

PHENOTYPIC VARIATION IN REMNANT POPULATIONS OF NORTH AMERICAN BISON

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Eight external characters distinguishing plains bison (*Bos bison bison*) and wood bison (*B. b. athabasca*) were analyzed in six extant populations of plains bison and five populations of animals with ancestry of wood bison to test whether panmixis occurred in Wood Buffalo National Park following the introduction of plains bison and to test whether the variation is ecophenotypic. Character states were polarized from wood to plains bison and scored numerically. Frequencies of individual scores and indices were analyzed by a series of tests, and populations were ranked according to phenotype. Analysis of overall phenotypic variation based on all eight characters revealed three significantly different groups: plains bison; the subpopulation from Pine Lake; the other subpopulations from Wood Buffalo National Park. Results indicate that panmixis has not occurred since the 1925–1928 introduction of plains bison to the Park and that the characters studied are genetically based.

Key words: *Bos bison*, phenotypic variation, conservation

A central goal in conservation biology is to maintain or restore biological diversity for its intrinsic values, to sustain the health of ecological systems, and to meet human needs (Salwasser, 1990). The bison (*Bos bison*), once an important biotic element of North American grasslands, contributed substantially to the material and cultural well-being of the aboriginal human population and, in part, supported the early colonization of the interior of the continent by Europeans. During the past century, the species was reduced to a few remnant populations ranging in size from a few to several hundred individuals, together comprising <900 bison (Roe, 1970). Conservation and recovery of bison have gained in popularity in recent years because of the cultural, biological, and commercial value of

this large herbivore. Consequently, there is a need to document the range of phenotypic and genotypic variation within and among historical and contemporary populations to provide a basis for conserving existing diversity within the species.

The near extermination of bison precluded comprehensive study of historical geographic variation. Analysis of skeletal, largely cranial, material preserved in museum collections (McDonald, 1981; van Zyll de Jong, 1986) has cast some light on the extent and nature of past geographic variation, but the geographic variation of external characters in historical populations will remain largely a matter of conjecture. Extant populations of plains bison (*B. b. bison*) are descended from small founding populations comprising animals from north-

ern and southern regions of the historical range. The exact proportion of each in the founding herds and their genetic contribution to extant herds can only be approximated. At the turn of the century, the largest remnant population of bison, the northern wood bison (*B. b. athabasca*), resided in and around the area that is now Wood Buffalo National Park. Under protection, this population increased to ca. 2,000 by the early 1920s (Soper, 1941). Despite genetic introgression resulting from the introduction of >6,000 plains bison from southern Canada into central Wood Buffalo National Park in 1925–1928, bison from one subpopulation near the Nyarling River showed closer morphological resemblance to the indigenous wood bison than to the introduced plains bison (Banfield and Novakowski, 1960).

External phenotypic variation in wood bison from the Nyarling River and plains bison from Elk Island National Park was first analyzed subjectively by Geist and Karsten (1977) and later by van Zyll de Jong (1986), who used a quantitative approach. The external phenotypic variation of the other subpopulations in Wood Buffalo National Park has not yet been studied. Efforts to re-establish wood bison in other areas of its historical range have focused solely on bison captured in the area of Needle Lake and the Nyarling River in 1963 and 1965. The number of founding animals was limited to 18 for the Mackenzie Bison Sanctuary and 23 for Elk Island National Park. The taxonomic status of remaining herds living in the area of Wood Buffalo National Park is of interest with regard to the possibility of conserving additional genetic variation within contemporary wood bison.

Here we present results of a quantitative analysis of external phenotypic variation in a number of remnant populations including those from the area of Wood Buffalo National Park, which were not studied previously. We discuss the results in relation to historical geographic variation of bison in

North America, infraspecific taxonomy, and conservation of biological diversity within the species. The study received its impetus from the Wood Bison Recovery Team and emphasizes bison from the area of Wood Buffalo National Park, the core of the historical range of the wood bison (Soper, 1941; van Zyll de Jong, 1986).

We postulated that hybridization of wood and plains bison, following the latter's introduction to Wood Buffalo National Park, was not the pervasive event it was assumed to be and did not result in a phenotypically homogeneous population (see Van Camp, 1989). We speculated that hybridization occurred primarily where the plains bison were released and in adjacent, easily accessible areas. More remote and less accessible indigenous populations were less affected. In the absence of unrestricted, random mating, these differential effects should still be measurable today. The hypothesis we test is that there was restricted mating, i.e., no free interchange of genes, among subpopulations in Wood Buffalo National Park. The alternative hypothesis is that panmixis occurred, resulting in phenotypically uniform subpopulations. To test our hypothesis, we predict that subpopulations in the area of Wood Buffalo National Park will show significant phenotypic differences. Those in areas nearest the introduction site, or easily accessible from it, will have the highest frequencies of traits characteristic of plains bison; those in areas farthest away, or least accessible, will have lower ones.

A second hypothesis we test dates to Hornaday (1889) and recently was revived by Geist (1991). It claims that phenotypic differences between wood and plains bison are ecophenotypic in nature (*sensu* Mayr, 1969), i.e., the phenotypes are induced by environmental factors and are nongenetic. In other words, there is no genetically based discontinuity in geographic variation in North American bison consistent with subspecies. To test this hypothesis, we predict that bison of the *B. b. athabasca* phenotype moved to the habitat of *B. b. bison* (or

vice versa) will assume the phenotype of the latter in the first succeeding and subsequent generations.

MATERIALS AND METHODS

Populations sampled.—Populations of bison sampled are grouped into three categories: 1) plains bison; 2) wood bison from the Nyarling River area; 3) taxonomically undetermined subpopulations in the area of Wood Buffalo National Park. Six populations of plains bison were sampled from: Custer State Park, South Dakota; Delta Junction, Alaska; Fort Niobrara National Wildlife Refuge, Nebraska; Elk Island National Park, Alberta, Canada; National Bison Range, Montana; Yellowstone National Park, Wyoming (animals from Grand Teton National Park were included in this sample). Wood bison from the Nyarling River area are represented by samples from Elk Island National Park, Alberta, Canada, and the Mackenzie Bison Sanctuary, Northwest Territories, Canada. The taxonomically undetermined category includes three subpopulations from the area of Wood Buffalo National Park: Pine Lake; Sweetgrass; Slave River Lowlands. Designations of subpopulations of bison in Wood Buffalo National Park follow those of Wilson and Milne (1992), except for the subpopulation from the area of the Little Buffalo that we combined with the one from Hook Lake to maximize the size of the sample and designated as Slave River Lowlands. Of the four subpopulations residing strictly in the park, only those from Pine Lake and Sweetgrass are represented in our study. No photographs were obtained from the areas of the Garden and Nyarling rivers. However, the latter is represented by animals from Mackenzie Bison Sanctuary and Elk Island National Park, descendants of animals caught near the Nyarling River in 1963 and 1965, respectively. Populations listed under categories 2 and 3, all from the area of greater Wood Buffalo National Park, are referred to collectively as such in the text. For reasons of economy and convenience, all populations, subpopulations, and samples are referred to in the text by the geographic name of the area of origin.

Data for external phenotypic variation were obtained from photographs and video recordings that show animals in profile. Photographic records used in this study are cataloged and deposited at the Canadian Museum of Nature, Ottawa, Ontario, Canada.

Nongeographic variation.—To prevent genetically controlled, nongeographic, intraspecific variation from confusing geographic variation (Thorpe, 1976), variation attributable to sexual dimorphism was isolated by analyzing each sex separately. Ontogenetic variation was eliminated by analyzing adults only. The effect of seasonal variation was neutralized by using photographs taken in July and August (i.e., during the breeding season).

The development and characteristics of the horns in males and females (Fuller, 1959; Hornaday, 1889) were the criteria used to assign individuals to the appropriate age class and to determine inclusion in the sample. The validity of criteria used to determine age classes for populations of bison in northern Canada (Fuller, 1959) was confirmed for both subspecies at Elk Island National Park where a large number of known-age bison were present. Mature males (≥ 7 years old) comprise two age classes defined as follows: B3 or adult, characterized by horns with tips curved in, but smooth; B4 or prime, characterized by similar curvature of the horn, but with a "step" a short distance from the tip or with moderate brooming. Individuals with heavily broomed horns were excluded. Mature females (≥ 3 years old) are characterized by horn tips commonly curved strongly over the head (in adult males the tips point inward, but do not curve over the frontal area).

Direct environmental induction.—To detect environmentally induced variation in the characters studied, genetically related populations from localities with widely different environmental conditions were included in the analysis. For example, we compared a population of plains bison introduced to Alaska in 1928 from Montana (Burris and McKnight, 1973), living under boreal conditions in the prehistoric range of the wood bison, with its sister population on the National Bison Range. Conversely, we compared descendants of wood bison transplanted from the area of the Nyarling River to Elk Island National Park, part of the historical range of the plains bison, with bison of the same stock moved to the Mackenzie Bison Sanctuary in the historical range of wood bison.

Characters examined and methods of scoring.—Eight external features, three describing the hump and five describing the pelage, were examined and scored. Variation in each character was divided into a number of states (Fig. 1),

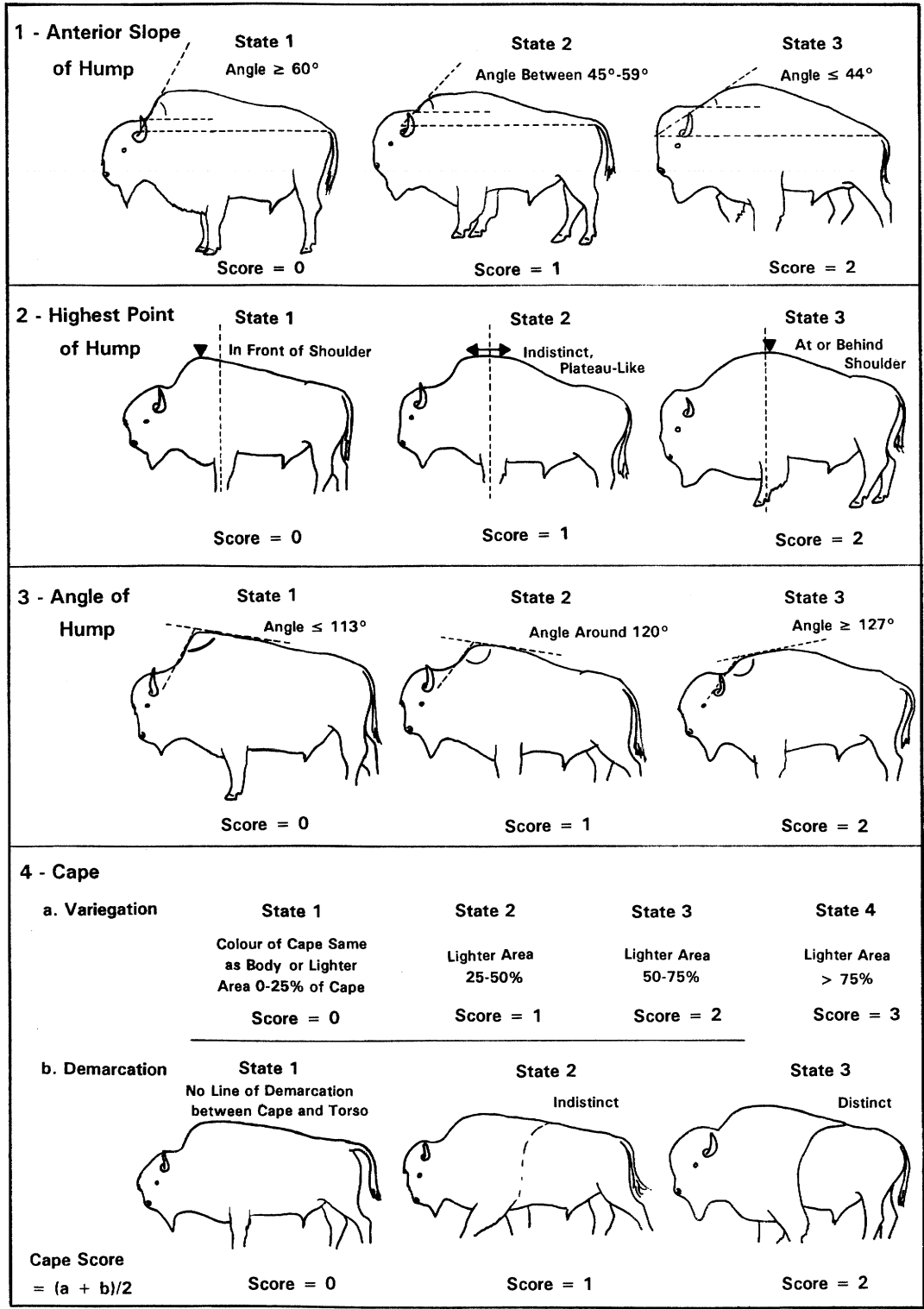



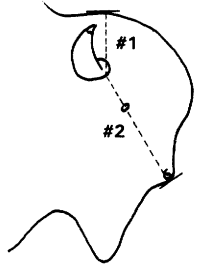
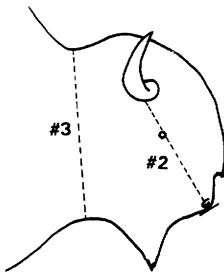





FIG. 1.—Character gradients, character scores and the calculation of the character index (sum of eight character scores) for adult male bison. Character states of *Bos bison athabasca* on the left, and those of *B. b. bison* on the right.

5 - Hair on Upper Front Leg				
	State 1 Short, Not Much Longer Than Nearby Areas of the Body	State 2 Longer Than in 1, But Not Forming Distinct "Chaps"	State 3 Long and Dense Forming Distinct "Chaps"	
				
	Score = 0	Score = 1	Score = 2	

6 - Frontal Display Hair				
	State 1	State 2	State 3	State 4
	Ratio #1/#2 = 0.20-0.40	Ratio #1/#2 = 0.41-0.60	Ratio #1/#2 = 0.61-0.80	Ratio #1-#2 > 0.80
	Score = 0	Score = 1	Score = 2	Score = 3

7 - Ventral Neck Mane				
	State 1	State 2	State 3	State 4
	Ratio #3/#2 = 1.20-1.40	Ratio #3/#2 = 1.41-1.60	Ratio #3/#2 = 1.61-1.80	Ratio #3/#2 > 1.80
	Score = 0	Score = 1	Score = 2	Score = 3

8 - Beard			
a. Shape	State 1	State 2	State 3
	 Pointed	 Rounded	 Blunt
	Score = 1	Score = 2	Score = 3

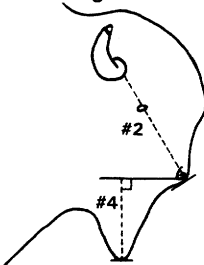
b. Length	State 1	State 2	State 3
	Ratio #4/#2 = 0.20-0.40	Ratio #4/#2 = 0.41-0.60	Ratio #4/#2 > 0.60
	Score = 0	Score = 1	Score = 2
	Beard Score = (a + b)/2		

FIG. 1.—Continued.

TABLE 1.—Frequencies of character scores for six characters in 11 populations of bison. The populations are ranked according to similarity, and those followed by the same letter are not significantly different.

Hump									Cape								
Population	n	Score							Population	n	Score						
		0	1	2	3	4	5	6			0.0	0.5	1.0	1.5	2.0	2.5	
Fort Niobrara	10	0	0	0	0	2	2	6	Custer State	19	0	0	1	0	2	16	a
National Bison Range	35	0	0	0	0	5	23	7 a	Fort Niobrara Elk Island National Park Plains	10	0	0	0	2	2	6	a
Delta Junction	18	0	0	0	3	3	10	2 ab		36	0	3	13	5	5	10	
Elk Island National Park Plains	38	0	0	0	7	17	12	2 b	Delta Junction	16	0	1	1	5	7	2	
Custer State	23	0	0	1	2	4	12	4 b	National Bison Range	34	0	0	3	3	9	19	b
Yellowstone National Park	43	0	0	1	4	13	23	2 b	Yellowstone National Park	40	2	2	5	3	16	12	bc
Pine Lake	21	0	3	3	7	6	2	0 c	Elk Island National Park Wood	28	1	5	3	5	8	6	c
Slave River Lowlands	6	1	0	1	2	2	0	0 c	Slave River Lowlands	6	2	0	1	1	0	2	c
Elk Island National Park Wood	28	8	2	9	6	3	0	0 c	Pine Lake	21	1	0	1	4	15	0	
Mackenzie Bison Sanctuary	32	1	9	13	4	5	0	0 c	Mackenzie Bison Sanctuary	31	13	5	1	11	1	0	d
Sweetgrass	16	8	2	5	1	0	0	0 c	Sweetgrass	15	8	5	1	1	0	0	d

forming a gradient. These states were assigned a numerical value, using a system of additive scoring (Sneath and Sokal, 1973). The lowest value represents the most extreme state in wood bison, and the highest represents the most extreme state in plains bison. Each character was weighted equally. Thus, in the two characters of the pelage, cape, and beard, where two aspects of a character were scored separately, the total was divided by two to obtain the final score (Fig. 1). Scoring was done in one of two ways. One involves comparing a character on the photograph to the standard characters in Fig. 1 and assigning it the corresponding value. The other involved measuring distances or angles on the photograph. Measurements were transformed to size-independent ratios by dividing them by a standard measurement. Angles and ratios were assigned scores based on their numerical value. Details are given in Fig. 1. Characters and methods used here are those described by van Zyll de Jong (1986), modified to increase objectivity and precision as described.

Scoring was done from photographs of profiles of mature animals with the head in a normal

position. Normal position of the head was defined by the angle between a line from the eye to the base of the tail and the horizontal axis of the body (Fig. 1) being ca. $4 + 2^\circ$. To reduce bias and inconsistency further, scoring was done by one observer on randomly selected photographs without information as to geographic origin.

Data analysis.—Frequency distributions of scores and indices in populations were examined in several ways. For each character, we tested the hypothesis that the distribution of its states did not differ in each pair of populations using the *G*-test and Williams' correction (Sokal and Rohlf, 1981). Second, the association between different characters in greater Wood Buffalo National Park (categories 2 and 3) was tested in the same manner to determine whether they were independent. Third, we added individual character scores for each individual to obtain a character index (Mayr, 1969; Simpson et al., 1960), which characterizes an individual's position along an axis of discrimination between the two forms compared. The character index, therefore, determines an individual's degree of phenotypic

TABLE 1.—*Extended.*

Chaps						Frontal display hair						
Population		n	Score			Population		n	Score			
			0	1	2				0	1	2	3
Custer State	20	0	0	20	a	Custer State	20	0	1	12	7	a
National Bison Range	34	0	0	34	a	Delta Junction	17	0	0	13	4	a
Fort Niobrara	12	0	0	12	a	Fort Niobrara	12	0	1	10	1	a
Yellowstone National Park	43	0	0	43	a	National Bison Range	44	0	2	31	11	a
Delta Junction	14	0	0	14	a	Elk Island National Park Plains	38	0	13	20	5	b
Elk Island National Park Plains	38	0	6	32	b	Yellowstone National Park	43	0	14	22	7	b
Pine Lake	21	2	5	14	b	Pine Lake	21	1	6	10	4	b
Slave River Lowlands	4	0	2	2	bc	Mackenzie Bison Sanctuary	31	0	13	16	2	b
Mackenzie Bison Sanctuary	31	7	17	7	c	Elk Island National Park Wood	27	0	12	13	2	b
Sweetgrass	8	4	2	2	c	Slave River Lowlands	6	0	6	0	0	c
Elk Island National Park Wood	28	13	10	5	c	Sweetgrass	16	5	8	3	0	c

resemblance to either subspecies and can be used in a quantitative analysis of phenotypic variation within and among populations. We employed a *G*-test using Williams' correction (Sokal and Rohlf, 1981) to examine the independence of phenotypic variation and populations. Finally, we used correspondence analysis (Greenacre, 1984) to determine the relative positions of the sampling units to one or more axes and to each other to maximize information about phenotypic similarities. Correspondence analysis allows one to compare frequencies of rows or columns in a two-way table by mathematically decomposing the chi-square into components similar to that of principal-components analysis. Unlike principal-components analysis, correspondence analysis uses frequencies or discrete data rather than continuous measurements. In correspondence analysis, chi-square distances can be computed and used to describe phenotypic relationships among populations quantitatively. Chi-square distance also was used to rank populations on the basis of frequency of character states. Calculations for *G*-test and correspondence analysis were performed using BIOM-pc and NTSYS-pc software (Rohlf, 1988, 1990).

RESULTS

There was essentially no difference in external phenotypic characters between

males and females (van Zyll de Jong, 1986). Therefore, we report only results obtained from adult males.

Variation in individual characters.—The scores for the three characters describing the shape of the hump were added and analyzed as one. All six populations of plains bison are more similar to one another with respect to shape of the hump than to any of the subpopulations from the area of greater Wood Buffalo National Park (Table 1). The population from Fort Niobrara is significantly different from other populations of plains bison (comparison with the most similar population; National Bison Range, $G = 6.48$, $d.f. = 2$, $P < 0.05$) and had the highest modal score (6). All other populations of plains bison form two overlapping nonsignificant subsets. The modal score characteristic of most of these populations is 5, except for Elk Island National Park where it is 4. All subpopulations from the area of greater Wood Buffalo National Park form a nonsignificant subset that differs significantly from all populations of plains bison ($G = 201.5$, $d.f. = 6$, $P < 0.005$). The modal scores from the area of greater Wood

TABLE 1.—*Extended.*

Ventral neck mane						Beard				
Population	n	Scores				Population	n	Score		
		0	1	2	3			0–0.5	1–1.5	2
Custer State	20	0	1	9	10	Delta Junction	14	2	9	3 a
National Bison Range	33	2	6	21	4 a	Custer State	20	4	14	2 a
Fort Niobrara	11	0	3	6	2 a	National Bison Range	32	7	25	0 a
Delta Junction	18	0	7	7	4 a	Fort Niobrara	10	5	5	0 ab
Yellowstone National Park	43	2	11	20	10 a	Yellowstone National Park	43	15	26	3 ab
Elk Island National Park Plains	35	1	15	11	8 b	Elk Island National Park Plains	38	13	23	2 ab
Pine Lake	21	4	9	7	1 bc	Elk Island National Park Wood	28	14	14	0 bc
Elk Island National Park Wood	27	1	16	9	1 bc	Mackenzie Bison Sanctuary	31	16	15	0 bc
Slave River Lowlands	6	2	4	0	0 c	Pine Lake	21	12	9	0 bc
Mackenzie Bison Sanctuary	30	8	16	6	0 c	Slave River Lowlands	6	4	2	0 bc
Sweetgrass	16	7	6	3	0 c	Sweetgrass	16	13	3	0 c

Buffalo National Park show a wider range of variation, with the highest in Pine Lake (3) and lowest in Sweetgrass (0). Nyarling wood bison from Elk Island National Park and the Mackenzie Bison Sanctuary have the same modal score (2).

A pattern of separation between plains bison and populations from the area of greater Wood Buffalo National Park also is evident in the cape, but is not as clear as it is in the hump (Table 1). The subsets National Bison Range–Yellowstone National Park and Yellowstone National Park–Slave River Lowlands overlap, evincing a less distinct separation between the plains bison and subpopulations from the area of greater Wood Buffalo National Park. Modal scores vary widely and are not concordant with the plains-greater Wood Buffalo National Park division.

Frequencies of the states of chaps show a clear division between most populations of plains bison and the subset Elk Island plains–Slave River Lowlands and overlapping subset Slave River Lowlands–Nyarling wood bison from Elk Island (Table 1). The modal score for all plains populations is 2. The modal score for subpopulations from

greater Wood Buffalo National Park varies widely from 2 in Pine Lake and 1 in Mackenzie Bison Sanctuary to 0 in Sweetgrass and Nyarling wood bison from Elk Island.

Frontal display hair shows a pattern of three non-overlapping subsets (National Bison Range versus plains bison from Elk Island, $G = 8.1$, $d.f. = 3$, $0.05 > P > 0.025$; Nyarling wood bison from Elk Island versus Slave River Lowlands, $G = 6.5$, $d.f. = 2$, $0.025 < P < 0.05$). The subset in the middle comprises plains bison and samples from greater Wood Buffalo National Park. Modal scores, similarly, show a relatively uniform pattern, being 2 for all populations except Slave River Lowlands and Sweetgrass.

A separation into plains bison and bison from greater Wood Buffalo National Park is discernible in the ranking of the groups on the basis of ventral neck mane, but they are linked by broadly overlapping nonsignificant subsets (Table 1). Custer State differs significantly from National Bison Range ($G = 9.81$, $d.f. = 3$, $0.025 < P < 0.05$). In most plains populations, the modal score is 2 or higher, except for plains bison from Elk Island where it is 1. In samples from

TABLE 2.—Frequencies of character indices in 11 populations of bison. The phenotypic gradient from left to right indicates increasing characteristics of plains bison. Populations followed by the same letter are not significantly different.

Population	n	Character index								
		2–3.5	4–5.5	6–7.5	8–9.5	10–11.5	12–13.5	14–15.5	16–17.5	
Custer State	21	0	0	0	0	2	2	11	6	a
Fort Niobrara	9	0	0	0	0	0	2	5	2	a
National Bison Range	37	0	0	0	0	1	8	23	5	a
Delta Junction	12	0	0	0	0	2	2	6	2	ab
Elk Island National Park Plains	37	0	0	0	3	12	11	9	2	b
Yellowstone National Park	43	0	0	0	3	10	13	14	3	b
Pine Lake	22	0	0	5	2	8	6	1	0	c
Elk Island National Park Wood	27	2	6	4	9	4	2	0	0	c
Mackenzie Bison Sanctuary	31	2	7	11	6	4	1	0	0	
Slave River Lowlands	4	1	1	1	0	1	0	0	0	cd
Sweetgrass	8	4	3	1	0	0	0	0	0	d

greater Wood Buffalo National Park the modal score is 1, except for Sweetgrass, where it is 0.

The pattern of frequency distributions for the beard is similar to that of the ventral neck mane. There is a definite ranking of plains bison and bison from greater Wood Buffalo National Park into two groups, which also is evident from the distribution of the modal scores (Table 1). However, overlap between non-significant subsets is even broader than for ventral neck mane.

In subpopulations of greater Wood Buffalo National Park significant association exists between cape and chaps ($G = 13.2$, $d.f. = 4$, $P = 0.01$), cape and frontal display hair ($G = 11.3$, $d.f. = 2$, $P < 0.005$), and frontal display hair and ventral neck mane ($G = 19.7$, $d.f. = 2$, $P < 0.005$). The hump and beard are not significantly associated with any of the other characters.

Overall phenotypic variation.—Comparison of overall phenotypic variation in the samples (Table 2) evinced a clear division into three groups. The first group comprises all samples of plains bison within which two overlapping nonsignificant subsets occur. The second group contains only Pine Lake, and the third, all other samples from greater Wood Buffalo National Park, which form two overlapping nonsignificant sub-

sets. Pine Lake is phenotypically clearly intermediate and differs significantly from the most similar plains sample ($G = 25.9$, $d.f. = 5$, $P < 0.005$) as well as from the most similar samples from greater Wood Buffalo National Park ($G = 22.1$, $d.f. = 5$, $P < 0.005$).

The extent to which subpopulations in greater Wood Buffalo National Park have been affected by past interbreeding with plains bison can be judged from the amount their character indices overlap those of populations of plains bison. To this end, we calculated the percentage and its 95% confidence limits of individuals in each sample having indices equal to or higher than the lowest observed index for plains bison (class 8.0–9.5). Of the subpopulations in greater Wood Buffalo National Park, Pine Lake overlapped most extensively with the populations of plains bison, 77%. Nyarling wood bison, represented by samples from Elk Island National Park and the Mackenzie Bison Sanctuary, overlapped less (45%, CI of 32–58). No overlap was observed between Sweetgrass and plains bison, but the Sweetgrass sample was small ($n = 8$) and the confidence limits correspondingly wide (CI of 0–33). In the even smaller sample from Slave River Lowlands ($n = 4$), the observed overlap was 25%.

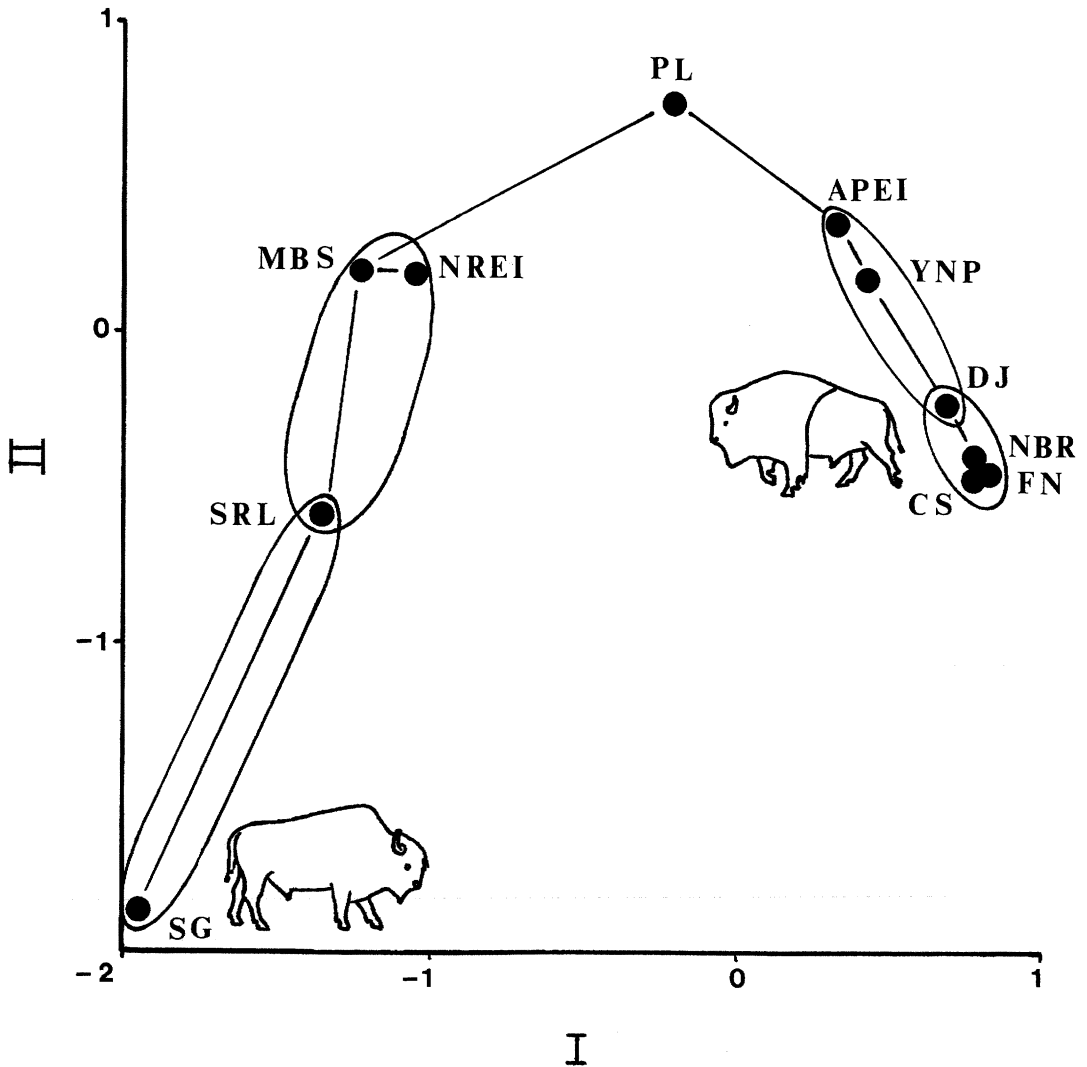


FIG. 2.—Results of correspondence analysis of external phenotypic variation in 11 populations of bison. A plot of row factors for the frequency data of Table 2 shows the ordination of the populations. A minimum-spanning tree connects nearest neighbors. Ellipses indicate nonsignificant subsets. Populations are from left to right: SG, Sweetgrass; SRL, Slave River Lowlands; MBS, Mackenzie Bison Sanctuary; NREI, Elk Island National Park wood bison; PL, Pine Lake; APEI, Elk Island National Park plains bison; YNP, Yellowstone National Park; DJ, Delta Junction; NBR, National Bison Range; CS, Custer State; and FN, Fort Niobrara.

Results of the correspondence analysis depict the ordination of populations based on phenotype (Fig. 2). The first axis represents most of the phenotypic variation. Phenotypes characteristic for wood bison are on the left; those characteristic for plains bison on the right of the graph. Pop-

ulations of plains bison are well separated from the majority of subpopulations from greater Wood Buffalo National Park except Pine Lake, which is intermediate. Distances indicated by the minimum-spanning tree may not accurately reflect the phenotypic inter-relationships between samples that did

not differ significantly in the previous analysis. Pine Lake, which differs significantly from either of its closest neighbors, is considerably closer to plains bison from Elk Island National Park than to Nyarling wood bison from the same park. Chi-square distances among all pairs of groups are listed in Table 3. Sweetgrass and Slave River Lowlands are most remote from plains bison from Elk Island, followed by Nyarling wood bison from the Mackenzie Bison Sanctuary and Elk Island National Park.

DISCUSSION

Impact of hybridization.—Our analyses reveal that subpopulations in greater Wood Buffalo National Park are phenotypically heterogeneous, with Pine Lake having the highest frequency of traits characterizing plains bison. The release of plains bison in 1925–1928 occurred at several points along the eastern boundary of the park below the confluence of the Peace and Slave rivers, i.e., in the area of the present subpopulation at Pine Lake (Fig. 3). Our observations are, thus, in general agreement with the predictions of the first hypothesis that there was no free exchange of genes. The finding that bison from Sweetgrass are phenotypically most remote from plains bison from Elk Island National Park was unexpected in view of their relative proximity to the release sites. The remoteness suggests that there has been relatively little reproductive contact between subpopulations at Sweetgrass and Pine Lake. Bison from Slave River Lowlands are represented by a small sample in this study. However, data indicate that bison in this area are phenotypically at least as distinct from those in the area of Pine Lake as those of the other subpopulations (Sweetgrass; Nyarling wood bison from Elk Island National Park and the Mackenzie Bison Sanctuary). The evidence supports the absence of panmixis since the introductions >60 years ago. The reasons for this are not clear. Information on movements of bison and on the stability of subpopulations in greater Wood Buffalo Na-

TABLE 3.—Chi-square distances between pairs of 11 populations of bison (males).

Population	Population										
	1	2	3	4	5	6	7	8	9	10	11
1. Custer State	0.000										
2. National Bison Range	0.650	0.000									
3. Fort Niobrara	0.437	0.339	0.000								
4. Yellowstone National Park	1.056	0.840	0.937	0.000							
5. Delta Junction	0.485	0.436	0.473	0.637	0.000						
6. Elk Island National Park Plains	1.243	1.101	1.187	0.278	0.839	0.000					
7. Sweetgrass	3.362	3.327	3.345	3.238	3.279	3.253	0.000				
8. Pine Lake	1.780	1.682	1.752	1.057	1.447	0.923	3.233	0.000			
9. Slave River Lowlands	2.359	2.351	2.391	2.087	2.192	2.048	1.581	0.000	0.000		
10. Elk Island National Park Wood	2.103	2.052	2.090	1.637	1.921	1.595	2.609	1.566	1.530	0.000	
11. Mackenzie Bison Sanctuary	2.183	2.142	2.178	1.834	2.020	1.811	2.593	1.405	1.266	0.849	0.000

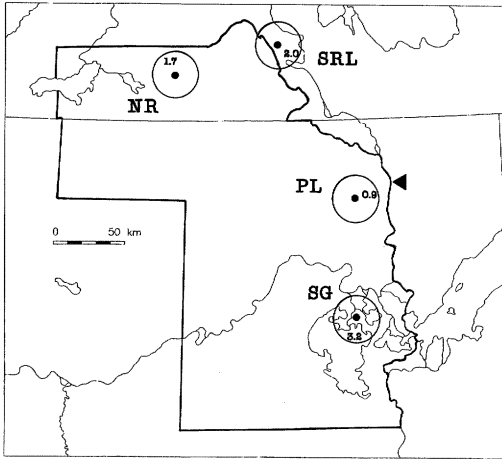


FIG. 3.—Approximate centers of distribution of subpopulations of bison in Wood Buffalo National Park in relation to the area where the release of plains bison took place in the period 1925–1928 (indicated by the black triangle). Chi-square distances of the subpopulations from the parental stock of plains bison (Allard-Pablo), shown in the circles, indicate the extent to which interbreeding has affected the external phenotype of present subpopulations. The subpopulations shown are: NR, Nyarling River; PL, Pine Lake; SRL, Slave River Lowlands; and SG, Sweetgrass.

tional Park in the past is lacking. Recent studies (Wilson and Milne, 1992) have yielded information that supports the existence of relatively discrete subpopulations (absence of significant seasonal movements and limited exchange between areas), which may constitute demes. This continuing study of movements of bison will provide further insight in the dynamics of subpopulations in greater Wood Buffalo National Park.

Concordance of genealogy and phenotype.—Results of our analysis strongly support a genetic basis for the phenotypic characters studied. This conclusion is based on the observation that the known genealogical (i.e., genetic) relationships of the populations studied are highly concordant with the phenotypic relationships. The “sibling” populations, those derived from the same “parent” population, show remarkable

agreement between genealogy and phenotypic similarity. Populations of plains bison from Delta Junction and the National Bison Range, descendants from the same stock, are neighbors in phenotypic space (Fig. 2). They do not differ significantly with respect to phenotype after >60 years apart in widely differing environments. Bison at Delta Junction are free-roaming and live in boreal forest. Bison on the National Bison Range, conversely, are fenced, live in temperate grassland-open forest and are managed quite intensively. Similarly, the two populations of wood bison from the Mackenzie Bison Sanctuary and Elk Island National Park were derived from the same subpopulation in Wood Buffalo National Park. They do not differ significantly in the morphological characters studied, after living separately under different environmental conditions since 1963. In the Mackenzie Bison Sanctuary, the animals live in boreal and subarctic woodlands, interspersed by marshes, where they lead a natural existence subject to predation and the environment. In contrast, their relatives in Elk Island National Park live in a fenced, temperate, aspen parkland, where they lead a semi-natural existence and are not subject to predation. Evidence provided by these sibling populations falsifies the hypothesis that phenotypic differences between plains and wood bison are environmentally induced.

The other populations, whose genealogies are more uncertain, show the same general concordance between phenotype and kinship. The populations in the nonsignificant subset Custer State-Fort Niobrara-National Bison Range-Delta Junction (Fig. 2) stem from founding stock containing northern plains bison with admixtures of southern (Texas) strains (Coder, 1975; N. S. Novakowski, in litt.). Custer State was established in 1914 with animals from Wyoming. Fort Niobrara originated in 1913 from six animals from Nebraska and two from the Allard estate (via Yellowstone National Park). The National Bison Range

dates from 1909, and its founding stock comprised Allard-Pablo (36) and Texas (10) stock. Delta Junction, as we have already seen, derives directly from the herd at the National Bison Range. Plains bison from Yellowstone National Park and Elk Island National Park, which form the other non-significant subset, differ from other plains bison to a greater degree. Yellowstone National Park's founding stock consisted of northern (Allard-Pablo) and southern (Texas) plains bison and a significant proportion (30–40%) of indigenous Yellowstone bison (Meagher, 1973). Plains bison in Elk Island National Park were derived from northern plains bison with an unknown admixture of Texas stock.

The results of our analyses support a genetic basis for the phenotypic characters that distinguish plains bison from bison in greater Wood Buffalo National Park. Our study indicates that the shape of the hump and the pelage characters are independent. Four of the five pelage characters, conversely, showed significant associations, which suggests that they may be genetically linked.

Relevance to infraspecific taxonomy.—The phenotypic variation in present remnant populations can only be partially interpreted in terms of the past geographic variation, because the exact composition of the founding herds is not known. However, results of our study agree with those based on cranial data from historical populations (van Zyll de Jong, 1986). Both show variation within plains populations to be much less than that between plains and wood (or present greater Wood Buffalo National Park) bison. It is probable that external phenotypic differences observed in modern populations reflect a past morphological discontinuity between plains and wood bison.

In the recent past, North American bison occupied a vast range, but they were most numerous on the central plains. The geographic variation in historical populations appears to have been largely clinal in a

south-north direction, but there was a morphological discontinuity in the northwestern part of the species' range in the area of the boreal forest-grassland transition (van Zyll de Jong, 1986, 1993). The distinctness of wood and plains bison probably was maintained by a combination of behavioral and ecological factors. Most important among these were seasonal movements of plains bison (Gordon, 1979; Moodie and Ray, 1976; Morgan, 1980), which ensured separation of the two forms during the rut. The subspecific status of the historical populations of wood and plains bison is well founded and fits the definition given by Avise and Ball (1990). As to the taxonomic status of present subpopulations in greater Wood Buffalo National Park, the situation is less straightforward. All could, strictly speaking, be designated as intergrades (*B. b. bison* × *B. b. athabasca*) because even the most remote of the subpopulations appear to have been affected to some degree by the introduction of plains bison. To combine all subpopulations in the same category would obscure detection of significant differences and that some subpopulations are closer to the original wood bison than others. It would be more useful and informative to designate the clearly intermediate subpopulation (Pine Lake) as an intergrading population (*B. b. bison* × *B. b. athabasca*) and the others (Sweet Grass, Nyarling, Slave River Lowlands), being considerably more distant from plains bison and closest to the original wood bison, as *B. b. athabasca*.

Conservation policy.—In Canada, present conservation policy encompasses infraspecific groups based on geographic distinctiveness. Any group below the species level may be designated by the Committee on Species of Endangered Wildlife in Canada (COSEWIC) as endangered or threatened, if it is geographically distinct based on discontinuity in gene flow, geographical barriers, breaks in breeding distribution, ecotypic variation, taxonomic differentiation, genetic analysis, or other compelling

evidence and the population represents a significant proportion of the historical range of the species in Canada. Based on our findings, we recognize that existing subpopulations in greater Wood Buffalo National Park and those populations derived from them represent the closest living relatives of the original wood bison. Despite hybridization, some subpopulations retain a high proportion of animals resembling indigenous wood bison. Consistent with the Committee's criteria, these subpopulations should be added to those already on the list (Nyarling wood bison in the Mackenzie Bison Sanctuary, Elk Island National Park, and populations derived from these).

While data now available, in our view, warrant formal recognition of contemporary plains and wood bison as subspecies, the debate on whether this recognition is valid should in no way affect their conservation as separate entities. The important issue is the conservation of genetically-based geographic variation in North American bison that reflects a pattern of evolutionary divergence and geographic discontinuity that has developed within the past 10,000 years. After their devastating impact on the species in the past, humans continue to control the evolutionary destiny of bison. There is thus an implicit responsibility to preserve as much of the intraspecific diversity as possible, to allow for continued adaptation and evolution as well as for utilitarian purposes. Geographic variation should be preserved in populations where natural processes and factors operate most freely. Accidental crossbreeding of northern and southern forms of bison resulting from escapes of privately-owned, commercial bison or the willful introduction of one form into the range occupied by the other will lead to further loss of intraspecific diversity and conflicts with one of the central objectives of conservation biology. Phylogeny is a time-dependent process, in part, resulting from accumulated genetic differences in the absence of gene flow. The possibility that geographic variants possess unique adapta-

tions and have the potential to evolve into new species are compelling reasons for conserving them (O'Brien and Mayr, 1991).

Managers of public and private herds of bison cannot afford to be complacent about conservation of geographic variability. Erosion of genetic variability tends to advance rapidly under domestication. Domestication places the species in a state of total dependence where natural selection is replaced largely by artificial selection based on economic and husbandry considerations. Experience with several traditional domestic animals indicates that recovery of original genetic diversity is difficult or impossible once domestication has progressed to a stage where existing breeds are highly selected for specific purposes and primitive breeds and wild stocks have become extinct (Crawford, 1984). Artificial selection and hybridization to obtain certain traits dictated by economic and animal husbandry considerations make good business sense, but rapidly diminish the genetic resource. Wild stocks, therefore, serve as a genetic bank that can be drawn upon to improve domestic breeds when the need arises.

It takes little reflection to conclude that the responsibility for conserving intraspecific diversity rests primarily with public agencies and not private interests. Only public agencies can provide the continuity and long-term protection of intact ecosystems large enough for all natural forces to act on a large-sized species such as bison. A conservative approach to the conservation of intraspecific diversity in bison would be to manage geographic variants separately in large, viable populations under conditions as close as possible to those of primeval times. Aldo Leopold implored "to keep every cog and wheel is the first precaution of intelligent tinkering" (Noss, 1989). We would be wise to bear this analogy in mind as we forge plans for the conservation of remnant populations of bison for present and future generations.

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