Genetic variation within and relatedness among wood and plains bison populations

G.A. Wilson and C. Strobeck

Abstract: There are two recognized subspecies of bison, wood (*Bison bison athabascae*) and plains (*Bison bison bison*) bison. The establishment of most bison populations from a small number of individuals has raised concerns about their genetic variation. To this end, 11 bison populations were surveyed with 11 microsatellite loci in order to calculate genetic variation and genetic distances. Mean number of alleles ranged between 3.18 at Antelope Island State Park (Utah) and 6.55 at Wood Buffalo National Park (Alberta and Northwest Territories). Mean heterozygosity ranged from 0.295 at Antelope Island State Park to 0.669 at Custer State Park (South Dakota). The amount of genetic variability present in the bison populations as measured by mean number of alleles and overall probability of identity was found to correlate with the number of founders for all sampled populations. The *G*-test for heterogeneity revealed some evidence for the existence of subpopulations at Wood Buffalo National Park, however very small genetic distances between these subpopulations suggest that nuclear material from the plains bison introduced into Wood Buffalo National Park has diffused throughout the park. Genetic distances between the sampled populations were generally larger between than within the two bison subspecies.

Key words: *Bison bison bison*, *Bison bison athabascae*, DNA microsatellites, genetic variation, genetic relatedness.

Résumé : On reconnaît deux sous-espèces de bisons, le bison de forêt (*Bison bison athabascae*) et le bison des plaines (*Bison bison bison*). Le fait que la plupart des populations de bisons sont issues d'un petit nombre d'individus suscite des inquiétudes quant à la variation génétique au sein de celles-ci. Afin de mesurer cette variation et d'estimer des distances génétiques, onze populations de bison ont été étudiées à l'aide d'onze loci microsatellites. Le nombre moyen d'allèles variait entre 3,18 (Antelope Island State Park, Utah) et 6,55 (Wood Buffalo National Park, Alberta et Territoires du Nord-Ouest). Le degré moyen d'hétérozygotie allait de 0,295 (Antelope Island State Park, Utah) à 0,669 (Custer State Park, Dakota du Sud). La variabilité génétique présente chez les populations de bison, telle qu'estimée à l'aide du nombre moyen d'allèles et de la probabilité globale d'identité, s'est avérée corrélée avec le nombre d'individus fondateurs pour chacune des populations échantillonées. Le test de *G* pour l'hétérogénéité a montré des indices suggérant l'existence de sous-populations à Wood Buffalo National Park. Cependant, la très faible distance génétique entre ces sous-populations suggère que du matériel nucléaire provenant des bisons des plaines, lesquels ont été introduits à Wood Buffalo National Park, a diffusé partout dans le parc. Les distances génétiques entre les populations échantillonées étaient généralement plus grandes entre les deux sous-espèces qu'à l'intérieur de celles-ci.

Mots clés : *Bison bison bison*, *Bison bison athabascae*, microsatellites, variation génétique, degré de parenté génétique.

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Introduction

Before the European settlement of North America, bison were among the most abundant local fauna. Herds of hundreds of animals roamed throughout most of North America. The amount of animal exchange between these herds is unknown, but has been suggested to be extensive (Roe 1970). Wood bison (*Bison bison athabascae*) existed in British Columbia, Alberta, and the Northwest Territories and plains bison (*Bison bison bison*) inhabited most of the remaining prairie regions. The amount of overlap of their ranges, if any, is unknown. Bison numbers were reduced to approximately 1000 by the late 1800s (Roe 1970), many of which were wood bison in what is now Wood Buffalo National Park (Alberta and Northwest Territories). The only other population containing indigenous animals is Yellowstone National Park (Wyoming), where between 22 and 50 animals existed in 1902 (Meagher 1973). The other remaining bison were found in a number of private herds throughout North America. Due to an intense restoration program by the governments of Canada and the United States, over 20 000 bison are currently found in public herds. However, the history of today's bison populations has raised concerns over the amount of genetic variability they contain.

Genetic variation is known to be greatly affected by the founder effect (Wright 1969; Nei et al. 1975). Populations originating from a small number of founders are expected to

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contain less genetic variation than those started from a larger number. Most of the public bison populations were founded from few individuals. Bison used to found these herds were mainly from ranch herds started from few animals themselves, further decreasing the amount of genetic variation expected in these herds. In an attempt to decrease the effects of inbreeding (and increase genetic variation), some herds were founded from more than one bison strain. A lack of genetic variation has been linked to inbreeding effects in some populations (O'Brien et al. 1985). However, not all genetically depauperate populations are affected by inbreeding depression (see for example Paetkau and Strobeck 1994), and inbreeding does not seem to decrease fecundity in all bison populations (Berger and Cunningham 1995). The amount of genetic variation present in a number of wood and plains bison populations will be examined.

The history of bison populations also affects the relatedness among them. Populations started with animals from similar locations should be more genetically related than those with different strains. Therefore, one would expect to find larger genetic distances between wood and plains bison, especially if they are different subspecies.

However, the subspecific designation for wood bison is in doubt. Wood Buffalo National Park was created to protect the last remaining wood bison population. Unfortunately, a large herd of plains bison was moved to the Pine Lake region of Wood Buffalo National Park from 1925–1928, and the wood and plains bison in the park hybridized. A herd of what was thought to be pure wood bison was found in a secluded area of Wood Buffalo National Park, and animals were taken from this area to start herds of wood bison in Mackenzie Bison Sanctuary (Northwest Territories) and Elk Island National Park (Alberta) in 1963 and 1965, respectively. Since that time it has been accepted that the bison used to start these herds had hybridized, at least to some extent, with the plains bison (Van Zyll de Jong 1986). Geist (1991) has argued that this hybridization has led to the extinction of wood bison while Van Zyll de Jong et al. (1995) believe that wood bison are still different enough from plains bison to warrant subspecific status. If *Bison bison athabascae* does in fact exist, we would expect to find these populations more genetically differentiated from *Bison bison bison* than from each other.

There may be regions of Wood Buffalo National Park that contain bison which are close to pure wood bison, and other regions which are mostly plains bison. Van Camp (1989) stated that wood bison may still exist in isolated areas. Van Zyll de Jong et al. (1995) described the bison of the Sweetgrass region of Wood Buffalo National Park as the most morphologically similar to pure wood bison, and Pine Lake individuals as intermediate between wood and plains bison. For this to be true, the bison population at Wood Buffalo National Park would need to be fairly heterogeneous, with little gene flow between regions of the park. The heterogeneity of the Wood Buffalo National Park bison subpopulations can be measured to see if it is possible that pockets of mostly pure wood bison still exist. If the Wood Buffalo National Park population is homogeneous, no pure wood bison could exist in the park.

It has been proposed that the bison indigenous to Yellowstone National Park were actually a type of bison called mountain bison, referred to as *Bison bison athabascae* (Meagher 1973). Again, this taxonomic issue is in doubt (for review, see Roe 1970). Plains bison were also added to the indigenous herd at Yellowstone, which diluted the amount of local input to the gene pool to about 40% (Meagher 1973). If mountain bison did exist in this park, the current population should be genetically distinct from other bison populations which do not contain any mountain bison input in their gene pool, or more similar to wood bison as mountain bison and wood bison share the same subspecific designation.

Highly variable regions of the genome must be used to examine genetic variation, diversity, and heterogeneity. Bison contain little to no variation at the chromosomal and protein level (Ying and Peden 1977; Bork et al. 1991; Cronin and Cockett 1993; Stormont 1993). More polymorphism was detected by restriction digesting the control region of the mitochondrial DNA, but still some populations were monomorphic (Polziehn et al. 1996). DNA microsatellites are highly polymorphic nuclear markers (Tautz 1989; Weber and May 1989) and have been used to analyze the genetic relationships among populations (for review see Bruford and Wayne 1993), including those that are genetically depauperate (Hughes and Queller 1993; Paetkau et al. 1995). In this study the genetic variability, diversity, and heterogeneity in a number of public North American bison herds were investigated with 11 microsatellite loci.

Materials and methods

Laboratory methods

The populations used in this study were: plains bison from Antelope Island State Park (Utah, AISP), Custer State Park (South Dakota, CSP), Elk Island National Park (Alberta, EINPP), Fort Niobrara National Wildlife Refuge (Nebraska, FNWR), National Bison Range (Montana, NBR), Wichita Mountains Wildlife Refuge (Oklahoma, WMWR), and Yellowstone National Park (Wyoming, YNP); wood bison from Elk Island National Park (EINPW), Mackenzie Bison Sanctuary (Northwest Territories, MBS), and Wood Buffalo National Park (Alberta and Northwest Territories, WBNP); and a feral herd of plains bison from Pink Mountain (British Columbia, PM). Table 1 summarizes the origins of these herds. EINPP had 45 founders as all other bison were shipped from the park to Buffalo National Park in 1909. While 18 and 24 animals were shipped from WBNP to MBS and EINPW, respectively, only 16 survived the trip to MBS. All of the adults were destroyed in EINPW to eradicate brucellosis, leaving 11 animals as founders (C. Gates, personal communication). To test the heterogeneity of the Wood Buffalo National Park population, samples from that park were split into the subpopulations of Garden River (GR), Little Buffalo (LB), Needle Lake (NL), Pine Lake (PL), and Sweetgrass (SW).

Sample sizes from the populations were: 30 from AISP, 32 from CSP, 30 from EINPP, 30 from FNWR, 30 from NBR, 21 from WMWR, 33 from YNP, 36 from EINPW, 28 from MBS, and 81 from WBNP. Of the WBNP samples, 8 were from GR, 13 from LB, 14 from NL, 24 from PL, and 22 from SW. DNA samples from AISP were kindly supplied by Julie Schneider. Tissue samples from PM, and DNA from all other populations were obtained from the DNA repository maintained by the Canadian Parks Service at the University of Alberta. As bison groups are quite fluid, and associations between individuals random, it can be assumed that these are random samples from the populations (Lott and

Table 1. Origins of the bison herds used in this study (Garretson 1938; Rorabacher 1970; Meagher 1973; Dary 1974; Coder 1975; Ogilvie 1979; Jenning and Hebbing 1983; Christiansen 1991; Malcolm 1993; Polziehn 1993; C. Gates, personal communication; R. Walker, personal communication; and T. Novak, personal communication).

Owner	Origin	Number	Year
Ranch herds			
Alloway/McKay	Saskatchewan	5	1873–4
Bedson	Manitoba (?)	3	1880
Bedson	Alloway/McKay	8	1880
Strathcona	Alloway/McKay	all	1887
Goodnight	Texas panhandle	6	1878
Goodnight	a Texas ranch (origin unknown)	1	1878
Goodnight	death, before breeding	–2	1878
Walking Coyote	Montana	4	1879
Pablo/Allard	Walking Coyote	12	1883
Pablo/Allard	Jones	26	1893
Conrad	Pablo/Allard	30	1902
Eaton	Pablo/Allard	60	1902
Dupree	Montana	6–7 (?)	1882
McCoy	Oklahoma (?)	2	1882
PWFC	McCoy	2	1886
Jones	Oklahoma	56	1886–9
Jones	Bedson	all (~75)	1889
Jones	Kansas, Nebraska ranches	10	1889
Corbin	Jones (From Bedson)	12	1889
Corbin	Jones	10	1892
Corbin	Banff NP	2	1904
Whitney	Wyoming (?)	13	1897
Whitney	Jones (from Oklahoma)	1	1897
Philip	Dupree	~75	1901–2
Gilbert	PWFC	3	1902
Gilbert	ranch in Iowa	1	1903
Public Herds			
AISP	Jones (from Bedson?)	12	1893
NYZG	Goodnight	4	1899
NYZG	Oklahoma	3	1899
NYZG	?	3	1900
NYZG	Wyoming	13	1903
NYZG	PWFC	1M, 3F	1904
NYZG	Whitney	13 (?)	1900–04
NYZG	Whitney (Oklahoma Jones animal)	1	1901
Banff NP	Goodnight	3	1897
Banff NP	Strathcona	13	1898
Banff NP	Corbin	2M	1904
YNP	native	22–50	1902
YNP	Eaton	18F	1902
YNP	Goodnight	3M	1902
WMWR	NYZG	6M, 9F	1907
WMWR	FNWR	4M	1942
WMWR	NBR	4M	1952
EINPP	Pablo/Allard	183	1907
EINPP	Banff NP	7M	1907
BNP	EINPP	all but 45	1909
Banff NP	Pablo/Allard	16M	1907
BNP	Pablo/Allard	298	1909–12
BNP	Banff NP	91	1909–14
NBR	Conrad	37	1909
NBR	Goodnight, Corbin, Jones	12	1910–11
NBR	WMWR	4M	1952

Table 1. (*concluded*).

Owner	Origin	Number	Year
NBR	YNP	2M	1953
WCNP	NYZG	7M, 7F	1914
FNWR	Gilbert	6	1913
FNWR	YNP	2M	1913
FNWR	CSP	8	1935–7
FNWR	NBR	5	1952
CSP	Philip	36	1914
CSP	Pine Ridge Reservation (origin unknown)	few	1940s
CSP	WCNP	~800	1950s
MBS	WBNP	16	1963
WBNP	native	200 minimum	
WBNP	BNP	6673	1925–28
EINPW	WBNP	11	1965
PM	EINPP	48	1971

Note: abbreviations: Page Woven Fence Company (PWFC), Antelope Island State Park (AISP), New York Zoological Gardens (NYZG), Yellowstone National Park (YNP), Wichita Mountains Wildlife Refuge (WMWR), Fort Niobrara Wildlife Refuge (FNWR), National Bison Range (NBR), plains bison at Elk Island National Park (EINPP), Buffalo National Park (Wainwright, BNP), Wind Cave National Park (WCNP), Custer State Park (CSP), Mackenzie Bison Sanctuary (MBS), wood bison at Elk Island National Park (EINPW), and Pink Mountain (PM).

Table 2. Remainder of the contents and amounts for the PCR reactions. Loci 1A, 1B, and 1C are *BM143*, *BM2830*, and *BM1225*, respectively. *RT29*, *BMC1222*, and *BM4513* are Primers A, B, and C in reaction mix 2, respectively. *RT27*, *RT24*, and *RT9* are multiplexed as loci 3A, 3B, and 3C, respectively. *Eth121* and *BOVFSH* are amplified separately using reaction mix 4.

	Reaction Mix 1 (μM)	Reaction Mix 2 (μM)	Reaction Mix 3 (μM)	Reaction Mix 4 (μM)
Primers A	0.19	0.19	0.18	0.16
Primers B	0.19	0.19	0.16	–
Primers C	0.17	0.13	0.16	–
dNTPs	160	160	160	120
Taq polymerase	0.68 units	0.48 units	0.6 units	0.6 units

Minta 1983; Van Vuren 1983). DNA was extracted from the PM tissue samples using a QIAamp® Tissue Extraction Kit.

The microsatellite loci used in this study were: *BM143*, *BM1225*, *BM2830*, *BM4513*, and *BMC1222* from Bishop et al. (1994), *BOVFSH* from Moore et al. (1992), *Eth121* from Steffen et al. (1993), and *RT9*, *RT24*, and *RT27* from Wilson et al. (1997). *RT29*, also used in the study, is *RT1* from Wilson et al. (1997) modified so that the primer sequences are GCCTTCTTTCATCCAACAAA and CCCATCTTCCCATCCTCTT. A FAM, HEX, or TET fluorescent dye group was added to the 5′ end of one primer from each of these loci. Where possible, these loci were multiplexed during PCR. Multiplexing in this context refers to the amplification of more than one locus in a single PCR reaction. All PCR reactions contained 2.5 mM $MgCl_2$ and approximately 60 ng DNA. The remainder of the PCR reaction contents, and multiplexes, are given in Table 2. The PCR was done on an ABI 9600 thermal cycler. Cycling conditions for the PCR reactions were as follows: 1 min at 94°C; then three cycles of 30 s at 94°C, 20 s at 54°C, and 5 s at 72°C; then 33 cycles of 15 s at 94°C, 20 s at 54°C, and 1 s at 72°C; then 30 s at 72°C. The PCR amplifications were then visualized with an ABI 373A DNA Sequencer and GENESCAN 672 software.

Data analysis

To examine variability in the bison populations, we first determined the allele frequencies of each locus for the populations. Allele frequencies are the prevalence of each type of allele in a population. We then used this information to calculate mean number of alleles, average heterozygosity, and overall probability of identity (*pI*). Mean number of alleles is the average number of alleles a population has present at any given locus. Average heterozygosity is the expected number of individuals having copies of different alleles at any locus. Unbiased expected heterozygosity was calculated at each locus using the formula from Nei and Roychoudhury (1974). This was then averaged over all loci to obtain the mean heterozygosity for each population. Probability of identity is the probability that an individual's genotype will be identical to another individual's genotype in the population, and can be calculated with formula [1]

$$[1] \qquad \sum_i p_i^4 + \sum_i \sum_{j>i} (2p_i p_j)^2$$

where p_i and p_j are the frequencies of the i^{th} and j^{th} alleles, respectively. We obtained unbiased probability of identity values using a formula from Paetkau et al. (1998). The overall *pI* for a population was calculated by multiplying together the probabilities of identity for all surveyed loci in that population. Three methods of measuring the original size of the bison populations were compared to these three measures of genetic variation using Kendall's rank correlation test (Sokal and Rohlf 1995). The three measures of original population size were defined as: (*i*) park founders, the number of animals originally used to found each of the herds, (*ii*) number in original stock, this value is similar to park founders but cannot exceed the lowest number of founders from the ranch populations,

Table 3. Allele frequencies, heterozygosities (*H*), and probabilities of identity (*pI*) for each population at each locus. The sample size (*n*) is given in the first table. If known, the size of the loci in cattle (CSize) is also given. Abbreviations can be found in Table 1.

Table 3A. Locus *BM143* (CSize 90–122).

		Allele frequencies									
Population	*n*	99	101	103	105	109	111	113	115	*H*	*pI*
AISP	30	0.017	0.75		0.167	0.033			0.033	0.414	0.37
CSP	32	0.094	0.094	0.109	0.281		0.172	0.031	0.219	0.826	0.053
EINPP	30		0.25	0.1	0.167		0.15		0.333	0.779	0.083
FNWR	30	0.117	0.567	0.083	0.117				0.117	0.642	0.154
NBR	30		0.533		0.2			0.033	0.233	0.631	0.192
PM	19		0.184	0.342	0.132		0.053		0.289	0.765	0.094
WMWR	21		0.286	0.095	0.238		0.381			0.725	0.128
YNP	33		0.212	0.242	0.076		0.333	0.045	0.091	0.781	0.081
EINPW	36	0.014	0.472		0.514					0.52	0.351
MBS	28	0.375	0.339	0.018	0.089	0.071	0.018		0.089	0.736	0.11
WBNP	81	0.179	0.506	0.049	0.167	0.031	0.025		0.043	0.682	0.135

Table 3B. Locus *BM2830* (CSize 149–203).

	Allele frequencies													
Population	141	143	147	149	151	153	155	157	159	163	165	167	*H*	*pI*
AISP			0.25	0.4	0.083				0.067	0.183		0.017	0.745	0.103
CSP			0.156	0.109	0.031	0.234	0.047	0.063	0.297	0.047	0.016		0.824	0.052
EINPP		0.017			0.133	0.083		0.067	0.417	0.25	0.033		0.746	0.098
FNWR			0.117	0.017		0.233		0.033	0.35	0.05	0.2		0.779	0.081
NBR			0.067	0.15	0.017	0.183			0.117	0.4	0.067		0.774	0.077
PM				0.053	0.132	0.184			0.421	0.211			0.744	0.101
WMWR			0.048	0.095	0.238	0.405		0.024		0.19			0.749	0.099
YNP	0.091		0.015	0.045	0.061	0.303			0.212	0.045	0.227		0.807	0.063
EINPW			0.25			0.583	0.139					0.028	0.585	0.228
MBS			0.321			0.5			0.054		0.036	0.089	0.646	0.183
WBNP		0.012	0.216	0.025	0.019	0.481		0.012	0.123	0.037	0.025	0.049	0.705	0.119

and (*iii*) number of strains, the number of different origins for the bison used to found the park herds.

The Monte Carlo approximation of the Fisher's exact test was used to detect deviations from Hardy-Weinberg equilibrium (Guo and Thompson 1992). Loci displaying an excess of homozygotes may contain null alleles, known to be present in a number of loci (Callen et al. 1993; Koorey et al. 1993; Paetkau and Strobeck 1995). Allele distributions were compared between populations using a *G*-test for heterogeneity (Sokal and Rohlf 1995). The *G*-test was chosen as it makes no assumptions about the method of mutation through which microsatellite alleles are derived. Pairwise comparisons between all populations at all loci were performed, and summed over all loci. The *G*-test was also used to examine the heterogeneity of the WBNP subpopulations. The assignment test, which compares an individual's genotype to the allele frequencies in all populations and assigns it to the population most likely to contain the genotype, was also calculated (Paetkau et al. 1995).

Statistical measures based on the infinite allele model (IAM), as opposed to the stepwise mutation model (SMM), were stressed as they give more reliable results with microsatellite data (Takezaki and Nei 1996; Paetkau et al. 1997). To obtain the genetic relatedness of the bison populations, Nei's standard (D_S, Nei 1972), Nei's minimum (D_M, Nei 1973), delta-mu squared ($\delta\mu^2$, Goldstein et al. 1995), and the genotype likelihood ratio (D_{LR}, Paetkau et al. 1997) genetic distance methods were calculated between all population pairs, and the subpopulations at WBNP. These measures were chosen because D_S and D_M are popular IAM methods of computing genetic distance. $(\delta\mu)^2$, based on the SMM, was designed specifically for microsatellites. D_{LR} is based on the assignment test. It is the log likelihood of a genotype occurring in a population other than its parent population. For example, a D_{LR} value of two means that genotypes are two orders of magnitude more likely to occur in the parent population than the other population being compared. Programs to calculate all of these genetic distances were designed by John Brzustowski and are available at http: //www.biology.ualberta.ca/jbrzusto/GeneDist.html. Unrooted trees from the population genetic distance data were created by PHYLIP 3.572 (Felsenstein 1995), using the neighbour-joining (Saitou and Nei 1987) and Fitch and Margoliash (1967) methods.

Results

Allele frequencies for all of the sampled populations at all loci, and their corresponding heterozygosities and probabilities of identity are given in Table 3. A range of variation was seen in the sampled loci. Average number of alleles was highest at locus *BOVFSH* and lowest at *BM4513* with values of 9.18 and 1.36, respectively. Locus *RT29* had the highest average heterozygosity with 0.767 and *BM4513* the lowest with 0.078. The lowest *pI* occurred for locus *RT29*, with a value of 0.092, and the highest at *BM4513*, with a value of

Table 3C. Locus *BM4513* (CSize 141–161).

Population	Allele frequencies 133	135	*H*	*pI*
AISP	0.917	0.083	0.155	0.72
CSP	0.813	0.188	0.31	0.519
EINPP	1		0	1
FNWR	0.917	0.083	0.155	0.72
NBR	1		0	1
PM	1		0	1
WMWR	1		0	1
YNP	0.864	0.136	0.239	0.601
EINPW	1		0	1
MBS	1		0	1
WBNP	1		0	1

Table 3D. Locus *BMC1222* (CSize 272–302).

Population	Allele frequencies 267	273	275	277	*H*	*pI*
AISP			1		0	1
CSP	0.094	0.156	0.656	0.094	0.536	0.246
EINPP	0.3		0.7		0.427	0.416
FNWR	0.183	0.05	0.767		0.382	0.418
NBR	0.15	0.033	0.717	0.1	0.46	0.318
PM	0.132		0.868		0.235	0.602
WMWR	0.024	0.024	0.952		0.094	0.816
YNP	0.03		0.97		0.06	0.883
EINPW		0.097	0.444	0.458	0.591	0.258
MBS	0.036	0.054	0.893	0.018	0.202	0.636
WBNP	0.043	0.123	0.525	0.309	0.616	0.212

Table 3E. Locus *BM1225* (CSize 227–253).

Population	Allele frequencies 238	240	244	246	248	252	264	268	270	272	*H*	*pI*
AISP		0.717				0.15	0.133				0.454	0.334
CSP	0.141	0.344			0.063	0.234	0.109	0.016	0.094		0.795	0.069
EINPP	0.017	0.467	0.15	0.017	0.083	0.15		0.033	0.083		0.734	0.095
FNWR	0.1	0.633				0.067	0.017	0.167		0.017	0.566	0.217
NBR	0.017	0.383		0.033	0.033	0.117		0.317	0.017	0.083	0.742	0.105
PM		0.368	0.211	0.026	0.053	0.079		0.079	0.184		0.791	0.07
WMWR		0.738				0.167		0.024	0.071		0.432	0.348
YNP		0.5				0.152		0.091	0.258		0.662	0.164
EINPW		0.042			0.111	0.583		0.264			0.584	0.229
MBS		0.196				0.643		0.161			0.532	0.269
WBNP		0.179	0.006	0.093	0.006	0.438	0.006	0.222	0.037	0.012	0.721	0.117

Table 3F. Locus *BOVFSH* (CSize 291–320).

Population	Allele frequencies 296	298	299	302	303	304	308	309	310	311	312	313	316	317	321	322	325	*H*	*pI*
AISP	0.017							0.983										0.033	0.933
CSP	0.125	0.125		0.016	0.328	0.047	0.016	0.109				0.125	0.047		0.063			0.838	0.041
EINPP	0.067	0.05		0.05	0.017		0.167	0.2	0.1			0.05			0.25	0.05		0.859	0.035
FNWR	0.167	0.383			0.017					0.167		0.05	0.05		0.1		0.067	0.791	0.066
NBR		0.017		0.683	0.05	0.017	0.017					0.017	0.017		0.183			0.504	0.274
PM		0.105		0.026	0.105		0.211	0.158	0.105			0.053			0.132	0.105		0.889	0.023
WMWR	0.048	0.024		0.095		0.071	0.048					0.429	0.286					0.733	0.106
YNP	0.015	0.152		0.03	0.106	0.182	0.015	0.273		0.136		0.015		0.015	0.03	0.03		0.849	0.039
EINPW			0.056	0.014	0.083			0.528		0.125		0.014		0.042	0.139			0.684	0.122
MBS		0.018	0.036	0.036	0.304		0.018	0.179		0.161		0.036		0.018	0.143	0.054		0.837	0.044
WBNP	0.025	0.025	0.031	0.062	0.123		0.049	0.333	0.012	0.136	0.006	0.043	0.012	0.037	0.093	0.012		0.84	0.039

0.869. Some alleles were fixed in various bison populations. Allele 133 at locus *BM4513* was fixed in populations EINPP, NBR, PM, WMWR, EINPW, MBS, and WBNP. Allele 275 at locus *BMC1222* was fixed in AISP. Alleles unique to a population were also discovered. At locus *BOVFSH*, allele 312 was found only in the WBNP population, and allele 325 was present only in FNWR individuals. YNP had two unique alleles, 209 and 211, at locus RT24.

As each locus for each population must be checked for Hardy-Weinberg equilibrium, there were a total of 121 genotype distributions to be examined using the Monte-Carlo approximation of the Fisher's exact test. However, eight of the allele distributions were monomorphic, so only 113 tests of the Hardy-Weinberg distributions were calculated. Eight of the genotype distributions were outside of the Hardy-Weinberg expectations at the 10% level and 5 at the 5%

Table 3G. Locus *Eth121* (CSize 173–212).

Population	Allele frequencies					*H*	*pI*
	186	188	194	198	200		
AISP	0.8	0.133		0.017	0.05	0.345	0.447
CSP	0.375	0.453	0.031	0.094	0.047	0.652	0.185
EINPP	0.433	0.1	0.05		0.417	0.637	0.205
FNWR	0.183	0.383	0.283	0.117	0.033	0.737	0.113
NBR	0.55	0.35	0.017		0.083	0.577	0.258
PM	0.237	0.079		0.079	0.605	0.58	0.22
WMWR	0.762	0.071		0.167		0.396	0.393
YNP	0.788	0.03	0.015	0.061	0.106	0.369	0.41
EINPW	0.403			0.111	0.486	0.597	0.249
MBS	0.911				0.089	0.166	0.704
WBNP	0.469	0.049	0.037	0.068	0.377	0.634	0.202

Table 3H. Locus *RT9*.

Population	Allele frequencies				*H*	*pI*
	113	115	117	119		
AISP	0.95	0.05			0.097	0.817
CSP	0.516	0.141	0.344		0.606	0.233
EINPP	0.617	0.067	0.317		0.524	0.306
FNWR	0.75		0.167	0.083	0.41	0.381
NBR	0.783	0.117	0.083	0.017	0.372	0.412
PM	0.316	0.158	0.526		0.615	0.22
WMWR	0.405	0.143	0.405	0.048	0.666	0.179
YNP	0.394	0.152	0.455		0.625	0.221
EINPW	0.694	0.056	0.25		0.459	0.354
MBS	0.786	0.089	0.125		0.366	0.423
WBNP	0.858	0.043	0.099		0.254	0.571

Table 3I. Locus *RT24*.

Population	Allele frequencies								*H*	*pI*
	205	209	211	213	225	227	229	231		
AISP	0.967						0.017	0.017	0.066	0.87
CSP	0.656				0.109		0.188	0.047	0.528	0.26
EINPP	0.7			0.05	0.15		0.05	0.05	0.488	0.283
FNWR	0.583				0.383	0.017		0.017	0.521	0.331
NBR	0.5				0.133	0.283		0.083	0.656	0.172
PM	0.868			0.026	0.053		0.053		0.246	0.564
WMWR	0.857				0.071		0.071		0.261	0.549
YNP	0.742	0.015	0.015	0.045	0.03	0.106		0.045	0.439	0.325
EINPW	0.625						0.306	0.069	0.518	0.308
MBS	0.661						0.339		0.456	0.397
WBNP	0.685			0.012	0.025	0.006	0.228	0.043	0.479	0.322

level. This number of values out of Hardy-Weinberg equilibrium is expected considering the number of tests performed. When the Dunn-Sidák experiment-wise error rate was used (Sokal and Rohlf 1995), two genotype distributions deviated from Hardy-Weinberg equilibrium at the 5% level, one of which also deviated at the 1% level. This was the *Eth121* allele frequency for the AISP population. A chi-squared goodness-of-fit test showed the observed number of heterozygotes for this genotype distribution did not deviate from the expected value at the 5% level. The deviation from Monte-Carlo expectations seems to be due to an inordinate number of 188/200 heterozygotes.

Table 4 shows the mean number of alleles, average heterozygosities and overall *pI* for all populations. The AISP population was the least variable with all three measures. The WBNP population was most variable when examining the mean number of alleles, while CSP displayed the most variation with the other two measures. All three methods of measuring variation showed that MBS and EINPW were both notably less variable than their founder population at WBNP. PM was also less variable than its founder population, EINPP, using all three methods of measuring variation.

The rankings used in the correlation analyses are given in Table 5. Rankings were calculated using the values from Table 1, but a few assumptions were made. (*i*) As CSP had 800 animals added to it from Wind Cave National Park, the number of founders for this park were added to the CSP population. (*ii*) For the rankings of the number of animals in the original stock, if the animals were moved more than once before reaching their final destination of the public herd, the smallest number of founders from the moves was considered. For example, in 1914, CSP was founded from 36 animals from Philip, who in turn had started his herd from about 70 Dupree animals. As Dupree had started his herd

Table 3J. Locus *RT27*.

Population	Allele frequencies				*H*	*pI*
	146	148	150	152		
AISP	0.133		0.867		0.235	0.606
CSP	0.422	0.031	0.453	0.094	0.617	0.227
EINPP	0.033	0.033	0.933		0.129	0.757
FNWR	0.4		0.517	0.083	0.576	0.272
NBR	0.2	0.1	0.65	0.05	0.534	0.257
PM	0.026		0.974		0.053	0.895
WMWR	0.214	0.048	0.738		0.417	0.385
YNP	0.091	0.091	0.818		0.319	0.479
EINPW	0.333		0.667		0.451	0.401
MBS	0.089		0.911		0.166	0.704
WBNP	0.173	0.012	0.802	0.012	0.328	0.488

Table 3K. Locus *RT29*.

Population	Allele frequences								*H*	*pI*
	206	212	214	216	218	220	222	224		
AISP	0.233	0.033			0.267	0.433	0.033		0.696	0.147
CSP	0.219	0.234	0.188		0.125	0.156	0.031	0.047	0.832	0.051
EINPP	0.083	0.267	0.117	0.05	0.133	0.133		0.217	0.837	0.047
FNWR	0.117	0.15	0.267		0.417		0.05		0.729	0.115
NBR		0.083	0.067		0.317	0.383	0.033	0.117	0.739	0.108
PM	0.053	0.395	0.053		0.158	0.263		0.079	0.758	0.092
WMWR	0.381				0.024	0.167	0.286	0.143	0.742	0.11
YNP	0.106	0.045	0.03		0.106	0.227	0.197	0.288	0.814	0.061
EINPW	0.25	0.125	0.014			0.167	0.417	0.028	0.73	0.114
MBS	0.036	0.393	0.018		0.018	0.268	0.179	0.089	0.745	0.103
WBNP	0.259	0.198	0.056	0.012	0.056	0.235	0.16	0.025	0.811	0.063

Table 4. Mean values for number of alleles, mean heterozygosity, and overall probability of identity (*pI*), the product of the *pI* values at each locus, for the bison populations. Abbreviations are given in Table 1.

	Mean no. alleles	Mean heterozygosity	1 / overall *pI*
AISP	3.18	0.295	4 100
CSP	5.64	0.669	7 600 000 000
EINPP	5.00	0.560	140 000 000
FNWR	4.64	0.572	42 000 000
NBR	4.91	0.544	15 000 000
PM	4.36	0.516	48 000 000
WMWR	3.91	0.474	1 600 000
YNP	5.36	0.542	67 000 000
EINPW	3.64	0.520	1 400 000
MBS	4.27	0.441	760 000
WBNP	6.55	0.552	57 000 000

from seven animals, the number of original animals starting the CSP population was then considered to be seven (excluding those from Wind Cave National Park). (*iii*) The number of strains in a herd was calculated by counting the number of strains in each addition of bison. For example, Mackenzie Bison Sanctuary, founded solely from animals from Wood Buffalo National Park, was assigned the same number of strains as the latter park. The number of strains could not exceed the number of bison added. (*iv*) If the number of animals added to a population was less than the number of founders for the emigrant population, the number of founders was added to the immigrant population instead of the actual number of individuals added. (*v*) Additions of less than eight animals to a public herd more than 20 y after it was originally founded were ignored. (*vi*) It was assumed that PM could not have a larger founding size than EINPP, as it was started solely from the latter population, so they were assigned a tie in the rankings. (*vii*) It was assumed that YNP had 50 native bison in the park in 1902 (Meagher 1973). And (*viii*) WMWR is known to have been founded from six strains of bison from the New York Zoological Gardens (Coder 1975). As Wind Cave National Park was also founded from New York Zoological Gardens, it was also assumed to have six strains of bison. The number of founders correlated with the mean number of alleles ($P < 0.01$) and the overall probability of identity ($P < 0.1$), while the number in original stock correlated with the mean num-

Table 5. Rankings assigned to the sampled bison populations used in Kendall's rank correlation test. The first value is the ranking, the second number in parenthesis is the actual value for the size of founding population measures. Actual values for the variability measures are in Table 4. Abbreviations are given in Table 1.

Table 5A. Size of founding population measures.

Park founders		Number of strains		Number in original stock	
FNWR	1 (8)	AISP	1 (2)	FNWR	1 (5)
EINPW	2 (11)	FNWR	2 (4)	AISP	2 (8)
AISP	3 (12)	WMWR	3 (6)	EINPW	3 (11)
WMWR	4 (15)	NBR	6 (8)	WMWR	4 (15)
MBS	5 (16)	YNP	6 (8)	MBS	5 (16)
EINPP	6.5 (45)	EINPP	6 (8)	CSP	6 (26)
PM	6.5 (45)	PM	6 (8)	PM	7.5 (37)
NBR	8 (49)	CSP	6 (8)	EINPP	7.5 (37)
CSP	9 (55)	WBNP	10 (9)	NBR	9 (42)
YNP	10 (71)	EINPW	10 (9)	YNP	10 (71)
WBNP	11 (240)	MBS	10 (9)	WBNP	11 (240)

Table 5B. Variability measures.

Mean no. alleles		Heterozygosity		Overall probability of identity	
AISP	1	AISP	1	AISP	1
EINPW	2	MBS	2	MBS	2
WMWR	3	WMWR	3	EINPW	3
MBS	4	PM	4	WMWR	4
PM	5	EINPW	5	NBR	5
FNWR	6	YNP	6	FNWR	6
NBR	7	NBR	7	PM	7
EINPP	8	WBNP	8	WBNP	8
YNP	9	EINPP	9	YNP	9
CSP	10	FNWR	10	EINPP	10
WBNP	11	CSP	11	CSP	11

Table 6. Assignment test results. Individuals assigned to their source population are in bold. Individuals assigned to the incorrect subspecies are in italics. Abbreviations can be found in Table 1.

	Population to which the individual was assigned										
Source	AISP	CSP	EINPP	FNWR	NBR	PM	WMWR	YNP	EINPW	MBS	WBNP
AISP	**30**										
CSP		**30**		1	1						
EINPP	1		**17**	1	1	10					
FNWR				**30**							
NBR	1	1			**28**						
PM			6			**12**		1			
WMWR							**21**				
YNP			1			1	2	**29**			
EINPW									**33**	2	1
MBS										**27**	1
WBNP	*1*	*1*		*1*		*2*			17	10	**49**

Table 7. Results of the assignment test for the Wood Buffalo National Park individuals, sorted by subpopulation. The total number of individuals in each subpopulation is in the first column (Total). The number of animals from each subpopulation assigned to WBNP, and all other populations, are in the other columns. Populations not listed had no WBNP animals assigned to them. Abbreviations for the populations can be found in Table 1.

					Plains bison populations			
	Total	WBNP	EINPW	MBS	AISP	CSP	FNWR	PM
GR	**8**	6	1	1				
LB	**13**	8	2	2		1		
NL	**14**	8	5	1				
PL	**24**	12	7	4				1
SW	**22**	15	2	2	1		1	1

Note: abbreviations for the subpopulations: Garden River (GR), Little Buffalo (LB), Needle Lake (NL), Pine Lake (PL), and Sweetgrass (SW).

ber of alleles ($P < 0.01$). None of the variability measures correlated with the number of strains per herd.

All pairs of populations had significantly different allele distributions when using the G-test ($P < 0.001$). However, of the WBNP subpopulations, only the allele distributions for the NL–GR, PL–GR, PL–LB, PL–NL, PL–SW, and NL–SW comparisons differed significantly at the 10% level using the G-test. Only NL–PL and NL–SW were significantly different when $P < 0.001$.

Of the 370 individuals used in the assignment test, 276 of them (75%) were assigned to the correct population (Table 6). Only five (1.4%) of the incorrectly assigned animals were placed in the incorrect subspecies, and all of these were WBNP bison assigned to various plains bison populations. Thirty-three percent of the WBNP animals were assigned to either EINPW or MBS. Thirty-three percent of the individuals from EINPP were specifically assigned to PM and 32% of the PM bison were assigned to EINPP. FNWR, AISP, and WMWR each had all of their individuals assigned to the correct population. Table 7 shows the number of individuals from each of the WBNP subpopulations that were assigned to the various populations. Of the five WBNP animals assigned to plains bison populations, three were from SW, one was from PL and one was from LB.

The genetic distances between all population pairs, and the WBNP subpopulations, can be found in Table 8. For D_S, the smallest distances between populations were the EINPP–PM and the WBNP–EINPW distances. The largest between population distance was between EINPW and FNWR. The smallest interpopulation distance with the D_M measure was between both WBNP–EINPW and EINPP–PM. The largest D_M distances were EINPW–AISP and AISP–PM. The D_{LR} genetic distance measure had the smallest interpopulation distance when comparing the EINPP and PM populations and the largest when measuring the EINPW–FNWR distance. $(\delta\mu)^2$ had the smallest interpopulation values when measuring the WBNP–EINPW distance and the largest when measuring the EINPW–AISP and NBR–AISP distances.

Unrooted trees for the populations were designed for all four of these genetic distance measures by PHYLIP 3.572, using the neighbour-joining (Saitou and Nei 1987) and Fitch and Margoliash (1967) methods. The unrooted tree made by applying the Fitch and Margoliash algorithm to the D_M distances is shown in Fig. 1. Aside from minor differences in branch lengths, both the neighbour-joining and Fitch and Margoliash algorithms gave trees identical to this one for the D_S, D_M, and D_{LR} distance measures, except the D_{LR} neighbour-joining tree has the (FNWR–CSP–NBR) and (WMWR–YNP) branches exchanged. Wood bison form one group on this tree. The unrooted tree created using $(\delta\mu)^2$ was not analyzed, as it was quite different from the other three. The $(\delta\mu)^2$ measure has been found to have high variance, and this could be the reason that its results differ from the other three (Paetkau et al. 1997). Takezaki and Nei (1996)

Table 8. Genetic distances between all bison populations, and the subpopulations at Wood Buffalo National Park (in bold). Distances between Wood Buffalo National Park and its subpopulations were not calculated. Population abbreviations can be found in Table 1, and subpopulation abbreviations are in Table 7.

Table 8A. D_S results are above the diagonal and D_M are below the diagonal.

	AISP	CSP	EINPP	FNWR	NBR	PM	WMWR	YNP	EINPW	MBS	WBNP	**GR**	**LB**	**NL**	**PL**	**SW**
AISP		0.261	0.204	0.261	0.215	0.290	0.217	0.184	0.280	0.209	0.171	0.239	0.201	0.221	0.155	0.179
CSP	0.147		0.162	0.151	0.225	0.192	0.172	0.168	0.257	0.195	0.181	0.224	0.205	0.237	0.185	0.177
EINPP	0.119	0.062		0.190	0.174	0.053	0.182	0.126	0.279	0.193	0.155	0.191	0.182	0.258	0.149	0.133
FNWR	0.145	0.057	0.077		0.194	0.272	0.258	0.251	0.377	0.302	0.231	0.253	0.236	0.292	0.266	0.209
NBR	0.124	0.085	0.073	0.08		0.269	0.240	0.230	0.320	0.226	0.19	0.208	0.211	0.255	0.195	0.187
PM	0.159	0.079	0.025	0.112	0.114		0.218	0.141	0.320	0.251	0.21	0.236	0.244	0.341	0.189	0.188
WMWR	0.126	0.079	0.084	0.113	0.108	0.102		0.090	0.303	0.204	0.218	0.246	0.282	0.289	0.199	0.212
YNP	0.109	0.067	0.054	0.100	0.095	0.064	0.044		0.296	0.159	0.196	0.253	0.260	0.282	0.163	0.185
EINPW	0.154	0.099	0.114	0.146	0.130	0.135	0.135	0.122		0.163	0.055	0.078	0.070	0.053	0.069	0.088
MBS	0.123	0.092	0.092	0.134	0.106	0.119	0.102	0.078	0.081		0.074	0.116	0.099	0.107	0.078	0.084
WBNP	0.104	0.069	0.065	0.092	0.079	0.091	0.098	0.082	0.025	0.081						
GR	0.135	0.085	0.080	0.101	0.087	0.102	0.110	0.104	0.036	0.059			0.038	0.063	0.045	0.043
LB	0.118	0.081	0.077	0.097	0.090	0.106	0.125	0.108	0.033	0.051		0.017		0.036	0.045	0.036
NL	0.128	0.095	0.109	0.120	0.120	0.144	0.131	0.119	0.026	0.055		0.030	0.017		0.061	0.063
PL	0.096	0.070	0.062	0.104	0.081	0.082	0.091	0.069	0.032	0.041		0.020	0.021	0.029		0.035
SW	0.107	0.069	0.057	0.085	0.079	0.083	0.097	0.079	0.040	0.044		0.020	0.017	0.030	0.016	

Table 8B. D_{LR} results are above the diagonal and $(\delta\mu)^2$ results are below the diagonal.

	AISP	CSP	EINPP	FNWR	NBR	PM	WMWR	YNP	EINPW	MBS	WBNP	**GR**	**LB**	**NL**	**PL**	**SW**
AISP		6.63	6.5	8.73	6.85	7.42	7.22	6.29	8.23	6.59	5.41	6.14	5.15	6.43	4.99	5.15
CSP	10.77		3.91	3.61	5.47	4.25	4.73	4.03	6.58	5.06	3.80	3.93	3.42	5.06	4.02	3.71
EINPP	12.43	7.27		5.14	4.25	0.46	5.89	3.46	8.32	5.85	4.55	4.54	4.57	6.75	4.48	3.61
FNWR	10.57	3.70	6.10		5.57	6.58	7.42	6.26	10.38	7.79	5.83	5.43	5.11	7.58	6.89	4.97
NBR	21.70	6.80	12.69	8.80		5.59	6.53	5.54	8.73	6.52	5.11	4.48	4.62	7.07	5.27	4.52
PM	13.84	10.21	3.68	10.05	15.99		6.36	3.40	8.34	6.02	4.74	4.86	4.95	7.28	4.23	3.95
WMWR	2.78	7.01	5.35	8.06	17.55	8.84		3.60	8.17	6.62	5.84	3.95	6.46	6.75	5.64	5.91
YNP	11.03	5.10	7.94	8.83	4.78	7.92	8.28		7.35	5.03	4.66	5.00	5.22	6.47	4.00	4.26
EINPW	20.72	11.38	14.80	13.47	9.48	10.76	17.81	10.66		3.53	1.48	1.15	1.21	1.08	1.52	2.06
MBS	9.82	6.00	11.53	8.11	4.99	13.15	8.92	5.11	5.64		1.45	1.31	1.11	1.85	1.70	1.55
WBNP	13.74	7.09	10.86	8.21	7.72	7.70	12.34	7.44	1.45	3.28						
GR	18.48	10.28	15.05	13.37	10.86	9.59	17.00	10.15	0.72	6.09			0	0	0	0
LB	13.23	6.92	11.46	6.15	7.12	8.44	13.29	7.16	2.96	4.11		2.31		0	0.08	0
NL	20.57	9.85	16.77	10.45	6.90	14.88	19.19	11.41	1.49	4.26		2.25	2.01		0.96	0.77
PL	14.43	6.70	10.33	8.48	7.39	7.88	11.97	7.50	1.51	3.07		1.35	1.75	1.90		0.20
SW	10.55	8.01	9.10	9.14	11.14	5.13	9.46	7.36	4.04	4.68		2.82	2.69	5.39	1.29	

also found that the $(\delta\mu)^2$ measure was less reliable than other methods for determining distances using microsatellites.

Discussion

The bison populations exhibited levels of microsatellite variability similar to other mammalian species, especially those recently undergoing population bottlenecks (Roy et al. 1994; Paetkau and Strobeck 1995; Houlden et al. 1996). Bison were also found to have variability levels similar to other large mammalian species in a study of allozymes (McClenaghan et al. 1990). The pre-bottleneck microsatellite variation must surely have been larger than it is today, as bottlenecks lower the amount of genetic variation in a population.

Wood Buffalo National Park was the most variable population when using mean number of alleles, while Custer State Park was the most variable with the other measures. This may be due to the fact that mean number of alleles tends to increase with number of individuals sampled. Wood Buffalo National Park had over two times the number of sampled individuals than the other populations, which may have increased the number of alleles detected. It is also of interest to note that each of the three sampled populations (Pink Mountain and Mackenzie Bison Sanctuary, and the wood bison at Elk Island National Park) which were started from one of the other sampled populations (plains bison at

Elk Island National Park, and Wood Buffalo National Park, respectively) contain less genetic variation than their founding herds. Pink Mountain had a larger number of founders than either of the other two populations, and is closer to its founding population in variability because of this.

The correlations of the mean number of alleles and probability of identity with the number of park founders, and mean number of alleles with the number in the original stock suggest that the amount of variation present in populations is indeed affected by the amount of potentially different genetic material in the populations. The number of founders has more of an effect on the amount of genetic variability in a population than the number of strains in that population does. Therefore, increasing the number of founders for a population is more effective in raising the amount of genetic variability in that population than increasing the number of strains. The failure of mean heterozygosity to correlate with any of the measures of original population size could be due to the fact that a number of the mean heterozygosity values are quite similar and may not be significantly different from one another, resulting in an incorrect ranking.

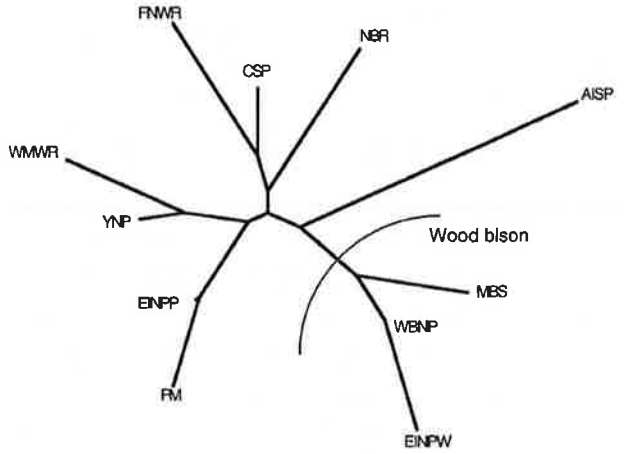
None of the variability measures were found to correlate with the number of mitochondrial alleles found in a study by Polziehn et al. (1996). It must be remembered that the mitochondria is only a single locus inherited maternally, and as such may not be a good indicator of the amount of variation present in populations which have undergone recent size changes.

Some individuals in the Custer State Park population have cow mitochondrial DNA (Polziehn et al. 1995). Known sizes of the loci used in this study in cattle are given in Table 3. Data from Bishop et al. (1994) involve the use of about 200 animals, while Moore et al. (1992) used 19 cattle. Most of the loci, when used in cattle, display a much wider range in allele sizes than bison. None of the bison at Custer State Park contained an allele in their genotype unique to their population, and all the alleles were within the size range found in other bison populations. Therefore, there is no evidence that any microsatellite alleles in the Custer State Park population originated from cattle.

Results of the *G*-test and the assignment test show that all the sampled bison populations are genetically distinct from one another. The founder effect and genetic drift, resulting from the small number of transfers between herds that have occurred, are probably responsible for the uniqueness of these populations. Most of the incorrect assignations of the assignment test were between Pink Mountain and the plains bison at Elk Island National Park, or between Wood Buffalo National Park and Mackenzie Bison Sanctuary or the wood bison population at Elk Island National Park. These are the only three instances of one sampled herd being directly established from another sampled herd, and all three occurred relatively recently.

The largest distances observed in this study were similar to those between widely separated North American polar bear populations, another mammal with a large home range (Paetkau et al. 1995). Founding effects and limited gene flow inflate genetic distance values, so we would expect genetic distances between bison populations to be larger than those obtained. If the bison inhabiting North America before

Fig. 1. Nei's minimum unrooted tree using the Fitch and Margoliash method. Abbreviations can be found in Table 1.



their near-extinction were essentially acting as a single metapopulation, with gene flow occurring between all areas, genetic distances between areas would be low. We would then expect to see low genetic distances between present herds despite the founding effects that have occurred. The extensive natural exchange of animals between herds on a daily basis within public parks today (Lott and Minta 1983; Van Vuren 1983) supports the idea of extensive gene flow in the past. Seton (1910) claimed that all of the plains bison present in Canada acted as one herd, at least before 1869. Roe (1970), also impressed with the homogeneity of bison, stated "in spite of the wide climatic variation, we are confronted with a species which is, broadly speaking, the same throughout this huge territory," with the possible exception of the wood bison. The physical similarity of North American bison should also be reflected in a genetic homogeneity, as is seen here.

As the D_S, D_M, and D_{LR} distance measures and both methods of designing trees all resulted in the same unrooted tree, there is some support for the relationships therein. The tree and the D_S, D_M, and D_{LR} distance measures all show the plains bison populations at Elk Island National Park and Pink Mountain to be the most closely related. Since the Pink Mountain population was founded recently from a fairly large number of Elk Island National Park individuals, this is not surprising. This suggests that the founding size of 48 animals for the Pink Mountain population was sufficient to obtain a representative sample of the genetic content of the Elk Island National Park population, though the genetic variation at Pink Mountain is smaller. If mountain bison existed and made a significant contribution to the gene pool of the bison at Yellowstone National Park, we would expect this population to be on a branch by itself or amongst the wood bison populations, as both mountain bison and wood bison were considered *Bison bison athabascae*. The genetic distances between the Yellowstone bison and the other populations would also be expected to be larger. As neither of these are supported by our results, the bison indigenous to Yellowstone were probably not mountain bison, but rather plains bison driven to the area by hunters. The relatively large genetic distances between the Antelope Island State Park pop-

ulation and all other bison populations, and its position on a branch by itself on the unrooted tree, could be a result of the extremely low genetic variability at Antelope Island. Low genetic variation increases the genetic distance between populations, as they may not share the same alleles by chance.

Genetic distances between wood and plains bison populations were larger than those within either of the two proposed subspecies. The three wood bison populations also form one group on the tree, and the genetic distances between these populations are low, relative to other bison populations. This is expected since the Mackenzie Bison Sanctuary and Elk Island National Park wood bison herds were founded solely from Wood Buffalo National Park. This grouping of the wood bison is strong, even after the introduction of numerous plains bison to Wood Buffalo National Park. The wood bison would surely have been even more distinct genetically from the plains bison had the introduction of plains bison to Wood Buffalo National Park not occurred. The clustering of these three populations implies that wood bison are functioning as entities distinct from plains bison, and should continue to be managed separately. The small genetic distances between these populations supports the idea that the founders of Elk Island National Park and Mackenzie Bison Sanctuary were wood–plains hybrids like the animals at Wood Buffalo National Park, and not pure wood bison.

It may be noted that the wood bison population at Elk Island National Park has larger genetic distances using all measures between itself and plains bison populations, while distances between Wood Buffalo National Park and the plains bison populations are smaller. This does not necessarily mean that the wood bison at Elk Island National Park are most like pure wood bison. This population was essentially founded from 11 individuals, as all of the animals shipped to the park from Wood Buffalo National Park were destroyed and only their offspring were kept. The reduction in founding stock could have increased the genetic distance between Elk Island National Park and all other populations. The power of the founder effect to lead to genetically different populations is illustrated by the genetic distance between Mackenzie Bison Sanctuary and the wood bison population at Elk Island National Park. These two populations were started at about the same time with animals taken from the same locale, but their genetic distance shows that their gene pools are quite distinct. Distances between Wood Buffalo National Park and the plains bison populations would be expected to be smaller than those of the other wood bison populations as Wood Buffalo National Park has a much higher genetic variability, and would share more alleles with the plains bison populations by chance.

The *G*-test indicates that the allele frequencies of the Pine Lake subpopulation at Wood Buffalo National Park are significantly different from all other subpopulations, and that the allele distributions at Needle Lake are also different from Sweetgrass and Garden River. All other comparisons were not significantly different. Pine Lake was the area chosen in Van Zyll de Jong et al. (1995) to be the most intermediate between wood bison and plains bison. The Pine Lake region was the site of the initial release of plains bison into the park, and this could have resulted in the uniqueness of this subpopulation, if it contains more genetic input from the introduced plains bison than other regions. However, genetic distances between all the regions of the park are extremely small. This suggests that while there may be differentiation between some of the subpopulations, there is still gene flow between all regions of the park, and no region should be free of genetic input from the introduced plains bison. Of the five animals from Wood Buffalo National Park misassigned with the assignment test to plains bison populations, three were from Sweetgrass, one was from Pine Lake, and one was from Little Buffalo. This also suggests that plains bison genetic material occurs throughout Wood Buffalo National Park. Even though Sweetgrass was chosen by external characteristics to be the most like pure wood bison (Van Zyll de Jong et al. 1995), more bison were assigned to plains bison populations from this region than from any other.

The correlation of the founding size of the bison populations with the mean number of alleles and overall probability of identity shows that microsatellites are good tools for examining the recent history of populations. Populations started from small numbers of animals have less genetic variation. Since the number of strains was not correlated with any of the measures of variation, it is more important to use a large number of animals irrespective of their origin to start herds with high genetic variation. The Pink Mountain population, founded relatively recently from 48 individuals, seems to contain a representative amount of the variation present in its parent population, judging from genetic distance data. This number of founders may then be a minimum level that could be aimed for when new bison populations are started. As the wood bison populations at Elk Island National Park and Mackenzie Bison Sanctuary do not contain as much variation as their founding population, Wood Buffalo National Park, they would not be suitable replacements if the latter population is to be extirpated. All wood bison herds existing today, either inside or outside Wood Buffalo National Park, contain some plains bison genetic material in their gene pool.

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