer than 800 animals, few of which were used in conservation efforts), plains bison would be expected to possess low levels of genetic diversity, and may potentially suffer from inbreeding effects. Bison display little to no variation at the chromosomal and protein level (Ying and Peden 1977; Bork *et al*. 1991; Cronin and Cockett 1993). However, a study of allozymes determined that bison have higher levels of genetic diversity than other mammalian species that have undergone significant decreases in population size (McCleneghan *et al*. 1990). An examination of blood groups also revealed that bison contain more diversity than might be expected for a species that passed through a precipitous decline in numbers (Stormont 1993). Levels of genetic diversity observed in a study of microsatellites revealed that bison have levels of diversity similar to most other North American ungulates (Wilson and Strobeck 1999).

In a study of eleven wood and plains bison populations, the plains bison population at Elk Island National Park was found to be one of the three most variable in North America (Wilson and Strobeck 1999). The Pink Mountain population also had relatively high levels of diversity. However, as genetic diversity in bison populations is correlated with number of founders, it is probable that the other plains bison populations in Canada are genetically depauperate (Wilson and Strobeck 1999).

It seems likely that North American plains bison essentially acted as a single herd, with extensive gene flow between regions due to their unpredictable and extensive movements. Today, because of the scattered nature of current plains bison populations, gene flow between populations in Canada is only through the shipment of animals between regions. While this lack of gene flow is contrary to what likely occurred with plains bison populations in the past, there are some good reasons to continue to minimize the movement of animals between regions. The exchange of bison between regions can result in an influx of unwanted genetic material and disease. The addition of unwanted genetic material to a population is irreversible after only a few generations, due to genetic mixing. The maintenance of genetic diversity in the small, isolated plains bison populations has been raised as a concern (A. Arsenault, pers. com., 2002; P. Fargey, pers. com., 2002; D. Frandsen, pers. com., 2002; H. Reynolds, pers. com., 2002).

Lack of consensus in legislation

Bison are considered wildlife in British Columbia and Saskatchewan, and are protected in national parks, but are considered domestic livestock in Alberta and Manitoba, and as such are not protected by any current legislation (Reynolds 1991). This issue may potentially impede the conservation of plains bison in Canada (A. Arsenault, pers. com., 2002; N. Cool, pers. com., 2002; H. Reynolds, pers. com., 2003).

Hunting

Unregulated hunting is permitted on the Cold Lake/Primrose Air Weapons Range by the Cold Lake First Nations Peoples in regions where access is granted, and there is controlled hunting on the Pink Mountain herd., Prince Albert National Park plains bison can be shot if they move onto privately owned land. There have been no studies on the effect of hunting on the demography of these populations (C. Gates, pers. com., 2003).

Game ranching

Geist (1996) outlined a number of potential conflicts between conservation and game ranching, including the displacement of native species through competition for land, an increase in poaching, the extinction of predators, the transmission of disease, and the loss of species due to hybridization. Possibly the biggest threat to the conservation of plains bison from ranched bison is the possibility of genetic pollution. At least 95% of bison in Canada today exist on game ranches (Boyd 2003). Bison ranching continues to grow due to the relative ease of raising bison compared to raising

cattle, and the increased popularity of leaner meats. Many new bison ranches are being established near areas that could be deemed suitable habitat for the reintroduction of wild bison. A wood bison ranch exists near the range of the Pink Mountain population (H. Schwantje, pers. com., 2003). The movement of an escaped ranched animal or animals into the range of a wild plains bison population could result in genetic mixing. This could have a large negative impact on the conservation and recovery of wild plains bison in Canada.

Artificial selection will likely result in bison that are faster growing and more docile, among other traits. While desirable in ranched animals, these traits are not selected for in wild populations. Selection for agricultural production will also result in a loss of genetic diversity in ranched bison (P. Fargey, pers. com., 2002). Despite undergoing this selection regime, ranched bison will remain ecologically viable for generations (C. Gates, pers. com., 2003). Mixing of ranched and wild animals, as a result of escaped commercial bison, will result in the dilution or potential replacement of traits that exist in wild bison as the product of generations of natural selection. The ranching of wood bison, or wood and plains bison crosses, has also recently gained favour, due to the larger size of wood bison. Mixing of ranched and wild bison could also result in the introgression of wood bison genetic material into the gene pool of North American plains bison (Reynolds 1991). The expanding game farm industry, especially that of bison game farms, is potentially a hazard for plains bison conservation.

Disease

There is little doubt that the most serious diseases affecting North American bison today, tuberculosis, brucellosis, and anthrax, are the result of infection from introduced livestock. Anthrax was likely introduced to the Wood Buffalo National Park region by domestic livestock in the late 19th or early 20th century (Dragon *et al.* 1999; D. Dragon, pers. com., 2003). However, it is possible that anthrax was present in the region of Wood Buffalo National Park in the early 19th century (Ferguson and Laviolette 1992). Tuberculosis and brucellosis were introduced to the region via the shipment of plains bison from Buffalo National Park in the 1920s, which in turn likely came into contact with these diseases through cattle. The presence of brucellosis in Yellowstone National Park plains bison is thought to be the result of either direct or indirect contact with domestic cattle (Meagher and Meyer 1994; M. Meagher, pers. com., 2003). Transmission of diseases from cattle to bison is an ongoing threat. The recent outbreak of bovine viral diarrhea in the plains bison at Elk Island National Park was likely contracted from surrounding cattle ranches (W. Olson, pers. com., 2003). Vaccination programs have been required to keep this disease at bay (N. Cool, pers. com., 2003).

Outbreaks of anthrax in the region of Wood Buffalo National Park have killed in excess of 20% of the animals within herds (Dragon *et al.* 1999). As this disease primarily targets males and is generally sporadic in nature, demographically healthy populations should be able to recover from an outbreak (Gates *et al.* 1995; Reynolds *et al*. 2003). However, the removal of a large number of males due to an anthrax outbreak can decrease genetic diversity, especially if it occurs in multiple years. As yet,

there have been no outbreaks of anthrax in Canadian plains bison populations, although this disease could arise in many areas (D. Joly, pers. com., 2002).

Brucellosis is present in Yellowstone National Park animals (Meagher and Meyer 1994). Plains bison at Elk Island National Park were initially brucellosis-positive (Nishi *et al*. 2002), the bison at Riding Mountain National Park were tuberculosis-positive**,** and the population at Buffalo National Park had a high prevalence of both tuberculosis and brucellosis. However, there are currently no public herds of plains bison infected with either tuberculosis or brucellosis in Canada. It should be noted that the elk population at Riding Mountain National Park is currently infected with tuberculosis at low rates, and there is the possibility that this disease could spread to the bison population.

The combined effects of tuberculosis, brucellosis, and wolf predation that have a significant effect on animal survivorship in the Wood Buffalo National Park population (Joly and Messier 2001). Therefore, although some diseases may negatively affect survivorship in wild plains bison, the perceived threat of bison as potential disease reservoirs to the health status of the game farm or commercial livestock industry may be a larger threat to population survival (Nishi *et al*. 2002; D. Joly, pers. com., 2002). The risk of infection of privately owned animals from wild populations could result in legislation requiring the eradication of infected wild populations. For example, the presence of Foot and Mouth disease in domestic animals results in a severe restriction in livestock exports. A bison herd infected with Foot and Mouth disease could be considered a threat to infecting cattle herds, especially given the wind-born transmission of this disease (D. Joly, pers. com., 2002). As such, the economic incentive for eradicating an infected free-roaming plains bison population would be high. The potential for transmission of disease to and from cattle could adversely affect plains bison conservation and the willingness of landowners to accept the presence of free-roaming bison (P. Fargey, pers. com., 2002; T. Fowler, pers. com., 2002; D. Frandsen, pers. com., 2002; D. Joly, pers. com., 2002; T. Jung, pers. com., 2002).

SPECIAL SIGNIFICANCE OF THE SPECIES

Plains bison were native to parts of British Columbia, Alberta, Saskatchewan, and Manitoba. At their peak distribution and population size, bison were the dominant herbivore in the prairies, and molded the plant and animal communities (Kerr 1995). Most plains bison populations in Canada today are either direct or indirect descendants of the Pablo/Allard herd, which in 1907 was one of the largest bison herds in existence (Lothian 1981; see A History of the Plains Bison Populations After 1870 section). The plains bison population at Elk Island National Park has great importance for the conservation of this species in North America for a number of reasons. This population had a large number of founders and, as a result, is one of the most diverse plains bison populations in North America (Wilson and Strobeck 1999). Also, there is no evidence that the bison in this population have hybridized with cattle, unlike some of the other more genetically diverse populations (Polziehn *et al*. 1995; Ward *et al*. 1999). Elk Island National Park has been used as the source for all of the public plains bison populations

in Canada and, given its level of diversity and purity from cattle genetic material, should continue to be the source for plains bison populations.

The histories of bison and Aboriginal Peoples in North America are inextricably linked. The large number of archaeologically significant bison kill sites is evidence of the importance of this animal to the survival of 500 generations of Aboriginal Peoples (for review, see Wyckoff and Dalquest 1997). While early kill sites consist of an assortment of large ungulates, sites younger than 10,000 years old contain bison as the dominant species (Guthrie 1980). Hunting pressures on bison were likely strong enough to affect the range of this species. Hunting probably ensured that bison did not exist in significant numbers in the Canadian Rockies (White *et al.* 2001). Hunting pressures may also have kept wood and plains bison separated (McDonald 1981; for further discussion see Appendix 1: Behavioural Ecology section). Bison were severely exploited in Canada during the fur trade, as their skins were highly valued as robes, and this was a primary factor in the decline in bison numbers in Canada (Geist 1996).

EXISTING PROTECTION OR OTHER STATUS

Global

The Nature Conservancy of Canada gives plains bison a global heritage status rank of G4TU (2002; NatureServe Explorer). The G4 indicates that *Bison bison* are globally common (>100 occurrences) and generally widespread, but may be rare in parts of their range and, although they are secure in their global range, they may be of long-term concern. The TU status refers to the subspecies and indicates that their status is uncertain and that further information is required (2002; NatureServe Explorer).

International

Plains bison are currently unranked in the USA (1996) by the Nature Conservancy (2002; NatureServe Explorer). Plains bison are not listed under the U.S. Endangered Species Act (USFWS 1999), nor by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendices (CITES 2003). The World Conservation Union, formerly known as the International Union for Conservation of Nature and Natural Resources (IUCN), Red Book lists bison as Lower Risk, conservation dependent (1996; IUCN 2002), indicating that bison, as a species, are currently the focus of a conservation program. If current conservation programs were to cease, the species would become vulnerable, endangered or critically endangered within 5 years. No distinction is made between the wood and plains bison subspecies.

National

Canadian plains bison are unranked by the Nature Conservancy (2002; NatureServe Explorer). The General Status of Species in Canada ranks bison as Sensitive, which indicates that the species is not at risk of immediate extirpation, but may require special attention or protection (Canadian Endangered Species

Conservation Council (CESCC) 2001). The General Status of Species in Canada ranking system (CESSC) does not separate subspecies. The Canada National Parks Act (2001) protects bison that reside within National Parks. As such, resource harvesting is not permitted within the four national parks that maintain plains bison, as long as the animals remain within the park boundaries, and the animals are managed to conserve their populations.

Provincial

British Columbia

Plains bison in British Columbia are on the Provincial Blue List, indicating that the subspecies is vulnerable or of special concern (B.C. Conservation Data Centre 2000). The Nature Conservancy of Canada also provides a provincial heritage status rank of vulnerable (S3), with rare to uncommon occurrences throughout the province (2002; NatureServe Explorer). The Nature Conservancy of Canada ranking suggests that large-scale disturbances could make the subspecies susceptible to extirpation. The British Columbia Wildlife Act lists plains bison as wildlife and big game (B.C. Ministry of Water, Land and Air Protection 1996). As the Pink Mountain herd is located on crown land, it is managed as a public wildlife resource. Therefore, the bison are protected from unregulated hunting, although a small amount of controlled harvesting is permitted with a guide outfitter (B.C. Conservation Data Centre 2000). Annual harvests ranged from 37 to 181 between 1996 and 2002 (Table 1). As game animals, bison may also be legally farmed under the *Game Farm Act* (Harper *et al*. 2000). Although restrictions may be placed to limit game farms in certain regions of the province, there are currently no restrictions on where bison farms may be located in B.C. (Harper *et al*. 2000). Bison is ranked by the General Status of Species in Canada (CESCC 2001) as Sensitive in British Columbia.

Alberta

The Nature Conservancy of Canada does not provide a provincial heritage status rank for Alberta plains bison (2002; NatureServe Explorer). The General Status of Alberta Wild Species (2000) lists plains bison as Extirpated. Plains bison have never been re-introduced as wild herds in provincially owned lands in Alberta. In the early 1900s, plains bison were re-introduced to federal, not provincial, lands and are consequently not listed under the Alberta Wildlife Act (G. Court, pers. com., 2002). The Alberta Wildlife Act lists *Bison bison* as endangered (G. Court, pers. com., 2002), but this refers to the wood bison in the bison protection area in northwest Alberta, as reported in the status report for wood bison in Alberta (Mitchell and Gates 2002). Any bison in this area are protected under the Wildlife Act.

Saskatchewan

Plains bison in Saskatchewan are given a provincial heritage status rank of S3, indicating that they are vulnerable, with rare to uncommon occurrences throughout the province, and that large-scale disturbances could make the subspecies susceptible to extirpation (2002; NatureServe Explorer; J. Pepper, pers. com., 2003).

In Saskatchewan, bison are listed as big game, and therefore wildlife, under the Saskatchewan Wildlife Act (1998). Consequently, a licence is required to kill or to disturb bison. As there is no open hunting season for bison in Saskatchewan, bison are protected from hunting by non-aboriginals. The Canada National Parks Act (2001), prohibits hunting and disturbance of wildlife within Prince Albert National Park.. The Saskatchewan Parks Act (1997) protects wildlife within Buffalo Pound Provincial Park. First Nations are permitted to hunt bison within Saskatchewan on any land for which they have right of access. A Cooperative Inter-Jurisdictional Plains Bison Management Strategy is being developed by Prince Albert National Park, Saskatchewan Environment, local rural municipalities, First Nations, and local and provincial land owners and stakeholders (D. Frandsen, pers.com., 2003).

Harvest pressure on plains bison is unknown (J. Pepper, pers. com., 2003). In addition to the above aboriginal harvest, domestic game farm operators may kill wildlife without a licence if that wildlife is of the same species as their game farm animals, and poses a direct threat to the game farm animals (D. Frandsen, pers. com., 2002). The threat could occur within the game farm, or from outside the fence.

The Department of National Defence (DND) offers protection to the Cold Lake/Primrose Air Weapons Range population by virtue of prohibiting trespassing on DND land. Therefore, the bison cannot be hunted, except by members of the Cold Lake First Nations (CLFN). As of July 12, 2002, CLFN are permitted to hunt, fish and trap wildlife, including bison, on the range under Range Access Agreements settled between the First Nations, the DND, and the Governments of Canada, Alberta and Saskatchewan (C. Gates, pers. com., 2003). Because the range is used for military operations, access by First Nations is regulated by the DND (C. Gates, pers. com., 2003). If bison roam from the range, they are not protected on public or private land and may be susceptible to hunting by aboriginals.

Bison is ranked by the General Status of Species in Canada (CESCC 2001) as May Be At Risk in Saskatchewan, which indicates that the species is possibly at risk of extirpation.

Manitoba

Plains bison in Manitoba are given a provincial heritage status rank of S1, indicating that the bison are extremely rare and susceptible to extirpation due to some factor of its biology (2002; NatureServe Explorer). Unlike wood bison, plains bison are not listed as wildlife under the Manitoba Wildlife Act (2004). They are listed in the Agricultural Act as "livestock behind a fence" (D. Bergeson, pers. com., 2002). Bison is ranked by the General Status of Species in Canada (CESCC 2001) as At Risk in Manitoba, which indicates that the species is at risk of extirpation.

SUMMARY OF STATUS REPORT

While plains bison were once widespread throughout the Canadian Plains region, today there are only three free-ranging, one semi-wild, and four captive display populations of plains bison in Canada. One of the free-ranging herds is in traditional wood bison habitat, and the other two are located in transition zones between wood and plains bison habitat. None are in typical traditional plains bison prairie habitat of open grassland. The total number of mature free-ranging Canadian plains bison is between 670 and 740 animals, occupying a range of approximately 2750-3000 km^2. The four captive display herds and the semi-wild herd are managed at a specific population size. The Prince Albert National Park population is increasing in size, but expansion of the herd range beyond the park boundaries is limited by agricultural land. The population on the Cold Lake/ Primrose Air Weapons Range in northwestern Saskatchewan may also be increasing in size, but the increase may be limited by recent agreements that permit hunting of this population by the Cold Lake First Nations. In general, little is known about the Cold Lake/Primrose Air Weapons Range herd, including total range area and precise population size. The other plains bison populations are relatively constant in size. Most of the range occupied by plains bison in Canada is currently protected, although hunting is permitted to some extent on each of the free-ranging herds. Under current management strategies, no decline in range size is expected. The small size of the herd on the Cold Lake/Primrose Air Weapons Range may be a concern. However, at the moment, none of the populations are in imminent risk of extinction. The small number of founders for the populations in Prince Albert National Park and Cold Lake/Primrose Air Weapons Range likely reduced the genetic diversity of these herds. Efforts should be made to ensure that genetic pollution through hybridization with either cattle or ranched bison does not occur. To date, only one of the Canadian plains bison populations (Elk Island National Park) has been examined for the presence of cattle mitochondrial DNA. Currently, the greatest threat to the conservation of plains bison in Canada is a lack of available habitat, as large portions of the original range have been lost to agricultural and urban development.

TECHNICAL SUMMARY

Bison bison bison

Plains bison (English), bison des prairies (French)
Range of Occurrence in Canada: British Columbia, Alberta, Saskatchewan, Manitoba

Extent and Area Information	
• *Extent of occurrence (EO)(km²)* **[Based on observations]**	2750-3000 km^2
• *Specify trend in EO*	Stable
• *Are there extreme fluctuations in EO?*	No
• *Area of occupancy (AO) (km²)* **[Based on observations – same as EO because there are no large areas of unused habitat]**	2750-3000 km^2
• *Specify trend in AO*	Stable
• *Are there extreme fluctuations in AO?*	No
• *Number of known or inferred current locations*	4 (3 free-ranging)
• *Specify trend in #*	Stable
• *Are there extreme fluctuations in number of locations?*	No
• *Specify trend in area, extent or quality of habitat*	Stable
Population Information	
• *Generation time (average age of parents in the population)*	9 years
• *Number of mature individuals*	670-740 in free-ranging populations, 250-270 semi-captive in Elk Island Park
• *Total population trend:*	Stable
• *% decline over the last/next 10 years or 3 generations.*	Minimal
• *Are there extreme fluctuations in number of mature individuals?*	No
• *Is the total population severely fragmented?*	Yes
• *Specify trend in number of populations*	Stable
• *Are there extreme fluctuations in number of populations?*	No
• List populations with number of mature individuals in each: • *Elk Island National Park, Alberta* 250-270 (enclosed) • *Pink Mountain, British Columbia 450* • *Prince Albert National Park, Saskatchewan* 175-220 • Cold Lake/Primrose Air Weapons Range, Saskatchewan 45-70	
Threats (actual or imminent threats to populations or habitats)	
- Lack of habitat - The presence of cattle-bison hybrids in some US herds - Potential lack of genetic diversity - Lack of intergovernmental consensus in existing protection - Potential conflicts with game ranching, and genetic pollution from ranched bison - Potential for domestic animals to act as disease reservoirs	

Rescue Effect (immigration from an outside source)	
• *Status of outside population(s)?* **USA: N4** [IUCN: Lower Risk, conservation dependent]	
• *Is immigration known or possible?*	No
• *Would immigrants be adapted to survive in Canada?*	Yes
• *Is there sufficient habitat for immigrants in Canada?*	Very little
• *Is rescue from outside populations likely?*	No
Quantitative Analysis [provide details on calculation, source(s) of data, models, etc]	Not available
Current Status	

Status and Reasons for Designation

Status: Threatened	**Alpha-numeric code:** **D1 + 2**

Reasons for Designation:

There are currently about 700 mature bison of this subspecies in three free-ranging herds and about 250 semi-captive mature bison in Elk Island National Park. The largest free-ranging herd, in the Pink Mountain area of BC, is outside the historical range of this subspecies. The population in Prince Albert National Park is increasing by about 10% a year. The greatest problem facing these bison in Canada is the lack of habitat, due to conversion to agriculture and urbanization. Additional threats include domestic cattle disease and the risk of genetic pollution from escaped ranched bison, including some that may carry cattle genes. The total number of free-ranging and semi-captive mature bison of this subspecies is just under 1000, and there are fewer than 5 populations**.**

Applicability of Criteria

Criterion A (Declining Total Population): The Canadian population has increased over the last 3 generations.

Criterion B (Small Distribution, and Decline or Fluctuation): The extent of occurrence is less than 5000 km^2 and there are fewer than 5 populations, but there is no evidence of continuing decline. The area of occupancy is more than 2000 km^2, and although there are fewer than 10 populations, there is no strong evidence of a recent decline in numbers.

Criterion C (Small Total Population Size and Decline): Although there are much fewer than 2500 mature individuals, there is no strong evidence of a recent or expected decline in numbers.

Criterion D (Very Small Population or Restricted Distribution): Threatened: there are fewer than 1000 mature individuals in Canada, and fewer than 5 populations.

Criterion E (Quantitative Analysis): Not available

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In 2001, Greg was awarded a doctorate for his thesis, entitled 'The Population Genetics of Wood and Plains Bison'. Research for this thesis was begun in 1996 with Dr. Curtis Strobeck at the University of Alberta. During the course of this research, Greg gained a great deal of knowledge about a number of taxonomic and ecological

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Keri Zittlau

Keri is currently completing her doctoral research on the population genetics of North American caribou. During the five years of her Ph.D. program, she has gained substantial knowledge of the taxonomy of North American ungulates as well as the genetic constitution of many wildlife populations. Through her research she has become very familiar with conservation issues of threatened and endangered wildlife in Canada. She has also worked with Greg Wilson on a number of bison projects, including establishing a breeding strategy for the wood bison herd at the Hook Lake Wood Bison Recovery Project, Fort Resolution, NWT.

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Appendix 1. Taxonomic review of all extant North American bison

Until the late 1800s, North American bison were considered to belong to a single subspecies, although most inhabitants of the region recognized a distinction between wood and plains bison. In their reviews of the genus *Bison*, Allen (1876) and Hornaday (1889) each described morphological and behavioural differences between what are now known as wood and plains bison (from Geist 1991). In 1897, Rhoads defined wood bison (*B. b. athabascae*) as a subspecies separate from plains bison (*B. b. bison*).

The taxonomic status of various groups can affect the amount of effort put towards their conservation. It may be more important to conserve groups that are more distantly related than those that are in the same taxonomic unit. As a consequence, a review of the taxonomy of extant bison in Canada is included in this report. The debate over the subspecific designation of plains (*Bison bison bison* Linnaeus 1758) and wood bison has raged for almost as long as European settlers have known of the existence of bison in northern Canada. This deliberation became more complicated with the 1920s introduction of plains bison to a region inhabited by the last remaining wood bison and subsequent hybridization of the two groups. Another reason for contention is the lack of morphological studies performed on "pure" wood bison, before the hybridization took place. The subsequent sections outline the history of wood bison, early reports on the potential existence of subspecies within this species, and any pertinent morphological, molecular, and ecological information that may aid in determining the validity of the subspecific descriptors. Photographs of plains and wood bison from Elk Island National Park can be viewed in Figures 1A and B, respectively.

A brief history of *Bison bison athabascae*

Evolution of modern North American bison

A number of theories exist on the evolution of modern North American bison (*Bison bison*). For the most part, they have little to add of relevance to a discussion of extant bison taxonomy, and will only be discussed briefly here. One popular theory is that *B. bison* is derived solely from the ancestor of *B. bonasus*, a forest bison of the east Siberian fauna that spread into North America relatively late across Beringia (Geist and Karsten 1977). A second theory is that the species *B. bison* is the descendant of *B. b. occidentalis*, which itself is the result of a hybridization event between *B. priscus*, a relatively recent arrival from Beringia, and a southern form (*B. antiquus*) (van Zyll de Jong 1986). Both of these theories suggest that modern North American bison then moved into the expanding grasslands, and continued evolving into *B. b. bison*. As such, *B. b. bison* is the most derived form, and *B. b. athabascae,* which continued to live in more Pleistocene-like conditions, should be less divergent from the ancestral state (Geist and Karsten 1977; Guthrie 1980; van Zyll de Jong 1986). Both of these theories of bison evolution agree that modern North American bison is a relatively recent evolutionary product, coming into existence about 4000 to 5000 Y.B.P. (Wilson 1980; McDonald 1981). From an evolutionary perspective, this is a very short time period, and likely exacerbates the difficulty of detecting differentiation and obtaining

monophyletic trees from morphological and genetic data for these two subspecies (see Appendix 1: Molecular Research section).

The hybridization of wood and plains bison

The number of wood bison historically occurring in northern Canada and Alaska is unknown. Soper (1941) estimated that the carrying capacity of their range was well over 100 000 in 1800, but predation and hunting pressures could have kept the population at lower levels. During the late 19th century, wood bison, like their plains brethren, underwent a precipitous decline in numbers to a single population of approximately 250 to 500 individuals (Seton 1911; Soper 1941). An effort was made to conserve the declining numbers of wood bison by the Canadian government with the passing of the Buffalo Protection Act in 1877 (Hewitt 1921). However, this Act was repealed a year later (MacEwan 1995). The wood bison population began to increase, and by 1922 it had reached a size of approximately 1500 (Graham 1923). At that time, Wood Buffalo National Park was created in the Northwest Territories and Alberta to protect the habitat of this wood bison population and for the preservation of this distinct subspecies (Lothian 1976; Lothian 1979).

About that time, the plains bison population at Buffalo National Park, Wainwright, Alberta, was experiencing overcrowding (see A History of the Plains Bison Populations After 1870 section). A decision was made to ship a number of the plains bison from this area to Wood Buffalo National Park as a more publicly acceptable solution to the excess plains bison problem (Graham 1924). This movement of plains bison into the historic range of wood bison was seriously challenged by the American Society of Mammalogists (Howell 1925) and by other biologists (Harper 1925; Saunders 1925), due in part to the risks of hybridization between these groups and the spread of tuberculosis in the wood bison herds (Lothian 1981). Nevertheless, commencing in 1925 and continuing for four years, a total of 6673 plains bison (332 three-year-olds, 1515 two-year-olds, and 4826 yearlings), the majority of which were female, were taken by railway to Waterways, Alberta, and from there by scow down the Athabasca, Rocher, and Slave Rivers (Soper 1941). These animals were then released at several localities along the west bank of the Slave River into the range of the wood bison population (Reynolds 1991).

By 1934, the population at Wood Buffalo National Park had increased to 12000 individuals (Soper 1941). Unfortunately, the original wood bison and plains bison introduced to the park were breeding with one another (van Zyll de Jong 1986; Polziehn *et al*. 1996). As a result, apart from skeletal remains, any further studies of pure wood bison were impossible at that point. The intermingling of wood and plains bison had the added disadvantage of introducing brucellosis and tuberculosis into Wood Buffalo National Park from the Buffalo National Park plains bison (Ogilvie 1979). The proportion of the wood and plains bison genome present in the Wood Buffalo National Park bison is unknown. Soper (1941) predicted that the wood bison strain made up 10 to 15% of the total. This value may be based on the estimated number of wood bison in the park (1500, Graham 1923), when the 6673 plains bison were introduced. However,

there are reasons to doubt this percentage. Due to the crowded conditions of the barges and the fact that the plains bison were placed in unfamiliar territory inhabited by wolves, a main predator of bison with which they had no experience, as many as 50% of those animals may not have been successfully introduced to Wood Buffalo National Park (Carbyn *et al*. 1993). Also, as the introduced animals were young, it is unlikely that many of the male plains bison could outcompete the larger, more mature wood bison for mates (van Zyll de Jong 1986; Carbyn *et al*. 1993). The likely lack of reproductive success in male plains bison introduced to Wood Buffalo National Park, combined with the female-biased sex ratio, ensured that most of the introgression of plains bison genetic material into the Wood Buffalo National Park population would be female-mediated. van Zyll de Jong (1986) used morphological analyses to attempt to quantify the introgression of plains bison genes into Wood Buffalo National Park, and obtained a value of approximately 5%.

By 1957, pure wood bison had essentially vanished from Wood Buffalo National Park (Fuller 1957). However, at that time a herd of about 200 animals was found in what was thought to be an inaccessible region of the northwest corner of the park, near the Nyarling River. Original reports stated that there were no travel lines between this area and other sections of the Park (Fuller 1957), and the terrain between the northwest corner and the rest of the Park was thought to be inhospitable and unproductive (Banfield and Novakowski 1960; Calef and Van Camp 1987). A comparison of five specimens from this region with wood bison samples taken before the introduction suggested that the bison in the Nyarling River area were morphologically representative of original wood bison, on the basis of large body sizes, pelage characteristics, and skull measurements (Banfield and Novakowski 1960). Sixteen of these bison were used to found a population in the Mackenzie Bison Sanctuary, Northwest Territories, in 1963. In 1965, another population of Nyarling River bison was established with 21 animals, this time at Elk Island National Park, Alberta.

Most current evidence suggests that the bison used to found the Mackenzie Bison Sanctuary and Elk Island National Park were not pure wood bison, but had been in contact with the hybrids existing in the rest of Wood Buffalo National Park. This terrain may not have been as inhospitable as originally thought. A 1957 distribution map of bison from aerial photographs showed small pockets of animals throughout the northern portion of the park (Van Camp 1989). Soper (1941) details a conversation with Sousi Marie of the Salt River Settlement, stating that as early as 1929 he saw Wainwright buffalo in the northern areas of the park, and that animal trails did exist into the Nyarling River area. Brucellosis and tuberculosis, introduced into Wood Buffalo National Park by the Buffalo National Park animals, were present in the Nyarling River animals, and the founders of the Elk Island National Park population (van Zyll de Jong 1986; Van Camp 1989). A study of cranial and post-cranial elements suggested that the bison originating from Nyarling River were similar to pure wood bison, but there was evidence that the level of hybridization with plains bison was approximately 5% (van Zyll de Jong 1986). Genetic evidence also supports the hybridization of the Nyarling River bison before Mackenzie Bison Sanctuary and Elk Island National Park were founded (Polziehn *et al*. 1996; Wilson and Strobeck 1999).

As a result of the introduction of plains bison from the Buffalo National Park to Wood Buffalo National Park, no pure wood bison exist today. All modern-day wood bison contain varying degrees of plains bison genetic material. This is especially unfortunate, in that only a few scientific studies of wood bison morphology and ecology were performed prior to the hybridization. However, some attempts have been made to resolve the taxonomy of extant bison, and their results are discussed below. For the purposes of this report, "pure wood bison" will refer to northern bison that were born before the introduction of plains animals in 1925. "Wood bison" will refer to northern bison that were born subsequent to the introduction and constitute modern-day wood bison, and wood and plains bison will continue to be referred to as subspecies.

Early reports on taxonomy

As mentioned, due to the hybridization of wood and plains bison in Wood Buffalo National Park, no living pure wood bison are available for taxonomic study. Exacerbating this problem is the fact that the external characteristics of pure wood bison were poorly documented. No high quality illustrations or photographs of wood bison made prior to 1925 appear to exist (van Zyll de Jong 1986; Geist 1991). A few museum skins exist from which pelage characteristics can be ascertained, and some skeletal remains are available, but descriptions by early settlers and Aboriginal Peoples are the primary tools available for a comparison of plains and pure wood bison. Furthermore, another difficulty is that few people were familiar with both subspecies.

Rhoads (1897) cites Sir John Richardson as providing the first description of a distinct form of wood bison, in his book "Fauna Boreali Americana", 1829. Within, he states that bison inhabiting wooded areas generally occur in smaller groups than those inhabiting plains regions, but are individually of larger size. In an 1858 report to the Legislative Assembly, Hind (in Roe 1970) states that hunters in the north describe wood bison as being different from plains bison in their size, colour, horns, and hair. He states that the wood bison exists exclusively in wooded areas, while the plains bison avoid such areas during the summer. It is unclear whether Hind believes in the existence of a distinct subspecies of wood bison (Rhoads 1897; Roe 1970).

Another early reporter on wood bison is Butler (1873). He states "it is still a matter of dispute whether the wood-buffalo is the same species as his namesake of the southern plains; but it is generally believed by the Indians that he is of a kindred race" (Butler 1873: 211). He describes wood bison as being larger, darker, and more wild, or shy. Butler is also impressed with the different habits of wood and plains bison, especially in the choice of habitat, where wood bison prefer thickly wooded areas, even if open prairies are available. Seton also described wood bison as different. Rhoads (1897) cites Seton as stating that the Aboriginal Peoples in the Peace River area, and an employee of the Hudson Bay Co. in the same area, felt that wood bison were a distinct species, and did not mix with plains bison. He was among the first to accept the subspecific designation of wood bison, describing them as being larger, and darker than plains bison with dense, silky hair and long, slender horns (Seton 1927).

Allen (1876, in Rhoads 1897; Geist 1991) did not recognize wood bison as a distinct subspecies of *Bison bison*, mainly due to some contradictory reports on its external characteristics. However, Allen did acknowledge the possibility that wood bison could theoretically exist. This opinion was also held by Hornaday in 1889, one of the leading authorities of bison, who felt that wood bison as a subspecies did not exist (Rhoads 1897; Roe 1970). However, from his experience with plains bison, and contrary to most reports at the time, Hornaday felt that plains bison would be the largest of the subspecies, and subsequently derived a theory for the potential smaller size of wood bison (Rhoads 1897; Roe 1970). Even before the description of wood bison as a subspecies, there was already debate on whether the external characteristics were caused by differences in genetics or the environment. Pike (1892) found the distinctions between wood and plains bison to be slight, and attributed them to differences in habitat, food quality, and climatic influences.

Rhoads (1897) reprints a letter by Mr. Moberly of the Hudson Bay Co. that addresses questions about the existence of wood bison. Moberly felt that wood bison were different than plains bison, and described them as being larger and longer limbed, with long, straight horns and long, silky fur. He felt the wood bison engaged in more browsing than grazing, and stated that wood and plains bison herds often meet, but never mix.

In a summary of early descriptions of wood bison, Roe (1970) notes that most observers portrayed them as being larger, darker, more shy, and non-migratory. However, he does not take the potential effects of seasonal differences into account on these descriptions (Geist 1991). Roe (1970) cites two further lines of evidence to support the distinction of wood and plains bison. First, he notes that early observers of wood bison never doubted which subspecies they were looking at. If interbreeding between the forms was common, there should have been reports of hybrid-looking animals. Second, Roe (1970) mentions that the Assiniboine have different names for wood (cha-tatanga) and plains (sena-tatanga) bison. Seton (1927) also mentioned different names Aboriginal Peoples have for wood (Ah-tuk-ard Moos-toosh) and plains (Mas-kootay Moos-toosh) bison. He did not specifically mention the band to which he was referring, but Roe (1970) felt it was either Chippewyan or Cree.

Rhoads (1897), a strong proponent of the differences between wood and plains bison, was the first to officially recognize *Bison bison athabascae* Rhoads 1897. The official description of this subspecies was “size larger, colors darker, horns slenderer, much longer and more incurved and hair more dense and silky than in *B. bison*”. He felt that these characteristics, along with the “opinions of many hunters and travelers”, were enough to warrant subspecific status. Unfortunately, Rhoads (1897) based his description of wood bison on a second-hand report of a single stuffed specimen in a sealed glass case (van Zyll de Jong 1986; Geist 1991).

Morphological studies

The first study that measured morphological traits of wood and plains bison functioned as a preliminary revision of the genus (Skinner and Kaisen 1947). In this examination of male horn-core and cranial characteristics of skulls from extant and extinct bison, Skinner and Kaisen (1947) described a number of differences in the means and ranges of these measurements between wood and plains bison. Of all bison examined, plains bison were found to be the smallest. They described the horn cores as being "small in size; length on upper curve seldom exceeding basal circumference or cranial width between horn-cores and orbits, subcircular in basal cross section; posteriorly directed with respect to longitudinal axis of skull and extending posterior to occipital plane; distal tips posteriorly twisted and pointed, superior longitudinal groove weak or missing, tips tending to be most posteriorly direct of bison, seldom rising high above the plane of the frontals and seldom strongly depressed, curvature varying from nearly straight to recurved … frontals flat to arched; cranium moderate" (Skinner and Kaisen 1947: 161). Wood bison were described as being similar, except with a larger skull, broader cranium, and larger and stubbier horn cores. They describe wood and plains bison as being closely related, but distinct subspecies. However, they considered this work preliminary, as they were only able to examine nine skulls from pure wood bison. It is also worth noting that the largest plains bison skulls they examined were larger than the smallest wood bison skulls. They also could not differentiate wood and plains bison based on dentition. A later study of three pure wood bison skulls observed measurements smaller than the minimum and larger than the maximum described by Skinner and Kaisen (Bayrock and Hillerud 1964). van Zyll de Jong (1986) also observed an overlap in skull measurements between adult wood and plains bison.

There is some concern about the use of horn cores - a secondary sexual characteristic - for comparisons between groups, as these characteristics may be more likely to show high inter-population variance due to environmental differences (Guthrie 1966). In an attempt to determine the potential for inter-population variance in horn core measurements, Shackleton *et al*. (1975) examined 157 plains bison skulls from Elk Island National Park. They found that horn core measurements had the highest variance of all measurements performed. They concluded that, as a result, basing taxonomic differentiation on horn core measurements might not be ideal. However, the plains skulls they examined were still generally smaller than those described by Skinner and Kaisen (1947). This study was intended to be preliminary, and they felt that the investigation of more wood and plains skulls would aid in determining whether a taxonomic differentiation on horn core measurements is justified (Shackleton *et al*. 1975).

Geist and Karsten (1977) performed a recent examination of external morphological characteristics, upon which most conservation efforts have been placed. On a single day in the fall of 1975, they examined 18 adult wood bison, eight of which were bulls, and an undetermined number of plains bison at Elk Island National Park. These "wood bison" were hybrids from Wood Buffalo National Park. They listed the

following ways in which wood bison bulls differed from plains bison bulls: the beard of the wood bison is smaller, shorter, and more sharply pointed; the hair on top of the head is shorter and less dense; the mane is very short; hair on the shoulders, rump, and neck is shorter and darker, blending in more with the hair on the rest of the body; the chaps, or long hair on the forelegs, are absent; the tail is longer, with more hair; the penis tuft is shorter and thinner; the line of the back from the top of the hump to the tail is more angled than in plains bison (Geist and Karsten 1977). Wood bison were also found to be less sexually dimorphic than plains bison, which was explained as an adaptation to their differing environments. As these differences were deemed at least as great as those between black-tailed deer (*Odocoileus hemionus columbianus*) and mule deer (*Odocoileus hemionus hemionus*), and greater than those between Rocky Mountain bighorn (*Ovis canadensis canadensis*) and desert bighorn (*Ovis canadensis nelsoni*), they felt that a subspecific differentiation between wood and plains bison was justified. A subsequent study suggested that the difference in cape colour and tail lengths were not as noticeable as described herein (van Zyll de Jong 1986).

A morphometric study based on 528 skulls, 143 mandibles, 36 post-cranial skeletons, skins, fresh carcasses and live animals was performed by van Zyll de Jong (1986). This study encompassed plains bison, hybrids, a small number of pure wood bison, and some extinct bison species, and tried to address whether wood bison were historically a legitimate subspecies, and if any pure wood bison still existed. Seven to eleven craniometric measurements and 15 mandibular morphometric analyses both suggested that these traits varied clinally north to south, but that a morphological discontinuity existed at approximately the grassland – boreal forest ecotone of the Canadian Plains and the Peace River, where the two groups likely came into occasional contact. The discontinuity of skull size and shape was suggested to support subspecific differentiation. Multivariate craniometric comparisons between pure wood bison and plains bison revealed that they both formed monophyletic groups, further supporting their differentiation. In the craniometric analyses, morphometric analyses of mandibles and post-cranial skeletal elements, and the comparison of external characteristics, hybrid bison usually appeared to be intermediate between wood and plains bison, but more similar to the former. This supports the theory that wood and plains bison in Wood Buffalo National Park did mix before the discovery of the supposedly pure wood bison in the Nyarling River area (see Hybridization of Wood and Plains Bison section). van Zyll de Jong (1986) also examined the possibility that the differences between wood and plains bison had an ecophenotypic, and not genetic, basis. He found only slight differences between the samples obtained from Elk Island National Park and Mackenzie Bison Sanctuary, despite the fact that these populations had existed in quite different environments for about 15 years. Also, differences between the wood and plains bison at Elk Island National Park were significant, despite the presence of these herds in nearly identical environmental conditions. van Zyll de Jong (1986) estimated that the level of introgression of plains bison genetic material into modern-day wood bison was approximately 5%.

Geist (1991) has become the most outspoken opponent of taxonomic differentiation in bison. His main concern was that wood bison have primarily been

defined by differences in size and pelage features - two characteristics that may vary with environmental differences - and therefore are a result of environmental, and not genetic, differences. This opinion was also held by others (see for ex. McHugh 1972; Berger and Peacock 1988). Geist felt that the size differences described by Rhoads (1897) may be due to the fact that wood bison lived in higher latitudes, and plains bison were smaller due to the cost of migration. He also considers the 10% difference in size, or 33% difference in mass, to be taxonomically meaningless. Unlike van Zyll de Jong (1986), Geist felt that the hybrids at Elk Island National Park and Mackenzie Bison Sanctuary were phenotypically distinct, which he attributed to the differing environments, and furthered his claim of wood bison being ecotypes. Old age and poor nutrition may bring about changes in the display hair of bison, resulting in wood bison-like pelage. Geist (1991) stated that the wood bison at Elk Island National Park, unlike the plains bison in the same park, undergo episodes of poor nutrition after the shedding of their winter hair, resulting in the reduced display pelage seen in these animals. If these animals were placed on superior food during this time, they would grow a plains bison-like, or normal, coat. The finding that a number of wood bison raised in zoos develop plains bison-like pelage backs up this claim. Geist (1991) also contended that the morphological differences between wood and plains bison at Elk Island National Park are due to the differences in density between the wood and plains bison populations, where the plains bison live in a dense population and also face higher competition for resources from elk (*Cervus elaphus*), resulting in their smaller size. In an examination of hump shape, Geist (1991) found that it was not consistent within wood and plains bison, and suggested that when held under identical conditions, they would converge in hump shape. Geist felt that the differences between wood and plains bison, if any, were much less than those described by van Zyll de Jong (1986).

Bison pelage characteristics can vary with age, gender, and season. However, males of the same age, when viewed during the same season, show consistent differences in their pelage, although there is some variability in these traits (W. Olson, pers. com., 2003). The density of wood and plains bison at Elk Island National Park has varied considerably through time. Plains bison numbered over 2500 in 1935, and have since been managed at a level of about 450 (Blyth and Hudson 1987; Olson 2002; Cool 2003). Wood bison started at a population size of about 20, and have since increased to about 400 animals (Olson 2002). Data collected for the population over this time has revealed little change in body mass, suggesting that there may in fact be a genetic basis for the differences in mass between wood and plains bison (Olson 2002; Olson, pers. com., 2003; Reynolds *et al*. 2003). Also, the claim that plains bison are more dense than wood bison seems unfounded given that, at the time of Geist's (1991) publication, plains bison and elk numbered around 450 and 800, respectively, on 136 km^2 of the main area of the park (densities of 3.31/km^2 and 5.88/km^2), while 350 wood bison (5.93/km^2) and 400 elk (6.78/km^2) inhabited the 59 km^2 of the wood bison area (Blyth and Hudson 1987; Olson 2002; Cool 2003). Wardens at Elk Island National Park do not believe that there is a difference in forage quality available to wood and plains bison in the spring, when they are replacing their winter hair (W. Olson, pers. com., 2003). Furthermore, prescribed fires could cause another potential difference between forage qualities in the two areas. There have been significantly more prescribed fires on the

plains bison range, which should have increased the forage quality of this area (N. Cool, pers. com., 2003). Despite this potential increase in range quality, plains bison are still smaller than wood bison.

van Zyll de Jong *et al*. (1995) expounded on the original study by van Zyll de Jong (1986), by obtaining observations of living animals from Wood Buffalo National Park, and a number of plains bison populations. One of the main purposes of this study was to determine whether the observed morphological distinctions between wood and plains bison were ecotypic, or were true genetic differences. As such, populations with similar genetic backgrounds existing in widely differing environmental conditions were included in the analyses. These populations were: plains bison from National Bison Range, Montana with their sister population transplanted to Alaska in 1928, currently residing in traditional wood bison range under boreal conditions; and wood bison from Mackenzie Bison Sanctuary with their sister population in Elk Island National Park, currently residing in traditional plains bison habitat. Bison at the National Bison Range are managed intensively, and live in temperate grassland-open forest, while the Alaskan plains bison are free-roaming in boreal forest. They found that the plains bison populations at the National Bison Range and Alaska were not significantly phenotypically different despite existing for greater than 60 years in these widely differing environments. Similarly, wood bison at Elk Island National Park and Mackenzie Sanctuary were not morphologically significantly different, despite the Elk Island National Park animals being semi-wild in temperate, aspen parkland while the Mackenzie Bison Sanctuary animals are free-roaming, subject to predation and exist in boreal and subarctic woodlands. The hump shape of wood and plains bison at Elk Island National Park was found not to have converged, despite existing in similar habitats for about 30 years. These findings suggest that there is a genetic difference responsible for the morphological distinctions between wood and plains bison, and that these differences result from a past morphological discontinuity between these two subspecies.

van Zyll de Jong *et al*. (1995) also examined morphological differences between the subpopulations in Wood Buffalo National Park to determine whether animals in some regions were more similar to pure wood bison. Pine Lake, the subpopulation closest to the introduction sites of plains bison from 1925-1928, was found to be the most plains bison-like. This population was morphologically closer to plains bison populations than to other wood bison subpopulations occurring within the same park. This suggests that there was no free interchange of genetic material within Wood Buffalo National Park after the introduction of plains bison. The Hook Lake region, located northeast of Wood Buffalo National Park, was thought to also potentially contain relatively pure wood bison, as the terrain between the two areas is fairly inhospitable (Van Camp 1989). Genetic studies have shown that the Pine Lake subpopulation is significantly different from other populations in the park, but that genetic differentiation between all areas of the park, including the Hook Lake region, is small (Wilson and Strobeck 1999; Wilson 2001). As such, there should be no region in Wood Buffalo National Park free of genetic input from plains bison.

Chromosomal Studies

A chromosome-level study also attempted to differentiate between wood and plains bison (Ying and Peden 1977). Karyotypes of both subspecies were compared, and each was characterized by a diploid number of 60 chromosomes. Twenty of these chromosomes plus the sex chromosomes were homologous. However, due to problems with obtaining viewable karyotypes, nine chromosomes could not be compared. It is not surprising that wood and plains bison both had similar karyotypes, as bison and domestic cattle also have identical karyotypes, with minor differences in the sex chromosomes (Bhambhani and Kuspira 1969).

Molecular studies

Using hemolytic (blood typing) tests with 13 different reagents belonging to six different systems, and carbonic anhydrase, polymorphism was examined in the wood and plains bison from Elk Island National Park, Wood Buffalo National Park, and two other plains bison populations (Peden and Kraay 1979). 78% of the wood bison from Elk Island National Park were characterized as being most similar to that same population, suggesting that the Elk Island National Park wood bison population was significantly different from the other populations. However, each of the other herds was also significantly different from one another. If subspecific status were awarded on these results alone, then each sampled population would constitute its own subspecies. The differences between the subspecies were not more significant than those observed among plains bison populations. The wood and plains bison populations at Elk Island National Park and Wood Buffalo National Park formed a group distinct from the other sampled plains bison populations. The results are not surprising given the number of individuals from Buffalo National Park, a sister population to the plains bison at Elk Island National Park, that were introduced to Wood Buffalo National Park (see Hybridization of Wood and Plains Bison section). It is likely that the wood bison populations would be more distinct had this hybridization not occurred.

Restriction fragment length polymorphism (RFLP) studies of four nuclear genes in the wood and plains bison populations at Elk Island National Park have also been performed (Bork *et al*. 1991). Of the 28 fragments identified in this study, two were polymorphic. The two alleles at fragment E had frequencies of 0.75 and 0.25 in wood bison and 0.20 and 0.80 in plains bison, while the two alleles at fragment S had frequencies of 0.85 and 0.15 in wood bison, and 0.50 and 0.50 in plains bison, showing that these two populations were significantly different. The number of net nucleotide substitutions between the two populations was estimated at 0.0007, which is indicative of recent divergence. This suggests that the two populations show differences at a level one would expect for geographically isolated populations. Again, it is possible that these two populations would be more distinct had the hybridization at Wood Buffalo National Park not occurred.

A study of the mitochondrial haplotypes of 269 bison from nine populations using RFLPs has also been completed (Polziehn *et al*. 1996). It should be noted that, while

nuclear DNA is inherited biparentally, mitochondrial DNA is inherited solely through maternal lines. Twelve variable sites were examined, constituting eleven unique haplotypes. The most parsimonious phylogenetic tree designed from these haplotypes shows that plains bison form a paraphyletic group, and wood bison form a polyphyletic group. Since neither subspecies forms a monophyletic group on this tree, where all individuals of a subspecies are derived from a single lineage, this study concluded that neither group is a well-defined taxon. The Wood Buffalo National Park population was the most variable of all populations examined. Of the eleven identified haplotypes, four were unique to wood bison and four were shared between wood and plains bison. The presence of unique haplotypes lends support to the recent divergence of these two subspecies. There are two possible explanations for the existence of shared and unique haplotypes. First, wood bison could have been historically separated from plains bison, resulting in genetic divergence and unique haplotypes. Under this scenario, wood and plains bison would be accepted historic subspecies. The shared haplotypes would then be a result of the hybridization between wood and plains bison. The second possibility is that there was enough gene flow between historic wood and plains populations that most haplotypes were shared between the two groups. Haplotypes not detected within wood or plains bison may in fact be present, but at low frequencies. Under this scenario, wood and plains bison do not make good subspecies. Unfortunately, as no data is available for genetic samples of wood bison obtained before the hybridization, it is not currently possible to determine which of these scenarios is more likely. Also, genetic samples obtained from Wood Buffalo National Park, the wood bison at Elk Island National Park, and Mackenzie Bison Sanctuary were very similar, which further suggests that these three populations have a common gene pool, and that hybridization occurred before the establishment of the latter two populations.

Further comment is warranted on the use of mitochondrial DNA for phylogenetic studies of the relationship between wood and plains bison. As previously mentioned, the sex ratio was highly skewed towards females in the plains bison introduced to Wood Buffalo National Park and it is unlikely that many of the male plains bison were able to reproduce for several years (see Hybridization of Wood and Plains Bison section). As a consequence, a study of mitochondrial DNA may not be indicative of the proportion of plains bison nuclear material present in Wood Buffalo National Park animals, due to its maternally inherited nature. Also, the use of monophyletic trees to define subspecific status may be unreasonable in this case. Haplotypic monophyletic trees are not expected to occur before $4N_e$ generations have passed, where N_e is the effective size of the population through time. A reasonable estimate of generation time in bison is five years (Gates *et al.* 2001). If a separation time of 5000 years for wood and plains bison is used (Wilson 1980; McDonald 1981), N_e would have to be less than 250 over this time period before a monophyletic tree would be expected. Up until the 20th century, wood bison may have numbered over 100 000 (Soper 1941), which makes it doubtful these two groups would be monophyletic. This also assumes that there is no gene flow between populations, so the hybridization of wood and plains bison would make it extremely unlikely current wood and plains bison populations would be monophyletic. Phylogenies developed from mitochondrial DNA data have been discordant with

species relationship in some deer (*Odocoileus*) species (Carr *et al*. 1986; Cronin *et al*. 1988). Mitochondrial DNA functions as a single locus, and the phylogeny of a single locus may differ from that of the species, or that derived from multiple nuclear loci (Pamilo and Nei 1988; Dowling and Brown 1989). Mitochondrial and nuclear DNA have been found to vary in their divergence within both Cervinae and Odocoileinae (Cronin 1991).

The most recent studies of divergence between wood and plains bison have made use of microsatellites (Wilson and Strobeck 1999; Wilson 2001). Microsatellites are highly variable and occur throughout the nuclear genome. Wilson and Strobeck (1999) examined the relationships between eleven North American bison populations, including Mackenzie Bison Sanctuary, wood and plains bison from Elk Island National Park, and Wood Buffalo National Park with eleven microsatellite loci. Each population examined was found to be distinct, so this alone cannot be used to define subspecies. However, genetic distances between wood and plains bison populations were larger than those within either of the two subspecies. This was not surprising, given that animals from Wood Buffalo National Park founded Mackenzie Bison Sanctuary and Elk Island National Park. The strong grouping of these three populations suggests that they are functioning as entities distinct from plains bison, and should be managed as such. It is also evidence that all three populations contain hybrid animals. Wood bison would likely have been more distinct had the hybridization event not occurred. An assignment test was also performed on the animals in these populations. With this test, each animal's genotype is compared to the allele frequencies in each population, and each animal is assigned to the population it is most likely derived from. Of the 370 individuals examined, only five (1.4%) were assigned to the incorrect subspecies. These were all individuals from Wood Buffalo National Park that were assigned to various plains bison populations. This is further evidence that the wood and plains bison genomes are currently genetically distinct. After the incorporation of additional individuals from the Hook Lake region (located just northeast of Wood Buffalo National Park; Wilson 2001) and the Hook Lake Wood Bison Recovery Project (Nishi *et al*. 2001; Wilson *et al*. 2002a) only four of the 258 wood bison examined (three from Wood Buffalo National Park and one from the Hook Lake region) were incorrectly assigned to plains bison populations. The Wood Buffalo National Park and Hook Lake region populations were found to be genetically similar, suggesting that the Hook Lake animals also hybridized with plains bison (contrary to Van Camp 1989).

Behavioural ecology

The key difference between wood and plains bison is their choice of habitat. However, it is difficult to prove whether differences in habitat use are an ecotypic response to environmental variation or due to underlying genetic differentiation. Wood bison prefer the northern forests and woodlands, where open areas are smaller and more scattered, while plains bison prefer open areas of the Great Plains (Geist and Karsten 1977). As a result, wood bison originally ranged across northern Alberta, Saskatchewan, and British Columbia, and portions of Alaska, the Yukon, and the Northwest Territories (Stephenson *et al*. 2001). Plains bison ranged across the

southern Prairie Provinces, and most of the United States east of the Rocky Mountains (Figure 2).

A potential difference in the behaviour of wood and plains bison is the undertaking of annual migrations. While it is debatable whether plains bison participated in a predictable migration each year (see Movements/Dispersal section), there is little doubt that the large herds of plains bison underwent frequent movements (Roe 1970; Moodie and Ray 1976). Wood bison, on the other hand, seemed to remain in their own habitat, either not migrating or migrating at an insignificant scale (MacEwan 1995). The seasonal movements of plains bison may have helped maintain the distinctiveness of the subspecies, as the plains bison moved south in spring away from possible contact with resident wood bison before the rutting season, thereby reducing the chance of interbreeding between these two subspecies (van Zyll de Jong *et al*. 1995).

There is some evidence that wood and plains bison may behave differently during the rut. While plains bison form large aggregates during this time, wood bison herds actually decline in size during the rut (Soper 1941; Melton *et al*. 1989). The small herds of wood bison may make them more controllable by a few dominant males, resulting in harem formation, rather than the dominance hierarchy of plains bison (Calef and Van Camp 1987). Wood bison tend to be more solitary than plains bison during the rut, with most aggressive interactions occurring when a lone male attempts to join a cow herd where a dominant male is already present (Melton *et al*. 1989). Dominant males within the cow herds often change during the breeding season (Komers *et al*. 1992); however it is possible that a smaller proportion of wood bison males, in comparison to plains bison, are reproductively successful each year. Again, it should be noted that this behavioural difference may result from habitat preference rather than from genetic differences.

Herd sizes tend to be smaller year round in wood bison than in plains bison (Komers *et al*. 1992). Most early observers describe wood bison as being more solitary and shy than plains bison (see Appendix 1: Early Reports on Taxonomy section). These different behavioural traits may be due to continued hunting pressures (Geist 1996). The formation of large plains bison herds in the Great Plains may have been a defense against hunting pressures and predation by wolves, as places to hide were minimal and solitary animals would be easier targets. Undertaking large, unpredictable movements would have been a way of avoiding hunting pressures (Geist 1996). However, in the northern areas where human density was lower, wood bison could escape hunters by hiding in wooded areas as solitary animals or in small groups. Hunting pressures would have kept northern bison shy and dispersed (Geist 1996). Dissimilarities between wood and plains bison could be a result of these differential hunting pressures in various parts of their range, which continued as long as modern bison have existed. McDonald (1981) believed that hunting pressures may have ensured that wood and plains bison were kept separate, as most hunting was done from the forest edges. Conversely, van Zyll de Jong (1986) came to the conclusion that hunting pressures in the northern regions were not strong enough to have a large effect on the bison inhabiting these areas.

In order for wood and plains bison to have developed into subspecies, gene flow between them would have to be minimal to nonexistent. Behavioural differences and habitat preferences may have kept these animals spatially and/or temporally isolated. Most reports suggest that the range of wood and plains bison overlapped at about the Peace River (see Roe 1970; van Zyll de Jong 1986; Geist 1991). However, the amount that wood and plains bison mixed is unclear. In a reprint of a letter in Rhoads (1897), Moberly states that wood and plains bison populations often met at the boundaries between prairies and woodlands, but that the two groups never mixed. It is also possible that wood and plains bison inhabited the same area for part of the year, but plains bison moved south before the breeding season, thus ensuring reproductive isolation (van Zyll de Jong 1986; Stephenson *et al*. 2001). Others suggest that there was little overlap of wood and plains bison ranges, and little if any opportunity for mixing (Roe 1970; van Zyll de Jong 1986). Unfavourable habitats may have kept the zone between the two subspecies sparsely populated by bison. A belt of heavy boreal forest may have acted as a semi-permeable barrier between wood and plains bison. However, it is possible that burning by Aboriginal Peoples maintained open grassland in the area where the range of wood and plains bison overlapped, allowing wood and plains bison to mix (Lewis 1977; Geist 1991). The differential selection pressures of the habitats of wood and plains bison, and differing hunting pressures in the two regions, may have ensured that any animal that moved into the range inhabited by the other subspecies was selected against.

Summary

The debate over the subspecific status of wood and plains bison has been long-running. Most early reports suggest that the bison inhabiting the northern regions were different than those living on the plains, but even at that time there was controversy over whether these were environmental or genetic differences. Opinions on morphological differentiation between wood and plains bison have ranged from being considered cause for subspecific status (such as the continued morphological and mass differences between wood and plains bison at Elk Island National Park), a result of environmental pressures, or nonexistent. As the sensitivity of genetic tests has increased, so has the ability to differentiate the subspecies. Genetic studies range from finding no differentiation between the two subspecies, to discovering significant differences between the subspecies, and even between populations of the same subspecies. There is some suggestion of ecological differences between wood and plains bison, but again it is unclear whether these are ecotypic, or the result of genetic differences. The potential for gene flow may or may not have been high between wood and plains bison in historic times. It is unfortunate that most of the morphological and ecological studies, and all of the genetic studies, have occurred after the hybridization of wood and plains bison in the 1920s. As a result, it is difficult to determine if wood bison were differentiated as a subspecies before this hybridization.

The morphological similarity of sister populations of wood or plains bison that have been existing in different environments, and the continued morphological and mass distinction of wood and plains bison at Elk Island National Park after existing in similar

habitats for many years, suggest that there is a genetic basis for the morphological differences observed between these two subspecies, despite having hybridized. This genetic differentiation is backed up by the genetic similarities seen between wood bison populations at Elk Island National Park, Mackenzie Bison Sanctuary, and Wood Buffalo National Park in studies of mitochondrial DNA and microsatellites, and the observation that genetic distances are generally smaller within than between the subspecies. That genetic and morphological differences exist suggests that these subspecies are distinct and should be managed separately. As evidenced by the hybridization at Wood Buffalo National Park, any mixing of these animals will be irreversible, and should not be undertaken lightly (Reynolds 1991).