

# Phantom Subspecies: The Wood Bison *Bison bison* "athabascae" Rhoads 1897 Is Not a Valid Taxon, but an Ecotype

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**ABSTRACT.** The proposal that the "hybrid bison" of Wood Buffalo National Park (WBNP) be exterminated and replaced with "wood bison" has no taxonomic justification. The subspecies *Bison bison athabascae* Rhoads 1897 is based on inadequate descriptions and taxonomically invalid criteria — i.e., body size and morphometrics. Its accepted pelage features are based on studies of the same herd of Nyarling River (NR) bison from Elk Island National Park (EINP). These pelage features, assumed to be genetically fixed, are ecotypic confinement effects, which NR bison share with EINP bull elk and moose. In bison the display hair acts analogous to deer antlers, which reflect their bearers' access to high-quality food during their growth. NR bison in captivity, in the Mackenzie Bison Sanctuary (MBS), and the original wood bison are "northern plains bison." Nor are WBNP bison distinguishable from MBS bison. A "wood bison" phenotype was also described as diagnostic for southern plains bison (*B. b. bison* Linnaeus 1758); the northern plains bison was named *B. b. montanae* Krumbiegel 1980. Consequently, *B. b. athabascae* = *B. b. bison*, as the latter has priority. Yet captive and introduced NR *athabascae* = *montanae*. Some WBNP bison resemble *B. priscus*, supporting the view that *B. bison* evolved as a hybrid between American and Siberian large-horned bison. Hybridization in large mammals need not be a tragedy for conservation.

**Key words:** wood bison, plains bison, taxonomy, phenotype plasticity, ecotype, display organs, morphometry, subspecies, conservation

**RÉSUMÉ.** Le plan visant l'extermination du «bison hybride» du parc national Wood Buffalo (PNWB) et son remplacement par le «bison des bois» n'a aucune justification du point de vue taxonomique. La sous-espèce *Bison bison athabascae* Rhoads 1897 se fonde sur des descriptions inadéquates et sur des critères qui ne sont pas valides du point de vue taxonomique, à savoir la taille et la morphométrie. Les attributs reconnus du pelage s'appuient sur des études du même troupeau de la rivière Nyarling (RN) dans le parc national Elk Island (PNEI). Ces attributs du pelage, que l'on suppose génétiquement déterminés, résultent de la limitation des écotypes, qui affecte le bison de la RN tout comme le caribou et l'original mâle du PNEI. Chez le bison, la hure (pelage de parade) joue un rôle analogue à celui des andouillers chez le cerf, tous deux reflétant l'accès des animaux à une alimentation très nutritive durant leur croissance. Le bison de la RN en captivité dans la Réserve de bisons Mackenzie (RBM) et le bison des bois d'origine sont des «bisons des plaines septentrionales». On ne peut plus faire de distinction entre le bison du PNWB et le bison de la RBM. On a aussi décrit un phénotype de «bison des bois» pour identifier le bison des plaines méridionales (*B. b. bison* Linnaeus 1758); on a appelé *B. b. montanae* Krumbiegel 1980 le bison des plaines septentrionales; ce qui fait que *B. b. athabascae* = *B. b. bison*, vu que ce dernier a priorité. Cependant le *athabascae* en captivité et relâché dans la RN = *montanae*. Certains bisons du PNWB ressemblent à *B. priscus*, ce qui confirme l'idée que *B. bison* est le produit d'une hybridation entre le bison américain et le bison sibérien à grandes cornes. L'hybridation chez les grands mammifères ne devrait pas constituer une tragédie pour la conservation.

**Mots clés:** bison des bois, bison des plaines, taxonomie, plasticité des phénotypes, écotype, organes de parade, morphométrie, sous-espèce, conservation

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"Change is not made without inconvenience, even from worse to better."  
— Dr. Samuel Johnson (1709-1784), quoting Richard Hooker.

## INTRODUCTION

Taxonomy has become important in conservation (O'Brian and Mayr, 1991). What is or is not a species, by what criteria to distinguish subspecies from ecotypes, transcends academic debate: answers to these questions are vital to the interpretation of laws, treaties and programs governing conservation. The naming of taxa in legislation makes them legal entities, actionable in courts of law. The implications to conservation are profound (Van Camp, 1989; O'Brian and Mayr, 1991). The designation of Wood Buffalo National Park bison as hybrids, for instance, deprives them of legal protection under the Alberta Wildlife Act. Such is granted only to bison designated as *B. b. athabascae*, provided, of course, that such can be identified.

For purposes of identification, all members of a subspecies listed in legislation must be recognizable as such or lose the protection of the law. Consequently, a subspecies has to be defined as a collection of populations whose individuals share common taxonomic — that is, hereditary (genetic) — traits. This would make into polymorphisms taxonomic characteris-

tics not shared by all individuals, though one can designate as a subspecies all populations containing one polymorphism or another. Put another way, subspecies are distinguished by at least one consistent taxonomic difference. Geographic location as an integral part of the definition of subspecies (O'Brian and Mayr, 1991), however, has drawbacks legally, since geographic origin is never a material part of a specimen and must be normally accepted on faith (Geist, 1991a).

The species can be defined as all subspecies not genetically segregated by reproductive barriers in nature (see O'Brian and Mayr, 1991) or as all subspecies sharing one or more taxonomic characteristics (e.g., species of *Ovis* are recognized by chromosome numbers linked to specific morphological features; see Nadler *et al.*, 1973) — that is, as the next cladistic level above the subspecies. If taxonomy is to reflect evolution, then taxonomic criteria must be hereditary ones, little affected by environment. I stress here differences in kind, not in degree (as does quantitative taxonomy) and dismiss subspecies based on comparative morphometrics, as this method is incapable of differentiating genetic, epistatic, environmental and true statistical variation. Experimental, but not comparative, morphometrics may give taxonomically valid results.

In 1989 Agriculture Canada, in concert with federal, provincial and territorial wildlife agencies, proposed to exter-

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minate the bison (*Bison bison* Linnaeus 1758) in Wood Buffalo National Park (WBNP) and replace these, allegedly "worthless hybrids" (*Bison bison bison* x *athabascae*; see van Zyll de Jong, 1986) and carriers of bovine tuberculosis and brucellosis, with so-called "wood bison" (*B. b. athabascae* Rhoads 1897) free of the diseases. The Bison Disease Task Force was struck to deal with matters of information and a panel formed by the Federal Environmental Assessment Review Office (FEARO) held public hearings on the plan 15-26 January 1990; the panel upheld Agriculture Canada's position (Connelly *et al.*, 1990). The purpose of this paper is to reassess bison taxonomy.

#### WOOD BISON TAXONOMY REVIEWED

In his major review of *Bison*, Allen (1876) considered the contradictory reports about wood and plains bison and chose not to formalize the distinction; neither did Hornaday (1887). However, Rhoads (1897) formally recognized wood bison as the subspecies *Bison bison athabascae* Rhoads 1897 but relied on second-hand descriptions of one specimen, which he did not examine. He admitted that the reports about differences between wood and plains bison were imprecise and contradictory (Rhoads, 1897; Roe, 1970:43-57). Rhoads used J. Macoun's description of wood bison: "Size larger, colors darker, horns slender, much longer and more incurved and hair more dense and silky than in *B. bison*." What taxonomic criteria are valid or not was not considered, but as van Zyll de Jong (1986) points out, criteria for subspecies distinction remain obscure and unsettled even now.

As determined by the careful and critical Roe (1970:43-57), there is little doubt that in historic times bison existed in at least two forms, a dark, large, shy, non-migratory wood bison in the north, and a smaller, lighter, aggressive, migratory plains bison in the south. There may have also been populations of mountain bison (Meagher, 1973), possibly analogous to the small mountain wisent (*B. bonasus caucasicus*) of Europe (Heptner *et al.*, 1961), as well as some regional differences that native people recognized (Seton, 1929:709). Roe (1970) was not concerned if these differences were taxonomically relevant, that is, of genetic origin, or if they were ecotypic, that is, a product of environmental circumstances; he was concerned if the differences reported had some foundation in reality. He concluded they had.

Roe (1970), in his evaluation of the historical literature, unfortunately did not take into account the notable seasonal and age-related differences in the characteristics of bison coats, nor, excepting colour, did he address within-population variability of pelage features in bison. Macoun's account of the wood bison specimen's pelage published in Rhoads (1897) would also fit a plains bison. Also, bulls may shed their long display hair in fall (Lott, 1979). Since bison push abrasive snow with their head during feeding, there may be wear on the head hair during winter.

One finds among plains and wood bison old bulls with fairly uniformly coloured hair on the body and with poorly developed chaps and display robes (see Figs. 1b, 3b). (Figures 1-11 are arranged in a sequence suitable for comparison.) The "Radford bull" described by Seton (1929) could have been an example of these. These old bulls may have regressed testes (analogous to what happens in old bulls of African buffalo *Syncerus caffer*; Sinclair, 1977). These bulls suggest that old age may bring about changes to the display hair.

No good illustrations of wood bison made prior to 1925 appeared to exist. The exception, Rowan's (1929) popular article containing one sketch and one photo of wood bison, escaped attention, as did his archives. Hewitt (1921:Plate 12) published a fuzzy photo of a distant wood bison bull obscured by vegetation. Garretson (1938:12) shows the photo of a mounted wood bison head with a short, erect frontal hair mop and a thin, pointed beard, no different from a plains bison. The best description is by Seton (1929) of a large bull shot on 1 December 1909 by Harry V. Radford 120 km southwest of Fort Smith and exhibited in Calgary in 1914; the mount has proven untraceable. It is surprising that Seton (1911), who habitually made high-quality sketches of plants and animals, would leave sketches of plains bison (Seton, 1909) but not of wood bison. Two photos of wood bison taken in the field (Seton, 1929:Plate CIV) show tiny, indistinct images, not only obscured by vegetation, but apparently retouched as well. I was unable to trace the original photos in the archives. The upper photo of Plate CIII in Seton (1929) shows two bison in captivity, one of which has "wood bison" characteristics, but Seton fails to comment. Were there no differences for him to notice?

William Rowan, of the University of Alberta, a zoologist with exceptional artistic abilities who was well acquainted with plains bison from Bison National Park and who observed and collected original wood bison in 1925, apparently saw no differences between them. He wrote: "They [the wood bison] are generally considered to be an offshoot from the plains race, but on what evidence I am unaware" (Rowan, 1929:360).

McDonald (1978), in a comprehensive taxonomic review of *Bison*, used size and horn core characteristics as taxonomic criteria. He upheld the subspecies *B. b. athabascae* but considered the differences from *B. b. bison* slight and not applicable to all individuals. While horn core differences are controversial taxonomic criteria interspecifically (Guthrie, 1966), they are doubtful taxonomic criteria intraspecifically due to allometric changes associated with body size. McDonald's (1978:463) assumption that *athabascae* is genetically larger than *bison* proved unfounded.

In the late 19th century the bison population in what is now WBNP went through a "bottleneck" of possibly 300-500 individuals (Seton, 1911:320); it increased to about 1500 in the 1920s. Some 6673 plains bison, mainly yearlings and two-year-olds, were introduced to WBNP from what was once Buffalo National Park near Wainwright, Alberta, commencing 25 June 1925. Many did not survive the relocation (Van Camp, 1989). The plains bison were carriers of bovine tuberculosis and brucellosis (Honest and Winter, 1956; McHugh, 1972; Broughton, 1987). Subsequently, plains bison bred with wood bison and infected them with the diseases.

However, due to N.S. Novakowski, of the Canadian Wildlife Service, bison that appeared to have escaped hybridization were discovered along the Nyarling River (NR) in WBNP in 1957. Two herds were salvaged from this stock, one in 1963 to the Mackenzie Bison Sanctuary (MBS) and one in 1965 to Elk Island National Park (EINP). The NR bison in the MBS originate from 6 males and 12 females, the herd in EINP from 4 males and 17 females. Both herds of wood bison are thus based on small samples of the wood bison gene pool. The claim that 37 (actually 39) wood bison, which formed the founding stock for the MBS and EINP herds, captured a "significant part" of the genetic diversity of wood bison (p. 57 of

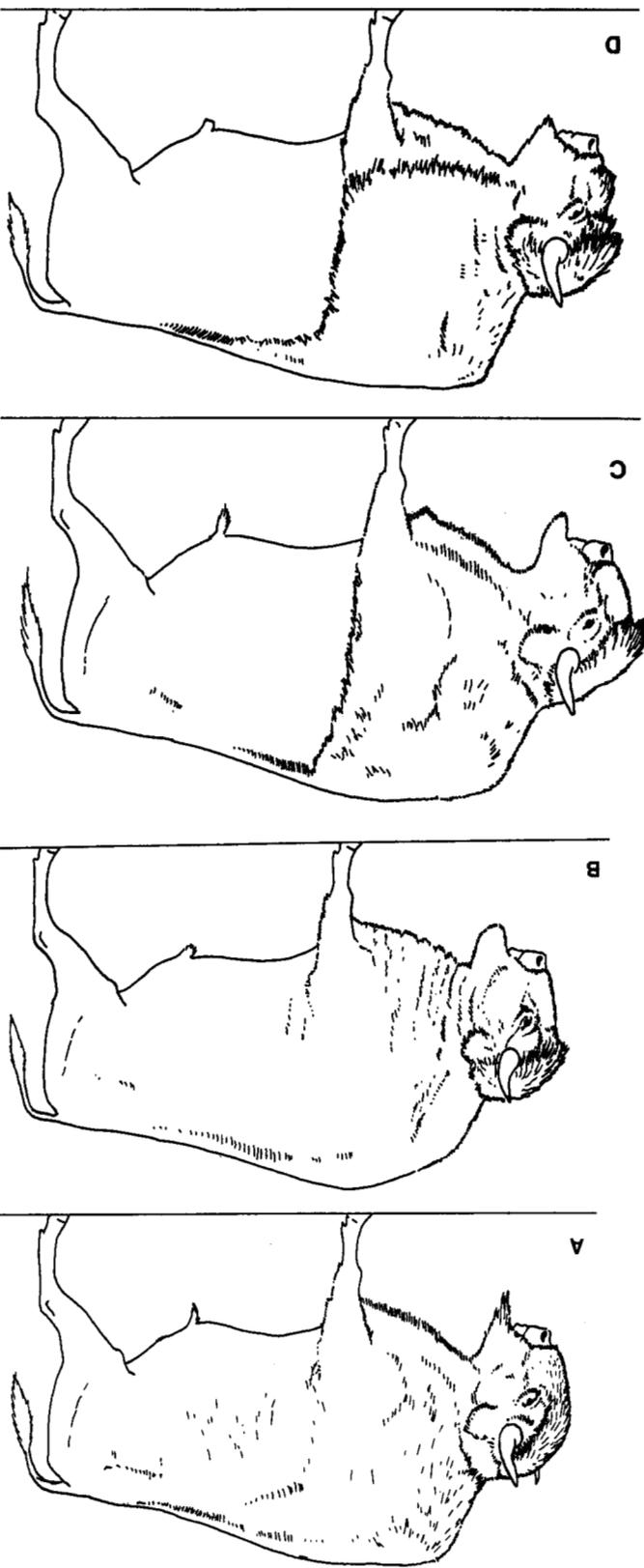


FIG. 2. Archetypal wood bison bulls of Nyarling River (NR) origin in Elk Island National Park (EINP), and southern plains bison bull. a) Old NR bull in summer coat (28 July 1980) without visible sign of a cape and short display hair on head and front legs (van Zyll de Jong, 1986:42, Fig. 1). b) Old southern plains bison bull during hair shedding in early summer, held in Hamburg zoo in 1923 (Krumblegel, 1980:154, Fig. 5). c) Younger NR bull in August 1977 (van Zyll de Jong, 1986:42, Fig. 3). d) NR bull in mid-winter 1979.

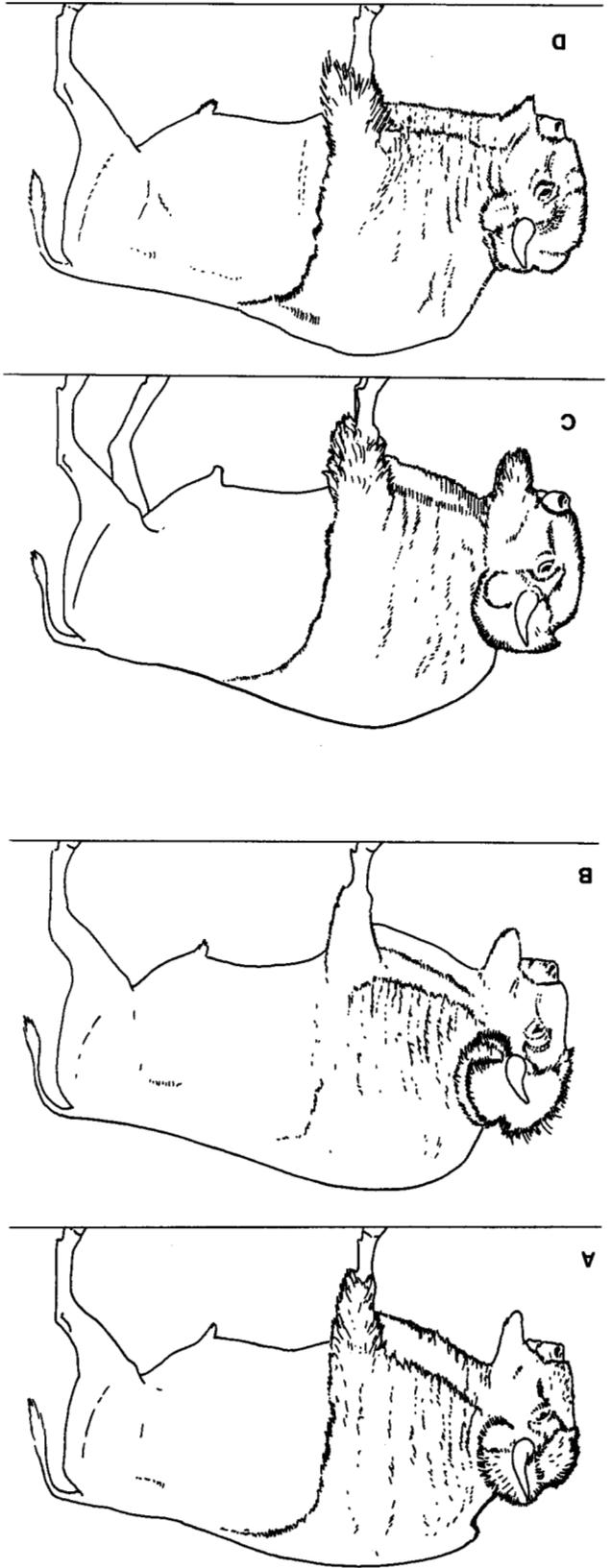


FIG. 1. Some variation in the coat and humps of bison bulls arranged and sketched for comparability: a) A Montana bull in late-winter coat with an unusual hump morphology (McHugh, 1972:198-199). b) A very old white Montana bison bull, called Old Medicine, in late winter coat. Note the absence of chaps or distinct long-haired cape (McHugh, 1972:198-199). c) Mature plains bison bull Black Dog in late-summer pelage (Garretson, 1938:5). d) Mature plains bison bull from Elk Island National Park (EINP) in mid-summer during mating season.

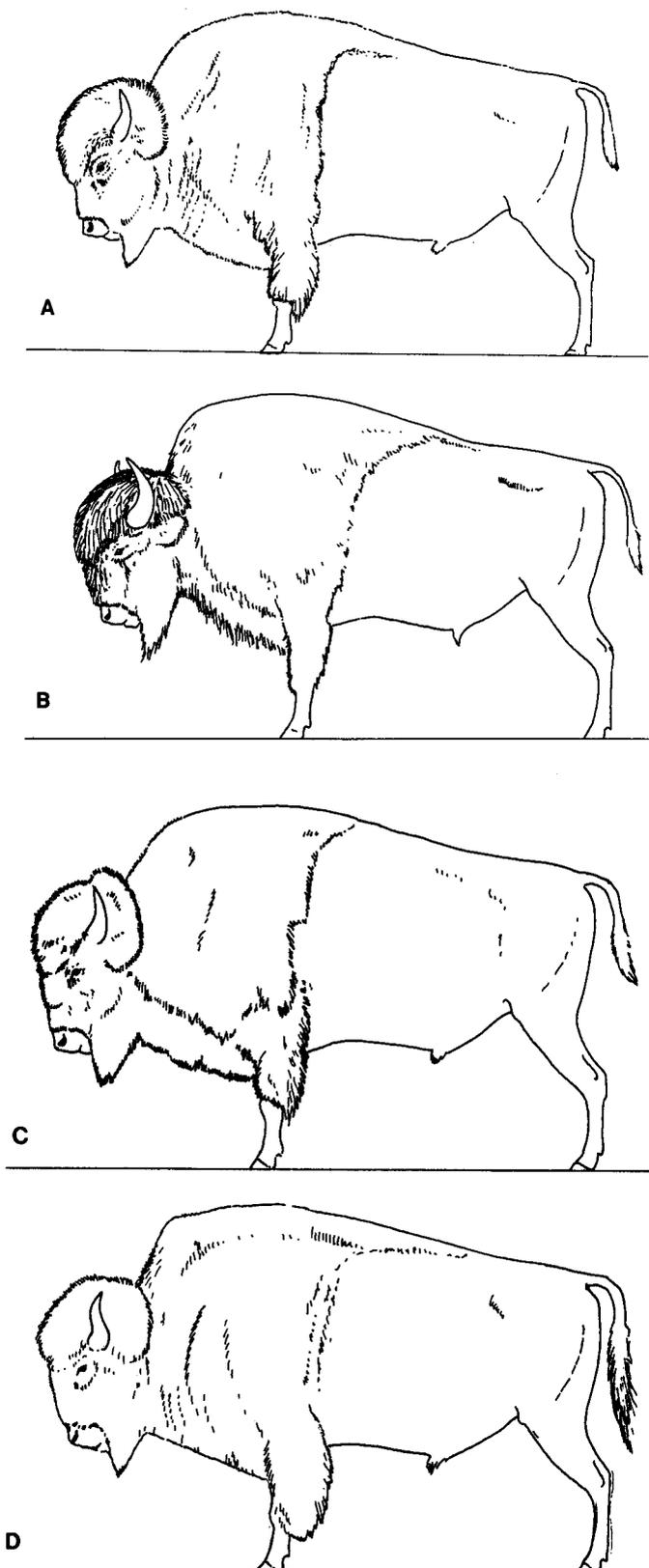


FIG. 3. More southern plains and NR bison: a) Fairly young bull from the Texas Goodnight herd, after archival photos. b) "Old Tex," very old bull originating from Texas bison in winter hair, renowned for his long record horns, held in captivity in Yellowstone National Park in 1926 (Maegher, 1973, Fig. 23). Note reduced chaps and long bonnet hair. c) NR bull from EINP in mid-winter (1979) with well-developed display coat. d) Young NR bull held captive in Calgary Zoo till 1991 in early summer coat.

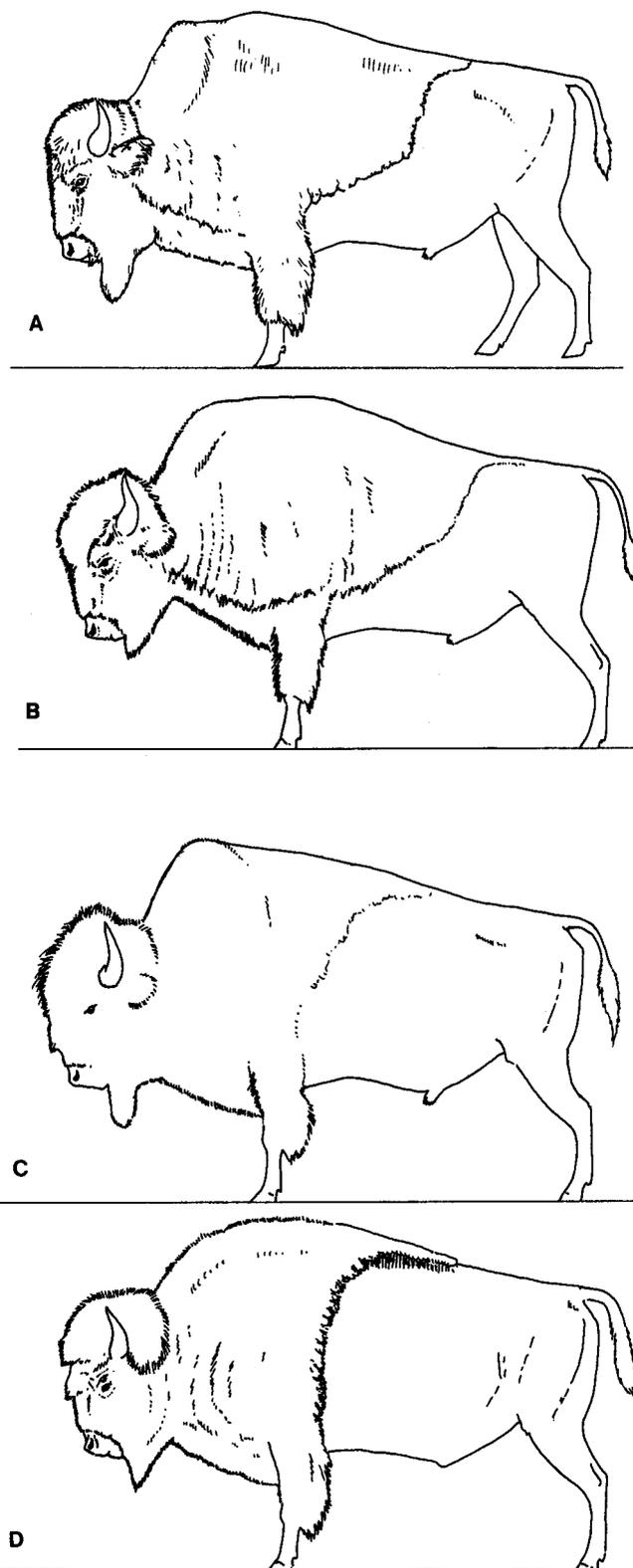


FIG. 4. Captive NR bulls originating in EINP but held captive *away from* Elk Island National Park. a) Four-year-old NR bull in August 1980 held on the Wildlife Reserve of western Canada, near Cochrane, Alberta. The display hair is well developed. This bull features the long cape. b) A three-year-old NR bull transferred to a paddock in the central Yukon, where natural forage was supplemented with hay. The bull shows a well-developed display coat one year after leaving EINP. c) Mature wood bison bull in Moose Jaw Wild Animal Park, with long-haired display coat (17 June 1983). d) Four-year-old NR bull held captive in display paddock in Banff National Park in February 1991. The display hair is long everywhere.

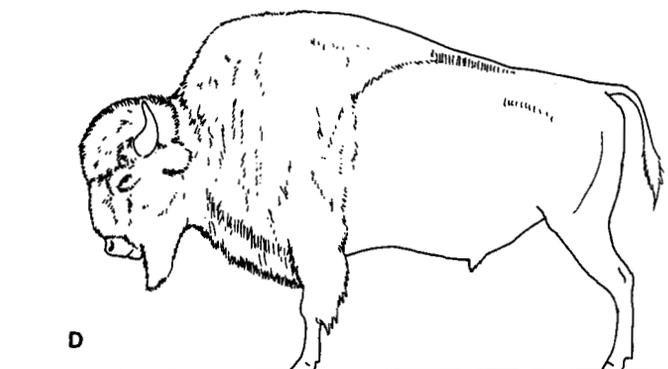
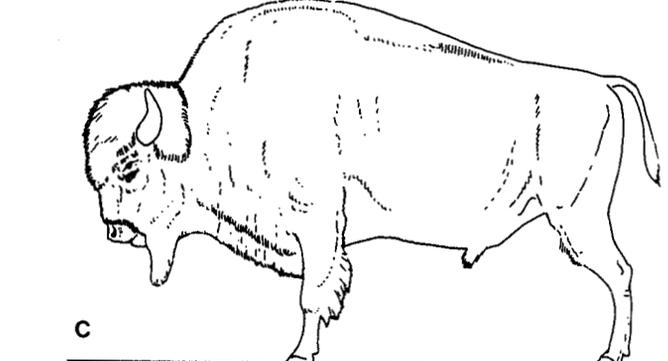
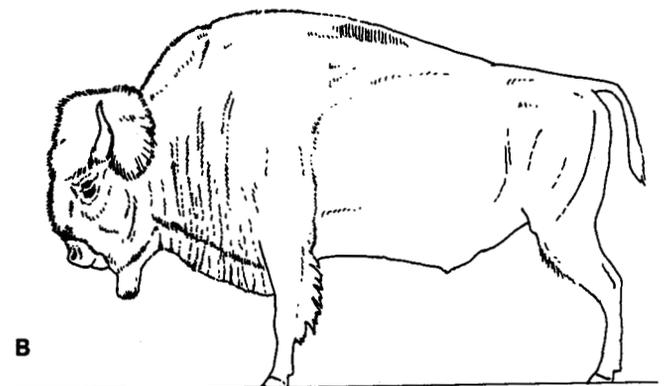
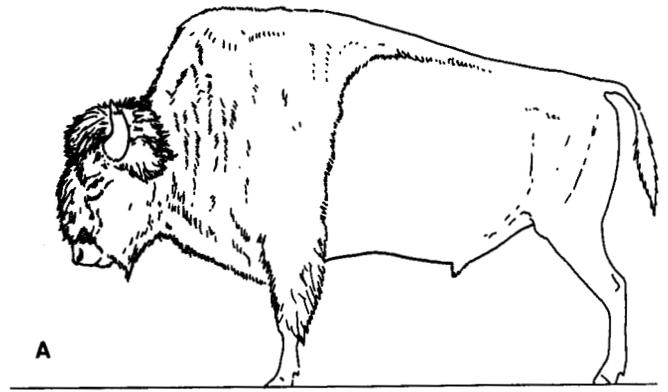
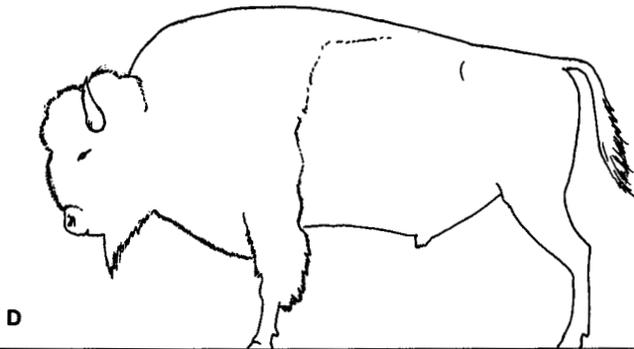
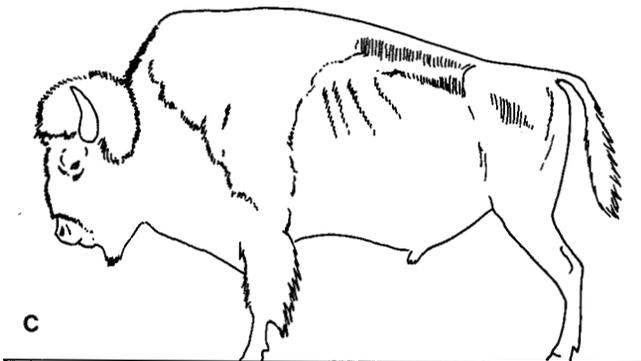
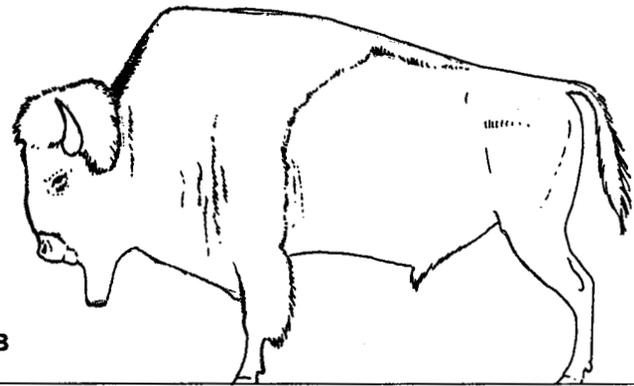
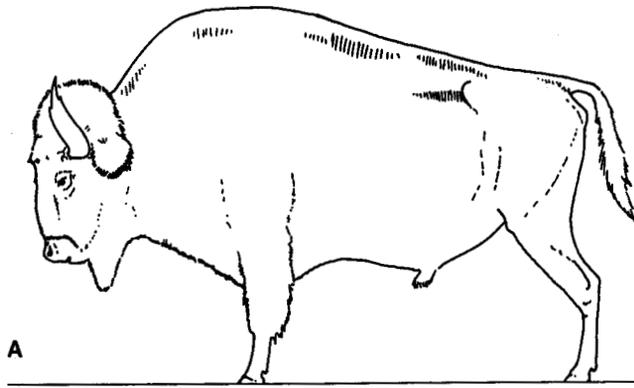


FIG. 5. NR bison in the Mackenzie Bison Sanctuary in May 1990. a) An old, emaciated bull well into shedding, with short chaps but long bonnet hair between the horns, a full beard and a tall hump that is not elevated anteriorly. b) Mature bull beginning to shed with long-haired display coat and anteriorly elevated hump. c) Mature bull with long display hair and elevated anterior hump. d) Young bull with low hump, depressed anterior and mid-length display hair and scraggly beard.

FIG. 6. Original wood bison bulls illustrated in or before 1925, plus bull from captivity. a) An old wood bison bull taken in early September 1925 and sketched from two sketches and one photograph left by William Rowan in the archives of the University of Alberta. Note short-haired display hair, patterned much as in plains bison. The hump shape is conjectural. b) Old bull in early fall with long-haired display hair, but still without a cape. From photo by Rowan. c) Mature bull with long-haired display hair but still without cape in late summer. From photo by Rowan. d) NR bull from EINP in captive herd in Toronto Metro Zoo, 3 September 1984 (van Zyll de Jong, 1986:43, Fig. 6).

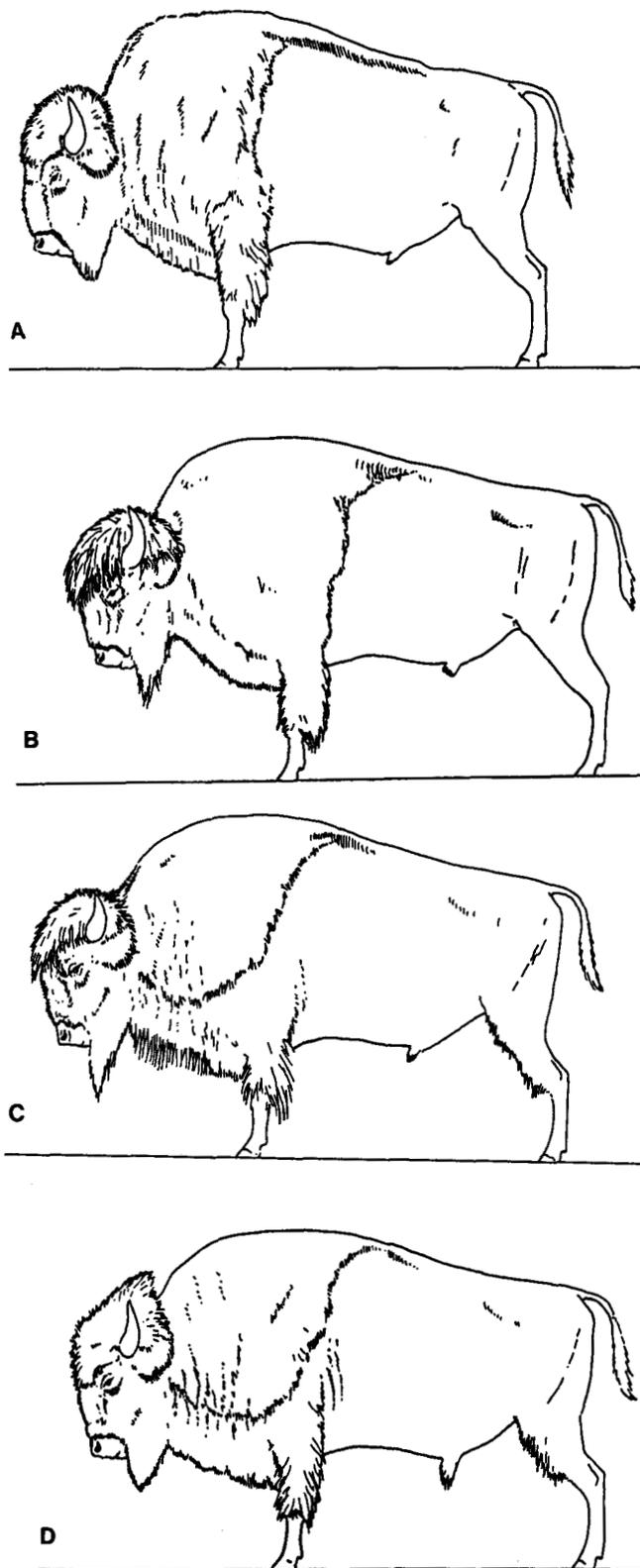


FIG. 7. Northern and southern plains bison bulls. a) A bull from Yellowstone National Park showing the high hump found in this bison population (Meagher, 1973). b) Captive southern plains bison bull with long, procumbent frontal hair (after Heck, 1936). c) A bull from the Wichita Mountain Reserve in summer, with features reminiscent of the southern plains bison as described by Krumbiegel (1980). Note the long frontal hair and thin, though long, display hair. d) Other bulls from the Wichita Mountain Reserve featured typical "plains bison" features (the display hair on this bison's head is blown back by wind).

the Compendium of Government Agencies Submissions) is unacceptable. It confounds absolute population size with effective population size and ignores the subsequent loss of genetic information through genetic drift, maternal relatedness and, especially, the male-dominance effect (see below).

The next authors to provide descriptions and illustrations of wood bison were Geist and Karsten (1977). They made detailed comparisons of NR bison and plains bison held separately in EINP. Their "wood bison" agreed with the partial description by Seton (1929) of the Radford Bull and was confirmed by van Zyll de Jong (1986), who used the same groups of plains and "wood bison" in EINP. Van Camp (1989) published a photo of a bull from Hook Lake, east of the Nyarling River, with classical "wood bison" features. The image of wood bison by Geist and Karsten (1977) became the archetype of the "wood bison phenotype," at which conservation efforts were henceforth directed.

However, following the publication of Geist and Karsten (1977), directors of zoos pointed out that captive wood bison did not conform to the published descriptions but had hair coats similar to northern plains bison. A herd of "wood bison" held captive near Edmonton and examined by Geist and Karsten on 24 October 1975 also had northern plains bison features. These bison, strikingly different from the wood bison in nearby EINP, were dismissed as potential hybrids. Peter Karsten, then a member of the committee for the rehabilitation of wood bison, notified the committee and voiced concerns about the "wood bison" phenotype. He made arrangements for two herds of NR bison to be established in or near Calgary to observe their development.

Krumbiegel (1980) proposed that plains bison be segregated into two subspecies, a "southern plains bison," the nominal subspecies (*Bison bison bison* Linnaeus 1758) and a "northern plains bison" (*B. b. montanae* Krumbiegel 1980). He followed here an earlier lead by Heck (1936), who drew attention to the differences between the bison German zoos acquired before the 1870s and those just before and after World War I. Krumbiegel's (1980) description of southern plains bison pelage is close to that of Geist's and Karsten's (1977) for wood bison (Fig. 2b); the same pelage appeared to grow on two purported subspecies, *B. b. bison* and *B. b. athabascae*. Krumbiegel (1980) published in German, but subsequently his views appeared in English (Krumbiegel and Sehm, 1989).

Van Zyll de Jong (1986) dismissed Krumbiegel's (1980) research of historic sources on the basis of inadequate sampling and because van Zyll de Jong's (1986) morphometric analysis failed to distinguish southern from northern plains bison. Unfortunately, craniometry distinguishes differences related to size, not necessarily differences related to genetics, and van Zyll de Jong's (1986) data shows that all plains bison had skulls of similar size. This is illustrated, for instance, by the findings of Bohlken (1967) that *B. bonasus* (wisent) is craniometrically closer to *B. b. bison* than the latter is to *B. b. athabascae*, even though *B. bonasus* is biologically quite different from *B. bison*. For instance, post-cranially, wisent are quite different from bison (Bohlken, 1967; Guthrie, 1989), much less adapted to cursorial life and, compared to the latter, notoriously difficult to keep in captivity, in part due to the wisent's adaptations to browsing (Heck, 1936). Wisent have much less-differentiated display hair and a different shedding pattern from bison, and the calves do not have the light neonatal coat.



FIG. 8. Four bison from WBNP in late summer, two bulls (above) and two cows. One bull has the light-coloured long cape, which extends back to the hips; both cows have the long cape. All have well-developed display hair. Photo: L. Carbyn.



FIG. 9. A bull from WBNP in late summer with blond long cape and short display hair on head and legs. Such a bull among bulls with long-haired display coats suggests a genetic polymorphism in display coat features. Except for the short horns and the lack of a large bulge over the neck, this bull resembles *B. priscus* in its pelage features. Photo: L. Carbyn.

Van Zyll de Jong (1986) accepted multiple photographic images for pelage analysis of wood bison from the inbred herd of NR bison in EINP. Relying for data on an inbred herd, no matter how well sampled, describes with increasing precision at best a small range of the natural variation. At the worst, it accepts phenodeviants as normal. Krumbiegel's (1980; Krumbiegel and Sehm, 1989) historic sources on bison covered a wide span in geography and time, which gives some credence to his conclusions. His claim that southern and northern plains bison are taxonomically distinct rests on pelage differences virtually identical to those accepted as valid taxonomically by van Zyll de Jong (1986). He published photos of captive EINP wood bison that had pelages typical of northern plains bison (Figs. 4c, 6d) but appeared unaware that captive wood bison assumed plains bison features.

Concurrent with conventional means of defining wood and plains bison taxonomically, attempts were made to analyze genetic differences among bison populations. The results were ambiguous. Peden and Kraay (1979) found that plains bison populations differed in blood-typing reagents and carbonic anhydrase alleles as much as did the NR bison from plains bison in EINP, even though different herds of plains bison

originated from the same limited stock at the turn of the century. One cannot assign individual bison to a given subspecies using unique genetic markers on chromosomes (Ying and Peden, 1977) or in blood proteins (Peden and Kraay, 1979), mitochondrial DNA (Cronin, 1986) or nuclear DNA (Bork *et al.*, 1991).

Moreover, there are fundamental difficulties with the genetic analysis when applied to current bison herds: any differences discovered are assumed to represent *evolved* differences, possibly related to differences in *adaptation*. Unfortunately, divergences in allelic frequencies between today's salvaged bison populations are expected for reasons other than adaptation or random mutation. These include differences based on the *founder effect* (reduction of the genetic diversity due to taking of a small sample of bison to found new herds), *genetic drift* (random fixation of alleles in small populations), the *maternal effect* (bison captured from the same herd have a high probability of being related by maternal descent, and have thus reduced genetic diversity) and the *male dominance effect* (disproportionate genetic contribution of the most dominant founder bull in tiny founding populations).

In a founder herd of only 4 bulls and 17 cows, such as that of NR bison turned loose in EINP, social competition among the bulls insures that only *one* bull will do virtually all the breeding for 4-6 years, including after 3-4 years his own daughters. Then he will be displaced by his sons. These, grown to larger size on the unoccupied, rich range, displace their father and breed their mothers, aunts, sisters and cousins. Inbreeding results in the fixation of meaningless phenodeviants. For this and other reasons, small founder populations of bison would rapidly diverge in allele frequencies and impoverish genetically, generating zoologically meaningless genetic "pseudo-subspecies" of little value to conservation.

Moreover, any close genetic relationship of NR bison and EINP plains bison could be, in part, due to hybridization. Van Zyll de Jong (1986) and Carbyn *et al.* (1989) marshalled evidence that the NR bison were not isolated from the park's southern populations. From 61 bison captured on the Nyarling River, 24 carried bovine diseases. When bison were numerous in the 1940s, the NR bison were not separated by 160-320 km of unsuitable habitat from other bison (Banfield and Novakowski, 1960) but were at the most 16 km apart (see Fuller's, 1950, distribution map). Granted the propensity of bison to move rapidly and capriciously over long distances in response to predation, granted a well-used trail system between the Nyarling and the Peace rivers, then there is little doubt about contact among bison throughout WBNP. The minor genetic differences among NR and EINP plains bison are taxonomically meaningless. Differences of the same order exist among plains bison herds that originated from the same founding stock at the turn of the century (Peden and Kraay, 1979).

It escaped notice that *all* recent taxonomic work on wood bison used only the inbred NR bison in EINP. Did these match the NR bison released in the MBS? How did wood bison look prior to 1925, before mixing with plains bison in WBNP? How did EINP wood bison change in captivity? How did they resemble "southern plains bison," and were such still extant?

Beninde (1937), in a study of transplanted red deer, found that different genotypes transplanted to the same environment converge on the resident phenotype. This was subsequently experimentally confirmed using passerine birds by James

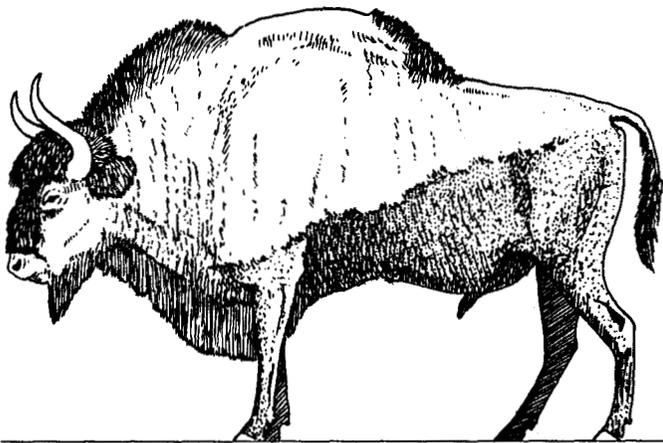


FIG. 10. External features of the extinct long-horned Eurasian-Alaskan steppe bison, *B. priscus*, regarded as an ancestor of *B. bison*, after Geist (1971) and Guthrie (1989).

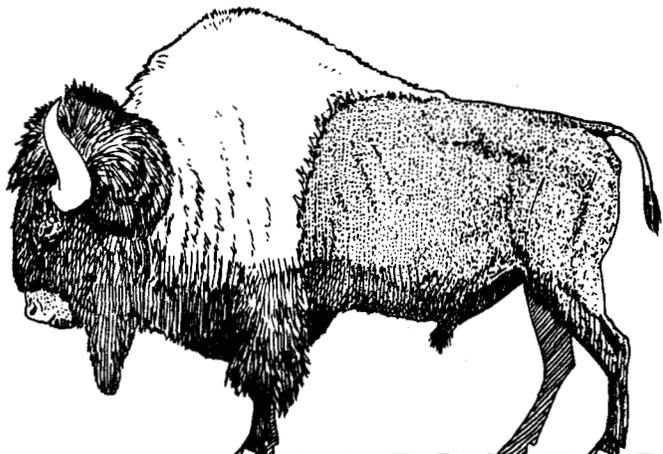


FIG. 11. Reconstruction of the extinct North American late Pleistocene thick-horned bison *B. antiquus*, regarded as an ancestor of *B. bison*.

(1983). This implies that plains bison transplanted into wood bison habitat and given time to overcome the tenacious phenotypic lag-effect to changes in environment, the maternal effect transmitted non-genetically over several generations (Vogt, 1948; Chandra, 1975; Denenberg *et al.*, 1962; Denenberg and Rosenberg, 1967; Beach *et al.*, 1982), will assume the wood bison phenotype. Do current "hybrids" in WBNP look like wood bison?

#### ARCHETYPAL WOOD BISON

The most distinct differences between the archetypal "plains" and "wood" bison from EINP (Figs. 1,2) are 1) the absence of long-haired, dense "chaps" in wood bison of both sexes; 2) the absence of a long-haired, usually light cape that terminates sharply behind the front legs; 3) the procumbent, long, thin frontal display hair, in contrast to the "Afro" hair-rolle of the plains bison; 4) the thin, short beard of the wood bison, compared to the full beard of the plains bison; 5) the short-haired ventral neck mane of the wood bison, compared to the long-haired neck mane of the plains bison; 6) a taller, more pronounced anterior hump in the wood bison, while plains bison (normally) had a lower hump with the anterior part of the hump lower than the main hump (Geist and Karsten, 1977; van Zyll de Jong, 1986). However, this is not a consistent characteristic, as plains bulls with wood bison humps are found, and vice versa.

In principle, the NR bison of EINP differ from northern plains bison by short display hair on the head, neck, cape and front legs. The display hair grows more slowly during spring, summer and fall than in plains bison. Thus in early fall the cape may be only outlined, but in winter the display hair has grown in place and is then reminiscent of plains bison, but shorter in length. In summer, after shedding the winter hair, big EINP wood bison may appear virtually "naked." Young bulls show more of a procumbent hair mop than do old bulls.

Southern plains bison bulls, as described and illustrated by Heck (1936), Krumbiegel (1980) and Krumbiegel and Sehm (1989), had a procumbent frontal hair mop of long hair; some had a short-haired display robe terminating behind the shoulders; some had full- and some had thin-haired chaps or no chaps at all (Figs. 2b,3b) and a short ventral neck mane. These claims are supported, in part, by two photos of southern bulls in captivity in Germany (one a very old bull — Fig. 2b) and by early 19th-century sketches of northern and southern plains bison. (In these sketches, both subspecies of plains bison have an elevated anterior hump, a feature considered diagnostic of wood bison [van Zyll de Jong, 1986], but not absent in plains bison. This identity may be due to artistic licence.)

These are the sources of southern plains bison I examined: 1) Wolfgang Frey kindly sent me photos of southern plains bison bulls from the Goodnight Herd, which he had found in the archives at the Historical Panhandle Plains Museum in Canyon, Texas, and in the Antonius Collection in Berlin. The remnants of the Goodnight Herd are the only unadulterated plains bison, derived entirely from stock captured in the Panhandle of Texas by Charles Goodnight, beginning in 1878 (Garretson, 1938). Three young bulls feature somewhat short, erect display hair on the head, while the fourth bull, a large mature male, has a long-haired "Afro," a full beard and long neck hair. All had robes cut off behind the shoulders and good chaps. None features a long-haired, procumbent hair mop. The hump line was typical for plains bison. 2) In Seton (1929),

Plate CIII has three photos of captive plains bison; the upper one shows two bison, one of which matches Krumbiegel's (1980; Krumbiegel and Sehm, 1989) description of southern plains bison. 3) Thomas and Toweill (1982:513) show a photo of a bison bull confronting a hunting party in Kansas in 1867. The bull, partially obscured, has a small hair mop on his head with procumbent frontal display hair, a diffuse cape and a low hump typical of plains bison. It appears to have chaps. 4) "Old Tex," a bull originating from Texas bison and held many years in Yellowstone National Park (Maegher, 1973; see Fig. 3b), fits Krumbiegel's description. 5) The southern plains bison phenotype can be identified today only with difficulty in photos of the Wichita Mountain herd. Seven of eight bulls are close to northern plains bison; one bull only approaches the phenotype of southern plains bison (Fig. 7b).

Van Zyll de Jong (1986), in addition to examining pelage characteristics, applied morphometrics to populations of plains and wood bison. He concluded that the NR bison were more similar to the original wood bison than to plains bison. Not unmindful of the pitfalls inherent in morphometrics as a tool to analyze taxa, van Zyll de Jong (1986) felt that his case was strengthened by what he thought were three relevant facts: 1) That bison collected before 1925 from the original wood bison range conformed closely to the EINP and MBS wood bison, while individuals from all three populations differed noticeably from the plains bison in EINP and from old plains bison samples. 2) That in EINP wood and plains buffalo were distinct, although they lived in the same environment. 3) That in captivity neither wood nor plains bison changed their respective appearances.

It turns out that all three contentions are invalid (see below); cranial similarities to original wood bison by NR bison from EINP and MBS are based on size, an unacceptable taxonomic criterion; comparative morphometry distinguishes populations, not taxa. EINP wood and plains bison live under different forage regimes, while the "wood bison" phenotype changes in captivity or in transplants to a "northern plains bison" phenotype.

#### CAPTIVE AND TRANSPLANTED WOOD BISON

Captive or transplanted wood bison from EINP look much like northern plains bison. In addition to the plains-bison-like wood bison bulls in captivity in Toronto and Moose Jaw (van Zyll de Jong, 1986:43), NR bison from EINP in four captive herds assumed a northern plains bison exterior (long-haired and dense chaps, long-haired and sharply bordered display coats, "Afro" hair mops, full beards and long ventral manes; some bulls have a high anterior hump, some do not; Figs. 4, 6d).

1) The EINP wood bison bull on Smeeton's game farm near Cochrane, four years old (Fig. 4a), had a hump reminiscent of NR bison in EINP (as did the large bull held captive in Moose Jaw, Fig. 4c), but had an upright hair mop, a large, broad beard, long nape hair and dense chaps. His cape, sharply set off from the short, dark body hair, however, was unusual; it was a "long cape," reminiscent of the extinct *Bison priscus* (Fig. 9). The two cows had regular northern plains bison features.

2) Four adult EINP bison of NR origin held in the display paddock of Banff National Park show classic plains bison features (Fig. 4d). The four-year-old bull has an exceptionally tall "Afro" hair style, a very light, long-haired cape distinctly set off just behind the front legs and a long beard, chaps and nape.

3) All four EINP wood bison held until early 1991 in the Calgary Zoo had northern plains bison features (see Fig. 3d).

4) Thirty-four EINP wood bison were released in a large enclosure in the central Yukon Territory on 6 March 1986. Photos from winter 1986/87 to fall 1987 were available. Three full-grown bulls appeared in their 1987 pelage as follows: one had plains bison features, except for a high first hump; one had "wood bison" features, except for a light, well-delineated cape and moderately long chaps; one had plains bison features, including the first hump lower than the second, but the display hair was short everywhere (Fig. 4b). From six adult cows only one had an elevated first hump; one had a high hump, but the first hump was not taller than the second. All had chaps and well-delineated capes, except the cow with the tall first hump. Her chaps were long but thin, and the cape, though well developed, blended into the body hair gradually.

5) In examining captive plains bison from EINP, the bison herd held in 1963 in the buffalo paddock of Banff National Park and bison from Waterton National Park, as well as pictures of wood bison in EINP in different seasons, one notices certain variations: since the cape grows out fully in late summer, plains bison in early summer may have little cape and feature no distinct delineation of the cape. The plains bison held in 1963 in Banff had very tall humps in which the height of the anterior hump varied with the posture, often exceeding the second hump. Body colour varied with the wetness of the fur. Plains bison in summer with wet fur are as dark as wood bison under the same condition. EINP wood bison in the Yukon holding enclosure looked a lot more like "wood bison" during the spring moult than at other times of the year; some had long, thin procumbent hair, a thin beard, virtually no ventral mane and short, thin chaps. Observations in the Leipzig Zoo suggest that the long hair in the chaps of wood bison can be pulled out readily (letter from W. Frey to S.N. Stuart, IUCN, 1987). The long display hair of plains bison bulls drops out before winter (Lott, 1979).

Van Zyll de Jong's (1986) assumption that wood and plains bison retain their phenotypic characteristics in captivity is not tenable.

#### NYARLING RIVER EINP AND MBS SPECIMEN COMPARED

I examined colour photos of nine male and four female bison from the Mackenzie Bison Sanctuary taken in May 1990. These descended from bison captured at the Nyarling River, as are the wood bison held in EINP (Fig. 5).

1) A bull, apparently three to four years old, has an erect hair mop between the horns, a short beard, good chaps, full tail; no noticeable cape development, but light (brown) hair slants down from tail-root to elbow. A short, black, mid-dorsal streak leads to the hump. The tall hump peaks anteriorly, as in EINP wood bison.

2) The remaining bulls were all older or very old animals in various stages of shedding. All had an erect, well-developed hair mop between the horns, as well as long-haired, thick chaps on the front legs. Three had massive beards, three did not; one was grazing and his beard was hidden. One had the long cape, four had a cape cut off behind the front legs and three were too advanced in shedding to tell. In five bulls the hump peaked anteriorly; in three it did not.

3) The bison cows were in a nursery herd. They were all tall-humped, with flat hump lines, peaking in front in two

cows but peaking over the shoulders in two other cows. All had erect hair mops and long, dense chaps.

These bison from the MBS, although of the same origin as the EINP wood bison, showed little similarity to the EINP animals.

#### NYARLING RIVER BISON AND WBNP BISON COMPARED

In a colour photo of WBNP bison, the animals are fully shed out with the capes growing in; the season is mid-summer. All twelve old, mature bulls have tall humps; in eleven the anterior is higher. In a second photo six of eight large bulls have the hump elevated anteriorly. Of fourteen unobstructed capes, only one is a long cape, seven are short capes and in seven others the colour extends back to the hip, but only over the shoulders is the cape hair long. Procumbent hair mops can be seen only in young bulls. The black dorsal neck stripe is well exposed because the cape hair is still short. All cows have capes of the extended type. In another photo three bulls have cut-off capes and big, erect hair mops on the head; the chaps are invisible in deep grass. All three have humps that peak anteriorly, possibly because they hold their heads high in the deep sedges. In another photo all five bulls have short capes, big chaps, erect hair mops and anteriorly elevated humps.

In a selection of slides taken in early fall in WBNP one sees bulls with long capes, short capes and barely distinct capes ranging in colour from straw-blond to reddish dark brown. All big bulls but one have big erect hair mops and chaps. One bull, however, has no chaps, a long cape and short head hair; he also resembles in colouration and hump shape a *Bison priscus* (Fig. 9). The bison bulls and cows of WBNP are not discernibly different from those in the MBS, and they share with EINP bison from the NR the high, anteriorly elevated hump. They look much like captive EINP wood bison or large plains bison. However, a few individuals resemble the "archetypical wood bison," except for having a long, light cape, and have humps reminiscent of those of *B. priscus* (Geist, 1971:Fig. 7; Guthrie, 1989:Fig. 5.13). Different hair styles segregating out in the same population suggest a strong hereditary polymorphic component for the hair patterns.

#### NYARLING RIVER AND ORIGINAL WOOD BISON COMPARED

In November 1990, W. Fuller, University of Alberta, mentioned a portrait sketch of wood bison made by the late William Rowan. John Foster kindly checked the Rowan Archives, where he found photos and sketches of wood bison, as well as an original of Rowan's (1929) article.

One is a portrait sketch of an old wood bison bull shot in early September 1925 and published in Rowan (1929). The bull has rather short but erect display hair all around; there is no procumbent hair mop between the horns (Fig. 6a). A poorly exposed photograph of apparently the same downed bull confirms the shortness of the hair between the horns. The head resembles a mature NR bull in van Zyll de Jong (1986:45 Fig. 6) that van Zyll de Jong considers to be similar to the "plains bison" phenotype.

Rowan, in a second sketch of a wood bison bull, attached said portrait to a plains bison bull body. This was not a technical sketch, but a Christmas card. The photo of the downed bull shows a darkish cape with hair only slightly longer than the body hair, with a light streak right behind the front leg. It

appears to be a classical short cape, as it extends on the back along the spine, but not over the ribs; I cannot discern a dark mid-dorsal stripe on the neck. The upper front legs are short haired, with sparse strands of long hair; the rear margins of the leg, where long chap hair is expected to grow, is not visible. Rowan's "Christmas card bull" does have big chaps.

The photo Rowan (1929) published of a wood bison herd at Graham's Ford in 1925 was augmented by a second one of the same herd, the negative of which was discovered by Ian MacLaren. Both show a distant herd and the images are small and somewhat obscured. There are bulls with large humps, but I see only one hump elevated anteriorly. They sport big, erect frontal display hair, but some have short-haired and procumbent hair mops; the cows have short beards and frontal hair. One can decipher several light, apparently short-haired capes, distinctly set off right behind the shoulders. The front legs are largely obscured by shrubs, but the few visible are noticeably thicker than the hind legs, indicating at least modest chaps.

Rowan's 1925 diary held additional sketches and loose photos, among them three photos of bison bulls (Fig. 6), of which only one resembles bulls from the NR herd in EINP. The bulls have not yet grown the display capes. Their heads resemble those of plains bison; the hump is tall, but not dissimilar to that of plains bison, and they have well-developed chaps on the rear margins of the front legs, and even some elongation of hair on the hind legs. Another photo of a herd of wood bison shows animals with light capes sharply cut off behind the shoulders and large, erect mops of hair on the heads. Unfortunately, these photos are not labeled, and only their presence in the 1925 diary suggests that they are photos of wood bison. These and the *bona fide* photos and sketches of wood bison suggest that, excepting possibly one bull at Graham's Ford, the phenotype of wood bison in 1925 in WBNP was not that of NR "archetypal wood bison" in EINP. The pre-1925 wood bison resemble present WBNP, MBS and EINP wood bison in captivity, or plains bison. Therefore the NR bison in EINP stand apart in their external appearance, excepting the lone Hook Lake bull whose photo was published by Van Camp (1989) and an occasional bull in WBNP (Fig. 9). Before explaining the "archetypal wood bison phenotype," we must turn to a discussion of taxonomic criteria commonly employed.

#### MORPHOMETRY NOT TAXONOMICALLY RELEVANT

A review of taxonomic papers on large mammals shows that while taxonomists have increasingly refined methods of detecting differences among populations, they have lagged behind in analyzing the nature of these differences (Geist, 1989, 1991a). Much faith is placed in skeletal measurements and the analysis thereof by means of sophisticated multivariate statistical methods, as exemplified in the taxonomy of American bison by van Zyll de Jong (1986).

The use of morphometry to detect genetic differences, however, is like using a rubber band to measure distance. While morphometry is a good tool to segregate *populations* (where factors of individual variation such as genetic relatedness, resource abundance, behavioural traditions, climatic effects, etc., vary in the *same* direction), it is an inadequate tool to segregate *taxa*. Comparative morphometry confounds genetic, epistatic, environmental and statistical variation, and thus confuses phenotype with genotype and homology with analogy.

Morphometrics applied to phenotypes cannot, in principle, isolate the hereditary differences among populations. That can be done only with characteristics whose expression depends on high penetrance of genes, and that can only be identified experimentally.

Body size and shape are not independent, and both are much affected by environment; body size changes with net nutrition, while shape changes with size (allometry) and with muscular forces (Ingebrigtsen, 1923; Vogt, 1936, 1948; Beninde, 1937; Iljin, 1941; Slijper, 1942; Du Brul and Laskin, 1961; Wood *et al.*, 1962; Klein, 1964; Gottschlich, 1965; Zeuner, 1967; Risinfeld, 1969; Meunier, 1977; Ellenberg, 1978; Klein *et al.*, 1987).

This old and well-demonstrated knowledge, which is the essence of the discipline of animal science and its "theory of centripetal growth" (Wilson, 1952, 1958; Palsson and Verges, 1952; Hammond, 1971) and of the practice of and research pertaining to orthodontics, has not been included in the practice or theory of taxonomy. Phenotype plasticity has been widely ignored in biology (Geist, 1978:116-144, 1989, 1991a), although this may be changing, as in 1989 a whole issue of *Bio Science* (Vol. 39, No. 7) was devoted to phenotype plasticity. Phenotype plasticity is reflected in adaptive phenotype extremes (ecotypic morphs), which were independently proposed by many authors. Stimulated by the early work of animal scientists, Geist (1971, 1978, 1989), Hutton (1972), Shackleton (1973), Horejsi (1976) and Bunnell (1978) identified high-quality (later "dispersal") and low-quality (later "maintenance") phenotypes. Other examples are: Fruehenticwiler and Spaeticwiler (Ellenberg, 1978); pedomorphs and paramorphs (Albrecht, 1979, in Balon, 1985); dispersers and biders (Packard and Mech, 1983:166). Similar conclusions were reached by ornithologists (Watson and Moss, 1972), entomologists (Wellington, 1960; Harrison, 1980), limnologists (Calow, 1980; Calow and Townsend, 1980), hesitantly approached by students of small mammals (Lidicker, 1975; Gaines and McClenaghan, 1980), but well accepted and incorporated into life history theory by ichthyologists (Balon, 1981, 1984, 1985; Noakes and Balon, 1982; see also Bruton, 1989). There are epigenetic studies dealing with this phenomenon (Waddington, 1957; Lovtrup, 1974). Models of mammalian ecotypic plasticity may be applicable to humans (Geist, 1978, 1989).

Rhod's designation *athabascae* became accepted because free-living wood bison are larger than plains bison in size (Roe, 1970; van Zyll de Jong, 1986). However, body size and size-related (allometric) differences in body proportions are poor taxonomic criteria. Thus wood bison may have been larger because they lived at higher latitudes (a phenomenon usually ascribed to the invalid Bergmann's Rule; Geist, 1987a). Plains bison may have been small because of the high cost of migration, analogous to small-bodied migratory reindeer (Reimers, 1972). Plains bison in zoos grow very large (Dathe, 1984), and under the same captivity regime plains and wood bison bulls grow to the same size (Renecker *et al.*, 1989). A 10% difference in linear dimensions (equivalent to a 33% difference in mass) between free-living wood and plains bison is taxonomically meaningless.

Consequently, bison may differ in size and shape due to differences in local ecology rather than differences in heredity, and the segregation of wood and plains bison on morphometric grounds (van Zyll de Jong, 1986) is taxonomically without

meaning. The differences in skull size between wood and plains bison samples are substantial. If so, then the shape of the skull and post-cranial skeletons will be affected by allometric growth; the sensitive multivariate analysis cannot but show a statistically significant difference here. This difference has biological, but not taxonomic, significance.

A quick check on whether conspecifics differ genetically in size is to check the length of tooth rows. Teeth are tissues of "high growth priority" that tend to be fully developed almost irrespective of the environment (Beninde, 1937). Table 3 in van Zyll de Jong (1986) indicates that tooth-row length is virtually identical for all bison populations he studied. This suggests that wood and plains bison are genetically of the same size, a conclusion upheld by Renecker *et al.* (1989) in an experimental study: bulls of both forms grew under the same conditions to the same body size. However, female wood bison grew larger than female plains bison. Even if this experimental difference is genetic, it may be due to an accidental selection effect, since van Zyll de Jong (1986) found no significant differences in sexual size dimorphism between wood and plains bison.

Van Zyll de Jong (1986) suggested that because the original wood bison and NR bison in the MBS and EINP were similar morphometrically and distinct from current and historical plains bison, the difference reflects genetic differences. That conclusion is unacceptable on ecological grounds: all samples of wood bison, current and historic, came from low-density (expanding), non-migratory populations. All wood bison not only had access to more resources for growth and development, but did not need to spend these resources in costly migration.

Moreover, wood and plains bisons in EINP do not live in the same environment as van Zyll de Jong (1986) assumed. The plains bison live in a dense population and are competing for resources not only with one another, but also with a dense population of elk. Wood bison in EINP, however, then lived at low density without competition from elk. Differences in resource availability are critical to growth and development, not identity of climate, land form and regional plant communities.

#### ARE PELAGE CHARACTERISTICS TAXONOMIC CRITERIA?

Social organs, in particular the nuptial pelage, have been used historically in ungulate taxonomy (e.g., Lydekker, 1915; Haltenorth, 1963; Geist, 1991a). They include manes, tassels, colour patterns on the face and rump patch, tail characteristics, the presence and size of skin glands and the presence, size and shape of horn-like organs. "Horns" may vary noticeably in size and complexity with environment, but pelage and gland characteristics have been assumed to be good taxonomic criteria, shaped by hereditary factors with a high penetrance — that is, pelage features were assumed to express themselves signature-like in individuals irrespective of environment and "breed true." Whether raised in the wild or in captivity, the races of ungulates can often be recognized by their pelage and "horns" — by their "uniform."

Also, the social markings of both parents are expressed in hybrids of the  $F_1$  generation, as shown by many examples in Krumbiegel (1954), including  $F_1$  hybrids of wisent and bison. Consequently, one can recognize not only parents, but  $F_1$  hybrids of most species pairs. While the number of hair folli-

cles and the characteristics of hair are influenced by nutrition (Ryder, 1983), nuptial pelages appeared resistant to nutrition. Taxonomic confusion has arisen when account was not taken of the age- and sex-related differences and the seasonal pelage changes due to rapid hair growth, wear and shedding (see Geist, 1991a).

While nuptial pelage features were the best available taxonomic criteria, there were troubling observations, in addition to the instability in the pelage of wood bison. Lion males (*Panthera leo*) show different amount of mane development depending on the size of prides they dominate, which in turn is a function of predator density (Guthrie, 1989). Thus large manes (a hindrance in hunting, but apparently a protection in fighting) are typical of male lions holding big prides, while short manes are found where lion prides are small and the population densities are low. There is considerable variation in the size of manes among males, even where prides are large.

#### IS BODY SHAPE DIAGNOSTIC OF BISON SUBSPECIES?

Much attention has been paid to the shape of the hump. "Wood bison" purportedly have a taller hump than plains bison, with the fore-hump often more pronounced and elevated (van Zyll de Jong, 1986). But Maegher (1977:132) points out that in Yellowstone National Park bison have higher humps compared to other plains bison (Fig. 7a). Unfortunately, van Zyll de Jong (1986: Figs. 29, 30) plots the absolute, not relative, lengths of neural spines, and wood bison, larger than plains bison, have longer neural spines.

Since wood bison exceed plains bison by about 10% in cranial dimensions (van Zyll de Jong, 1986:Table 3), a 10% increase in the length of neural spines in plains bison (van Zyll de Jong, 1986:Table 12) brings them to within one standard deviation of the same lengths as those of wood bison. Since hump size increases rapidly during ontogeny, it suggests that neural spines elongate with positive allometry. If so, then the height of the hump in large bison should be relatively greater than in small bison.

Guthrie (1989), in a study of humps in extinct and extant bison, showed that in a wood bison bull shot prior to 1925 the hump must have been *longer* than in plains bison due to the great length of neural spines on T3-T7. The old plains bison bull used in comparison had rather short spines, and the EINP wood bison was intermediate. Unfortunately, this pattern is not reflected in the data published by van Zyll de Jong (1986).

The apparent height and size of the forward hump may vary with how a bison holds its head (Mohr, 1952; Guthrie, 1989). With the head raised, the splenius and rhomboideus muscles contract and bulge, enlarging the anterior hump and making it rise; with the head lowered, so is the relative height of the anterior hump. Bison that habitually have to scan for predators with an elevated head (ancestral steppe bison of Eurasia; wood bison) or who feed with their heads elevated on tall vegetation (wood bison, wisent) are expected to have a larger front hump than bison that feed almost continually on short sward (American plains bison). One expects that wood and plains bison held under the same conditions will converge in hump shape.

Furthermore, the hump appears more accentuated in the EINP wood bison because the anterior hump line, unlike that of plains bison, is not obscured by long hair radiating from the head. A plains bison with an "Afro" appears to have "less"

hump than a wood bison, even though the distance from horn base to hump peak may be the same. Clearly, the hump as a taxonomic characteristic is in need of further study.

#### BRIEF REVIEW OF BISON HISTORY

Two discoveries made during this investigation (the "long cape" in some EINP and WBNP bison, and the segregation into short- and long-haired display coats in WBNP bulls) necessitate a brief review of American bison evolution prior to explaining the "wood bison phenotype" of the NR bison in EINP. These differences, linked to Guthrie's (1989) data on extended neural spine lengths on T3-T7 in an original wood bison bull, point to isolated *B. priscus* characteristics in WBNP bison.

Two hypotheses describe the origin of *Bison bison*: the first contends that it is derived solely from the late glacial Siberian immigrant *B. occidentalis* (Geist and Karsten, 1977; Flerov, 1977), which was part of an east Siberian fauna that spread south into America with the extinction of the Rancholabrean megafauna. Here the large, long-horned Siberian bison dwarfed into the small, short-horned *B. bison* of today (Wilson, 1980).

Guthrie (1989) attributed the dwarfing to a change in predator fauna: the long-horned bisons confronted large cats (lions, tigers, homotherms, saber-tooth cats) and the large, cursorial, predacious short-faced bears (*Arctodus*); the extant bison, shy and less fleet-footed (Smiley 1978), contended primarily with wolves. Fossil evidence suggests a replacement of indigenous *B. antiquus* by Siberian bison about 10 000 B.P. (Wilson and Churcher, 1984), shortly after the severe cold pulse known in Europe as the Younger Dryas Stadial (Nilsson, 1983).

The second hypothesis maintains that *B. bison* is indigenous in origin, derived from *B. antiquus*, whose two subspecies *occidentalis* (northern) and *antiquus* (southern) hybridized into *B. bison* after the Altithermal warm phase (McDonald, 1978). Earlier, Skinner and Kaisen (1947) suggested that *B. bison* is derived from hybrids of Siberian *B. occidentalis* and indigenous *B. antiquus*; this is considered likely by Guthrie (1989). The late Pleistocene/early Holocene expansion of *B. antiquus* postulated by McDonald (1978) finds a parallel in *Ovis canadensis* (Geist, 1985): a big-horned southern sheep, very large in the late Pleistocene, radiated northward towards a thin-horned sheep (*O. dalli*) entering from Beringia (Geist, 1985). In the case of *Bison*, but not *Ovis*, the two forms may have met and hybridized.

The absence of Siberian bison in North America, as postulated by McDonald's hypothesis (1978), is unlikely, granted that the large mammals from eastern Siberia are nearly identical to those in North America. Thus Altai and American wapiti (*Cervus elaphus canadensis*) appear indistinguishable and represent the same subspecies (Flerov, 1952). The large east Siberian *Rangifer tarandus phylarchus* has the dark withers and belly typical of primitive caribou, not Eurasian reindeer (Flerov, 1952; Heptner *et al.*, 1961). The moose *Alces alces gigas* is found on both sides of the Bering Strait, and according to Flerov (1977), so was the wood bison. The pachyercine sheep (*Ovis nivicola/dalli*) are remarkably similar, as are brown bears (*Ursus arctos*), wolves (*Canis lupus*), small mammals and the people. It is unlikely for elk, caribou, moose and thin-horned sheep to enter, but not Siberian bison. Under either scenario, *B. bison* is a recent evolutionary prod-

uct, only some 4000-5000 years old (McDonald, 1978; Wilson, 1980).

In opposition to the hybridization hypothesis are the differences in hair coats of the late Pleistocene *B. priscus* (Fig. 10) and *B. bison* and the shape of the hump, which in *B. bison* resembles that of *B. antiquus* (Guthrie, 1989:196-199). Bison in Pleistocene Alaska had a distribution of neural spine lengths similar to that of European steppe bison (*B. priscus*) and still retained by the European wisent (*B. bonasus*), despite shorter neural spines. The pattern of neural spine lengths in *B. bison* is similar to that of *B. antiquus*. It is here where the occasional *priscus*-like characteristics of bison in WBNP become significant.

The fossil record indicates that the distribution and abundance of bison varied greatly in the Holocene. Wood bison may have been left behind on patches of relict prairie and riparian meadows as boreal forests closed in about 4500 B.P., after the Altithermal period. Another southern shift in bison distribution correlated with cool climates about 700 B.P. (McDonald, 1978). The segregation was not complete even in recent historic times, as plains and wood bison did meet. This happened along the Peace River, where an old plains bison bull was shot in 1866. Roe (1970:51, 54) examined this incident, which had been reported to Ernest Thompson Seton by Elzear Mignault, and considered Mignault a reliable witness. Note that this meeting of southern and northern bison took place at a date well after bison had been severely depleted in Alberta (Hewitt, 1921). Moreover, our notion of continuous forests segregating plains from wood bison is based on a false landscape image: burning by natives maintained open grassland where today, untouched by fire or buffalo grazing, continuous aspen and conifer forests cover the land (Lewis, 1977; McCormack, 1990).

#### ON THE ORIGIN OF CANADIAN PLAINS BISON

While Seton (1929), Garretson (1938) and the June 1948 issue of *The Beaver* shed light on the origins of the Canadian plains bison in the former Bison National Park (BNP) at Wainwright, Alberta, the most detailed account is by G.D. Coder (1975) in an unpublished Ph.D. dissertation. All plains bison originate from six primary captures of wild bison calves between 1873 and 1889; at least five of these contributed to the Canadian herd assembled in BNP by 1914: "Buffalo" Charles J. Jones captured 56 calves in northern Texas and added 10 other bison bought from owners in Kansas and Nebraska; (Sam) Walking Coyote's 4 calves, captured probably in northern Montana, started the Pablo-Allard herd; the Alloway brothers captured 5 calves, and Samuel Bedson captured 3 calves in Saskatchewan; Charles Goodnight started his herd with 5 calves and 2 adult Texas bison; Fredric Dupree's herd originated probably from 5 calves that were caught along the Yellowstone River.

The BNP herd began in 1873 from 4 calves caught by (Sam) Walking Coyote from the Pend d'Oreille Tribe near the Milk River, close to Buffalo, Montana, according to Garretson (1938:215), but in southern Alberta, according to *The Beaver*. They were brought to the Flathead Reservation in Montana, where they multiplied. In 1883, 12 of the bison were bought by C.A. Allard and M. Pablo. In 1893, 26 bison were added to their herd from the herd of C.J. (Buffalo) Jones; an additional 18 cattle × bison hybrids were isolated on Wild Horse Island in Flathead Lake. Buffalo Jones's herd originated mainly from

Texas bison caught in the wild, but in 1889 he bought 58 Saskatchewan bison and 8 catello from Samuel Bedson of Stony Mountain, Manitoba. The remainder of Bedson's herd went to Sir Donald A. Smith (later Lord Strathcona), who donated 13 of these bison to Banff National Park. Three of Goodnight's Texas bison had been brought to Banff in 1887. Bedson's bison came from the McKay-Alloway herd based on 5 calves captured in Saskatchewan in 1873 and 1874; Bedson secured 3 additional calves. Between 1 June 1907 and 6 June 1912, M. Pablo delivered 716 bison, of which 631 went to BNP and the others to EINP. On 31 October 1909, 77 bison were added to BNP from the Banff herd, and 10 more on 31 March 1914; in 1910 and 1911 another 30 bison were added from the Conrad herd (based on bison from Allard's estate) near Kalispell, Montana. Only the Dupree herd appears not to have contributed to the plains bison in BNP. It is this mixture of southern and northern plains bison that was in turn mixed with wood bison in WBNP beginning in 1925. If the Canadian plains bison are hybrids of two subspecies, then the formal designation should be *B. b. bison* × *montanae*, and the current subspecific designation *B. b. bison* is invalid.

#### THE "WOOD BISON" PHENOTYPE EXPLAINED

The display coat of *Bison* acts analogous to antlers in elk. Keeping all factors equal, the display hair increases in length with nutrition — the richer the forage in nutrients essential for hair growth, the longer and denser the hair in the cape, beard, nape and the hair mops on the head. The coat of bison thus acts as a luxury organ that reflects the owner's competence at foraging. Consequently, the short-haired display robe of the "archetypal EINP wood bison" is ecotypic. Placing these bison on better food changes them into long-haired "plains bison"; one expects that the richer the food in summer in hair-building amino acids, such as supplied by plants growing on sulfur-rich prairie soils, the better the growth of display hair. Also, analogous to antlers, the growth of the display coat is likely to be retarded in young and in old bulls.

In EINP the wood bison mimic what happens to bull elk and moose. A sample of 26 bull elk 4.5 years of age and older shot 2-12 December 1980, when the bulls had little fat, gave an average body weight of 379 (SD=30) kg (Table 1). This makes bull elk in EINP the largest-bodied recorded in North America, much heavier than the 330 kg (Flook, 1970) for a comparable sample of bull elk in Banff National Park (BaNP). Yet the antler length of the EINP bull elk was only 109.6 cm (n=17, SD=6.2 cm); the largest antlers weighed only 7.2 kg. Bull elk in BaNP averaged a (low) 10 kg in antler mass, while the antlers averaged 119 cm (n=54, SD=10.1 cm) in length and weighed maximally 13.3 kg. The antlers of EINP bulls were short, short-tined, straight-beamed and narrow in spread — that is, they were juvenile-like or paedomorphic in form. Moreover, big antlers, cut off and put in water to measure the specific gravity, usually floated; they were spongy and of low specific gravity. Therefore, the large bull elk from EINP had a much lower antler mass than the smaller-bodied bulls from Banff.

A sample of 30 bull moose from EINP 3.5 years of age and older, taken at the same time as the elk, averaged a respectable lean whole weight of 456 kg (SD=44.0). The antlers averaged only 7.8 tines (n=12, SD=1.7) and 99.1 cm in spread (n=10, SD=13.0); the largest antlers had only 119.5 cm spread and 9

tines. The largest three sets of antlers weighed 6.1, 5.7 and 5.1 kg respectively (Table 1). For big bulls one expects 14-18 kg of antler mass and at least 18 tines. Thus the big bull moose and elk from EINP grew rather poor antlers, a parallel to the big-bodied wood bison bulls, which grew a short-haired display coat.

The following hypothesis explains the anomaly in body size and size of display organs in elk, moose and bison in EINP: the bulls are subject in spring to an intense flush of nutritious young foliage, forbs, sedges and grasses, because of productive soils; EINP is fairly even in elevation. This flush allows a rapid intake of a high-protein diet, which permits rapid skeletal growth. However, the phenology progresses rapidly, and the forage turns not only fibrous, but also toxic under the browsing pressure of many ungulates in EINP. Consequently, the ungulates soon experience a shortage of nutrients essential for hair and antler growth. They cannot satisfy the demand by moving to sites with better nutrition (e.g., riparian communities fertilized annually by alluvium, or by following the phenology pulse in elevation, as is possible for ungulates living in mountains), because all movements are cut short by tall fences. Therefore, in summer antlers of EINP elk and moose and the display hair of wood bison grow at reduced rates. Large-bodied males are expected to be more affected than small-bodied males, as the growth and maintenance needs of the former exceed those of the latter.

TABLE 1. Body (whole, (kg)<sup>1.35</sup>lean), antler (kg) and relative antler masses (grams per wt (kg)<sup>1.35</sup>) in bull elk and moose

	n	x <sub>1</sub> (wt)kg body	n	x <sub>2</sub> (wt)kg antler	g(wt·kg) <sup>1.35</sup>	
1. moose	29	479	35	18.2	4.39	Maine, U.S.A.
2. moose	—	565	145	22.9	4.40	Alaska
3. moose	—	500	—	20.0	4.50	Eastern Siberia
4. moose	1	450	1	14.5	3.80	British Columbia
5. moose	1	492	1	14.0	3.25	Ontario
6. moose	1	542	1	24.0	4.90	Alberta
7. moose	1	455	1	6.1	1.57	Elk Island N. P.
EINP	1	405	1	5.8	1.74	Elk Island N. P.
	1	466	1	5.1	1.27	Elk Island N. P.
8. elk	1	479	1	15.3	3.74	Manitoba
	1	326	1	11.5	4.66	Manitoba
9. elk	—	333	8	10.0	3.98	Banff N. P.
10. elk	—	350		13.8-15.5	5.1-5.7	New Mexico
11. elk	—	350		9.1-14.5	3.3-5.3	Alberta
12. elk	—	300		14.0	5.1	Mongolia
13. elk	25	379		7.2	2.4	Elk Island N. P.

1. A sample of trophy bulls from Maine, courtesy R. Arsenault, Gorham, Maine.
2. Alaska bulls.
3. East Siberian moose.
4. A big bull from southern British Columbia.
5. A large, but not trophy-sized, Ontario bull.
6. A large trophy bull from Alberta.
7. Three bull moose from EINP.
8. Two large bull elk from Riding Mountain National Park.
9. Averages reported for old bulls from Banff National Park.
10. Trophy antler weights from New Mexico.
11. Antler weights of mature bulls from Alberta.
12. Siberian wapiti from Altai Mountains, Mongolia.
13. EINP bull elk and the heaviest set of antlers weighed. (No. 2-6, 8-13 from Geist, 1987b.)

The long procumbent display hair arises from lack of annual shedding, normal in vigorous bulls (Lott, 1979), and from a reduced growth of under wool in summer; the "Afro" arises when the display hair is lifted by a vigorous growth of under wool.

Bison phenotypes with reduced display pelage (wood bison) are thus expected to arise where nutrition limits hair growth after the shedding of winter hair. This could happen to some northern "bog-bison," as well as to "desert bison" in southern states on marginal habitat or to old bulls in captivity. In short, Heck (1936), Krumbiegel (1980) and Krumbiegel and Sehm (1989) probably reported something real about southern bison, just as did Geist and Karsten (1977) and van Zyll de Jong (1986) about "wood bison" held in EINP. However, as they reported, it appears on ecotypic differences only. Still, a few bulls in WBNP may be short-haired in display coats for genetic reasons, making such a hair pattern (Fig. 9) a *polymorphism*. I suggest that the species *Bison bison* is void of subspecies. The foregoing has implications to an understanding of both the evolution of bison and their conservation.

#### EVOLUTION

Some bison of WBNP appear to share characteristics with *B. priscus* (Fig. 10), whose appearance is fairly well known (Geist, 1971; Guthrie, 1989). This suggests that *B. bison* is a hybrid of *B. antiquus* and Siberian steppe bison; it allows one to identify the luxurious plains bison pelage as similar to what *B. antiquus* probably carried (Fig. 11). This bison lived in southern latitudes and was exposed to a high heat load from the sun in summer, when the bulls were maximally active during the rut. That would explain both the blondness of the cape as a reflector of solar radiation and the near "naked" condition of American bison after the loss of winter hair in early summer. With dense display hair on the forequarters, there is a great need to shed heat when running on hot days. European wisent do not show a comparable nakedness, but grow a hair coat simultaneously with the moult.

Male bison have relatively and absolutely larger humps than cows, suggesting that the hump's musculature is crucial in combat (Guthrie, 1989). Since increased body size is associated with increased social competition (see adaptive ecotypic morphs), one would expect relatively larger humps and more sturdy skulls in large-bodied bison. The skeleton of *B. antiquus*, such as the specimen in the Los Angeles County Museum, shows an exceedingly tall hump, with T3 as the longest neural spine, as compared to T1 and T2 in *B. bison* and T5 in *B. priscus*. The skull of *B. antiquus* was massive and thick horned, suggesting forceful combat.

According to Guthrie (1989), the hump permits a high suspension of the front legs, increasing stride length and speed. *B. antiquus* must have had a very long stride length and high speed. This was also concluded by Smiley (1978), who showed that these bison had muscle insertion patterns on their front legs favouring speed over power. This is plausible granted big, long-legged Rancholabrean predators. Severe culling predation would select, in addition, for large horns and for display hair that functions antler-like as a luxury organ (Geist, 1987b, 1991b). It would have augmented the horn display in *B. antiquus* and made it a fronto-lateral display, as opposed to a broadside display in *B. priscus* (Guthrie, 1989).

That would have made a large tail significant in *priscus*, but not in *antiquus*. With increasingly cursorial adaptations one expects an elaborate courtship display with luxury organs that reflect a male's success in foraging and saving nutrients from maintenance and growth towards luxury. Running from predators in open plains selects for mothers able to bear large, highly developed young at birth that can soon run as fast and long as their mothers. Such young, fed on rich milk, rapidly outgrow the dangerous neonatal period. Their mothers would enhance the fitness of daughters by selecting as fathers superior foragers, those who have the big luxury organs to prove it. The bull's display hair functions analogously to antlers for it is shed after the mating season (Lott, 1979).

#### CONSERVATION AND HYBRIDIZATION

Lack of attention to phenotype plasticity in bison taxonomy has created peculiarities. The assumption that pelage features are fixed would, following Krumbiegel (1980), make *B. b. athabascae* Rhoads 1897 a *nomem nudum*, as *B. b. bison* Linnaeus 1758 has priority — that is, *B. b. bison* = *B. b. athabascae*. However, "wood bison" bulls from EINP placed on superior food would, by growing a normal coat, become "northern plains bison" — that is, *B. b. athabascae* = *B. b. montanae*. They would now lose their legal protection under the Alberta Wildlife Act, because not even experts might distinguish them from plains bison. The view that WBNP bison be killed off and replaced by genetically impoverished "wood bison" from EINP would destroy the largest continuous, well-tested gene pool of the species *B. bison* and give priority to the impoverished gene pool of an inbred phantom subspecies. Even if the bison of WBNP were hybrids of valid subspecies, which they are not, I agree with O'Brian and Mayr (1991) that such hybridization is not a biological tragedy, and is absurd in view of the evolution of bison, or of other mammals.

The American *B. bison* emerges as a dwarfed hybrid of indigenous southern big-horned *B. antiquus* and thin-horned northern Siberian *B. occidentalis*. It fluctuated greatly in abundance and range in the Holocene. Its prairie populations penetrated virtually to the edge of its northern distribution, insuring continuing mixing of populations, thereby minimizing geographic differentiation and excluding from this process probably not even the dispersed populations of wood bison.

Wood and plains bison were in contact in historic times, particularly if forests were periodically removed by native-set fires. There was probably gene flow between southern and northern bison. Our surviving plains bison are hybrids of northern and southern plains bison, and the salvaged NR bison are hybrids of wood bison and hybrid plains bison. Hybridization between closely related subspecies is, in nature, common enough in North America:

1) White Dall's sheep (*Ovis dalli dalli*) met grayish-black Stone's sheep (*O. d. stoni*) and left a mass of gray integrates, the "fannin sheep," across northern British Columbia and the Yukon Territory; we classify all "fannins" as Stone's sheep.

2) Mule deer (*Odocoileus hemionus hemionus*) hybridized extensively with black-tailed deer (*O. h. columbianus*) in British Columbia on the heights of the Coastal Ranges (Cowan, 1936; M.A. Cronin, Yale Univ., pers. comm. 1989), as do the subspecies *sitkensis* and *columbianus* in coastal British Columbia (Cowan, 1936). The subspecies *injoensis* may be a hybrid of *hemionus* × *californicus* (Wallmo, 1981).

3) Consider the mule deer: its mitochondrial DNA show it to be a hybrid of white-tailed deer mothers (*O. virginianus*) and black-tailed deer fathers (*O. hemionus*); it arose from such a cross repeatedly (Cronin, 1986; Carr *et al.*, 1986; Stubblefield *et al.*, 1986). Currently, the two ethological barriers that segregate breeding between white-tailed and mule deer are breaking down due to human action (Lingle, 1989). Are we to conclude that mule deer, because they originated as hybrids, are a worthless life form?

4) Hybridization among white-tailed deer subspecies is a subject beyond resolution, because white-tailed deer recolonized this continent, alone or with human help, after their near demise at the turn of the century (Seton, 1906; Bersing, 1956). It is impossible to determine what met and mixed or from where various releases of white-tailed deer originated.

5) The Columbian white-tailed deer (*O. v. leucurus*) appears to have done some hybridizing with Columbian black-tailed deer (Gavin, 1985). Does that warrant abandoning its protected status?

6) Note the "hybridization" of elk (*C. e. canadensis*): it is a late Siberian immigrant to North America, identical in external appearance and social signals to elk in northern Mongolia. Today elk across North America are largely derived from reintroduced Yellowstone elk, plus an admixture of local elk that survived the commercial slaughter at the turn of the century (Robbins *et al.*, 1981).

Hybridization is genetic pollution and a biological tragedy when it destroys a population's ability to survive under extreme environmental conditions, such as severe predation or weather, narrow seasonal windows or resource shortages. For instance, reintroduced Alpine ibex (*Capra ibex*) mixed with either Nubian ibex (*C. nubiana*; Turcek, 1951) or domestic goats (*C. hircus*; Grodinski and Stuwe, 1987) became extinct because births were spread over much of the year, including winter, instead of being concentrated within a narrow period in spring. The young born in winter died of exposure; those born in summer failed to reach survivable size before winter and also died of exposure. Crosses of Siberian roe bucks (*Capreolus pygargus*) and European roe deer females (*C. capreolus*) led to birth complications due to larger than normal fetuses (Turcek, 1951; Stubbe and Passarge, 1979). European wild boar (*Sus scrofa*) appear to have various admixtures of domestic pig, recognizable by the presence of spotted individuals. Spotting is associated with decreased survival, lower oxygen-binding capacity in the blood, decreased thermoregulatory ability and poorer development of the under wool (Briedermann, 1986:94). Huge antlers, a common goal of so-called "improvement" through hybridization of deer, were found to be detrimental to their bearers because stags with large, complex, unwieldy antlers were prone to be killed by smaller-antlered stags in fighting; in the Rominten Heath, where red deer were managed for large trophy antlers, this was a painful concern since stags with outstanding antlers might be killed in fighting, instead of by dignitaries hunting there as guests (Frevert, 1977). Hybridization of mule and white-tailed deer results in offspring that have neither parent's anti-predator behaviour (Lingle, 1989).

The test of the effects of hybridization is survival under severe environmental conditions. Using this criterion, then the "predator pit" within which WBNP bison are currently found (Carbyn *et al.*, 1989) should eliminate whatever detriments hybridization might have had. Considering the foregoing, the

1925-28 mixing of plains and wood bison in WBNP, while culturally tragic, because it was avoidable, is not a biological tragedy. There is no evidence for subspecies in *B. bison*, and no taxonomic justification for destroying the bison of WBNP.

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#### REFERENCES

- ALLEN, J.A. 1876. The American bison, living and extinct. Cambridge, Mass.: Memoirs of the Museum of Comparative Zoology 9(10).
- BALON, E.K. 1981. Saltatory processes and altricial to precocial forms in the ontogeny of fishes. *American Zoologist* 21:573-596.
- . 1984. Life history of Arctic charr: An epigenetic explanation of their invading ability and evolution. In: Johnson, L., and Burns, B.C., eds. *Biology of Arctic charr*. Proceedings of the International Symposium on Arctic Charr, Winnipeg, Manitoba. Winnipeg: University of Winnipeg Press. 109-141.
- . 1985. Reflections on epigenetic mechanisms: Hypothesis and case histories. In: Balon, E.K., ed. *Early life histories of fishes*. Dordrecht: Dr. W. Junk Publishers. 239-270.
- BANFIELD, A.W.F., and NOVAKOWSKI, N.S. 1960. The survival of the wood bison (*Bison bison athabascae* Rhoads) in the Northwest Territories. National Museum of Canada Natural History Paper 8.
- BEACH, R.S., GERSHWIN, M.E., and HURLEY, L.S. 1982. Gestational zinc deprivation in mice: Persistence of immunodeficiency for three generations. *Science* 218:469-471.
- BEAVER, THE. 1948. Saving the buffalo. *June*:10-13.
- BENINDE, J. 1937. Zur Naturgeschichte des Rothirsches. Monographie der Säugetiere. Vol. 4. Leipzig: P. Schoeps.
- BERSING, O.S. 1956. A century of Wisconsin deer. 2nd ed. Madison: Game Management Division, Wisconsin Conservation Department. Publication No. 353-66.
- BOHLKEN, H. 1967. Beitrag zur Systematik der rezenten Formen der Gattung *Bison*. *Zeitschrift fuer Zoologische Systematik und Evolutionsforschung* 5:54-110.
- BORK, A.M., STROBECK, C.M., YEH, F.C., HUDSON, R.J., and SALMON, R.K. 1991. Genetic relationship of wood and plains bison on restriction fragment length polymorphisms. *Canadian Journal of Zoology* 69:43-48.
- BRIEDERMANN, L. 1986. *Schwarzwild*. Melsungen: Verlag Neumann-Neudamm.
- BROUGHTON, S. 1987. Diseases affecting bison. In: Reynolds, H.W., and Hawley, A.W.L., eds. *Bison ecology in relation to agricultural development in the Slave River lowlands, NWT*. Canadian Wildlife Service Occasional Paper No. 63:34-38.
- BRUTON, M.N., ed. 1989. *Alternative life-history styles of animals*. Dordrecht: Kluwer Academic Publishers.
- BUNNELL, F.L. 1978. Horn growth and population quality in Dall sheep. *Journal of Wildlife Management* 42:746-775.
- CALOW, P. 1980. Resource utilization and reproduction. In: Townsend, C.R., and Calow, P., eds. *Physiological ecology*. Sunderland, MA: Sinauer Associates. 246-270.
- CALOW, P., and TOWNSEND, M.F. 1980. Energetics, ecology and evolution. In: Townsend, C.R., and Calow, P., eds. *Physiological ecology*. Sunderland, MA: Sinauer Associates. 3-19.

- CARBYN, L.N., HUISMAN, D., STREET, E., and ANIONS, D. 1989. An analysis of the decline of bison in Wood Buffalo National Park from 1971 to 1981 and a review of the status to 1989. Draft ms. Available at Canadian Wildlife Service, Edmonton, Alberta.
- CARR, S.M., BALLINGER, S.W., DERR, J.N., BLANKENSHIP, L.H., and BICKHAM, J.W. 1986. Mitochondrial DNA analysis of hybridization between sympatric white-tailed deer and mule deer in west Texas. Proceedings of the National Academy of Sciences USA 83:9576-9580.
- CHANDRA, R.K. 1975. Antibody formation in first and second generation offspring of nutritionally deprived rats. *Science* 190:289-290.
- CONNELLY, R.G., FULLER, W., MERCREDI, R., WOBESER, G., and HUBERT, B. 1990. Northern diseased bison. Ottawa: Federal Environmental Assessment Review Office. Report No. 35.
- COWAN, I.M. 1936. Distribution and variation in deer (*Genus Odocoileus*) of the Pacific coastal region of North America. *California Fish and Game* 22:155-246.
- CRONIN, M.A. 1986. Genetic relationships between white-tailed deer, mule deer and other large mammals inferred from mitochondrial DNA analysis. M.Sc. thesis, Montana State University, Bozeman, Montana.
- DATHE, H. 1984. Zur Akzeleration bei Zootieren. *Der Zoologische Garten, Neue Folge*, Jena 51(6):369-376.
- DENENBERG, V.H., and ROSENBERG, K.M. 1967. Nongenetic transmission of information. *Nature* 216:549-550.
- DENENBERG, V.H., OTTINGER, D.R., and STEPHENS, M.W. 1962. Effects of maternal factors upon growth and behavior of the rat. *Child Development* 33:65-71.
- DU BRUL, E.L., and LASKIN, D.M. 1961. Preadaptive potential of mammalian skull: An experiment in growth and form. *Journal of Anatomy* 109:117-132.
- ELLENBERG, H. 1978. Zur Populationsoekologie des Rehes (*Capreolus capreolus* L. Cervidae) in Mitteleuropa. *Spixiana* (Supplement 2). 211 p.
- FLEROV, C.C. 1977. Die fossilen Bisonreste von Taubach und ihre Stellung in der Entwicklungsgeschichte der Gattung Bison in Europa. In: Kahlke, H.D., ed. *Das Pleistozän von Taubach bei Weimar. Quartaerplaentologie* 2. Berlin: Akademie Verlag. 179-208.
- FLEROV, K.K. 1952. Musk deer and deer. *Fauna of U.S.S.R. Mammals*. Vol. 2. Moscow: Academy of Sciences of the U.S.S.R. (English trans., U.S. Department of Commerce.) 257 p.
- FLOOK, D.R. 1970. A study of sex differential in the survival of wapiti. Canadian Wildlife Service Report, Series No. 11. Ottawa: Queens Printer.
- FREVERT, W. 1977. Rominten. Hamburg: P. Parey Verlag.
- FULLER, W.A. 1950. Aerial census of northern bison in Wood Buffalo National Park and vicinity. *Journal of Wildlife Management* 14:455-461.
- GAINES, M.S., and McCLENAGHAN, L.R., Jr. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics* 11:163-196.
- GARRETSON, M.S. 1938. *The American bison*. New York: New York Zoological Society.
- GAVIN, T.A. 1985. Pacific Northwest. In: Halls, L.K., ed. *White-tailed deer*. Harrisburg: Stackpole Books. 487-496.
- GEIST, V. 1971. The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research* 1:285-315.
- \_\_\_\_\_. 1978. Life strategies, human evolution, environmental design. New York: Springer-Verlag.
- \_\_\_\_\_. 1985. Game ranching: Threat to wildlife conservation in North America. *Wildlife Society Bulletin* 13:594-598.
- \_\_\_\_\_. 1987a. Bergmann's Rule is invalid. *Canadian Journal of Zoology* 65:1035-1038.
- \_\_\_\_\_. 1987b. On the evolution of optical signals in deer: A preliminary analysis. In: Wemmer, C.M., ed. *Biology and management of the cervidae*. Washington, D.C.: Smithsonian Institution. 235-255.
- \_\_\_\_\_. 1989. Environmentally guided phenotype plasticity in mammals and some of its consequences to theoretical and applied biology. In: Bruton, N.M., ed. *Alternative styles of animals*. Dordrecht: Kluwer Academic Publisher. 153-176.
- \_\_\_\_\_. 1991a. On the taxonomy of giant sheep (*Ovis ammon* Linnaeus, 1766). *Canadian Journal of Zoology* 69:706-723.
- \_\_\_\_\_. 1991b. Bones of contention revisited: Did antlers enlarge with sexual selection as a consequence of neonatal security strategies? *Applied Animal Behaviour Science* 29:453-469.
- GEIST, V., and KARSTEN, P. 1977. The wood bison (*Bison bison athabasca* Rhoads) in relation to hypotheses on the origin of the American bison (*Bison bison* Linnaeus). *Zeitschrift fuer Säugetierkunde* 42:119-127.
- GOTTSCHECH, H.J. 1965. Biotop und Wuchsform — eine craniometrisch — allometrische Studie an europäischen Populationen von *Cervus elaphus*. *Beiträge zur Jagd- und Wildforschung* 4:83-101.
- GRODINSKI, C., and STUWE, M. 1987. With lots of help, alpine ibex return to their mountains. *Smithsonian Magazine* 18(9):68-77.
- GUTHRIE, R.D. 1966. Bison horn cores: Character choice and systematics. *Journal of Paleontology* 40:328-340.
- \_\_\_\_\_. 1989. *Frozen fauna of the mammoth steppe*. Chicago: University of Chicago Press. 323 p.
- HALTENORTH, T. 1963. Klassifikation der Säugetiere: Artiodactyla. *Handbuch der Zoologie* 1(18):1-167.
- HAMMOND, J. 1971. *Farm Animals*. 4th ed. London: Arnold.
- HARRISON, R.G. 1980. Dipersal polymorphism in insects. *Annual Review of Ecology and Systematics* 11:95-118.
- HECK, H. 1936. Bisons in unseren Zoologischen Gärten. *Das Tier und wir* 5:12-14.
- HEPTNER, W.G., NASIMOVITCH, A.A., and BANNIKOV, A.A. 1961. *Mammals of the Soviet Union*. Jena: Gustav Fischer, Verlag. (German trans.)
- HEWITT, C.G. 1921. *The conservation of the wildlife of Canada*. New York: C. Scribner's Sons.
- HONESS, R.F., and WINTER, K. 1956. Diseases of wildlife in Wyoming. *Bulletin* 9. Cheyenne: Wyoming Game and Fish Department.
- HOREJSI, B.L. 1976. Suckling behaviour in relation to lamb survival in bighorn sheep (*Ovis canadensis canadensis* Shaw). Ph.D. thesis, University of Calgary, Calgary, Alberta. 256 p.
- HORNADAY, W.T. 1887. The extermination of the American bison with a sketch of its discovery and life history. Washington, D.C.: Smithsonian Report.
- HUTTON, D.A. 1972. Variation in the skulls and antlers of wapiti (*Cervus elaphus nelsoni* Bailey). M.Sc. thesis, University of Calgary, Calgary, Alberta. 139 p.
- ILJIN, N.A. 1941. Wolf-dog genetics. *Journal of Genetics* 42:359-414.
- INGEBRIGTSEN, O. 1923. *Das Norwegische Rotwild*. Bergens Museum Aarbok. Naturvidensk. raekke nr. 7.
- JAMES, F.C. 1983. Environmental component of morphological differentiation in birds. *Science* 211:184-186.
- KLEIN, D.R. 1964. Range related differences in growth of deer reflected in skeletal ratios. *Journal of Mammalogy* 45:226-235.
- KLEIN, D.R., MELDGAARD, M., and FANCY, S.G. 1987. Factors determining leg length in *Rangifer tarandus*. *Journal of Mammalogy* 68(3):642-655.
- KRUMBIEGEL, I. 1954. *Biologie der Säugetiere*. Vol. 1. Krefeld: AGIS, Verlag. 355 p.
- \_\_\_\_\_. 1980. Die unterartliche Trennung des Bisons, *Bison bison* (Linne, 1788), und seine Ruckzuechtung. *Säugetierkundliche Mitteilungen* 28(2):148-160.
- KRUMBIEGEL, I., and SEHM, G.G. 1989. The geographic variability of the plains bison. A reconstruction using the earliest European illustrations of both subspecies. *Archives of Natural History* 16(2):169-190.
- LEWIS, H.T. 1977. Maskuta: The ecology of Indian fires in northern Alberta. *The Western Canadian Journal of Anthropology* 1(1):15-52.
- LIDICKER, W.Z. 1975. The role of dispersal in the demography of small mammals. In: Perusewitz, K., Golly, B.F., and Ryskowski, B., eds. *Small mammals: Productivity and dynamics of populations*. New York: Cambridge University Press. 103-128.
- LINGLE, S. 1989. Limb coordination and body configuration in the fast gaits of white-tailed deer, mule deer and their hybrids: Adaptive significance and management implications. Master's Degree Project, Faculty of Environmental Design, University of Calgary, Calgary, Alberta. 289 p.
- LOTT, D.F. 1979. Hair display loss in mature male American bison: A temperate zone adaptation. *Zeitschrift fuer Tierpsychol* 49:71-76.
- LOVTRUP, S. 1974. *Epigenetics*. London: J. Wiley.
- LYDEKKER, R. 1915. *Catalogue of the ungulate mammals in the British Museum* (Natural History). Vol. 4. London: British Museum.
- McCORMACK, P.A. 1990. Saving Canada's wild bison: The story of Wood Buffalo National Park and the last free-ranging bison in North America. Unpubl. ms. Available at the Provincial Museum, Edmonton, Alberta.
- McDONALD, J.N. 1978. *The North American bison: A revised classification and interpretation of their evolution*. Ph.D. dissertation, University of California, Los Angeles.
- McHUGH, T. 1972. *The time of the buffalo*. New York: E.A. Knopf.
- MEAGHER, M. 1973. *The bison of Yellowstone National Park*. Washington, D.C.: National Park Service Monograph Series No. 1. 167 p.
- MEUNIER, K. 1977. Analyse der Groessen und Proportions-verhältnisse. In: von Bayern, A., and von Bayern, J., eds. *Über Rehe in einen Steirischen Gebirgs-revier*. 2nd ed. BLV, Munich: Verlags-gesellschaft. 141-146.
- MOHR, E. 1952. *Der Wiesent*. Wittenberg-Lutherstadt: Neu Brehm-Buecherei.

- NADLER, C.F., KOROBISINA, K.V., HOFFMAN, R.S., and VORONTSOV, N.N. 1973. Cytogenetic differentiation, geographic distribution and domestication in Palearctic sheep (*Ovis*). *Zeitschrift fuer Säugetierkunde* 38(2):109-125.
- NILSSON, T. 1983. *The Pleistocene*. Dordrecht: Reidel Publishing Co.
- NOAKES, D.L.G., and BALON, E.K. 1982. Life histories of tilapia: An evolutionary perspective. In: Pullin, R.S.V., and Lowe-McDonald, R.H., eds. *The biology and culture of tilapia*. ICLARM Conference Proceedings 7. Manila, Philippines: International Centre for Living Aquatic Resources Management. 61-82.
- O'BRIAN, S.J., and MAYR, E. 1991. Bureaucratic mischief: Recognizing endangered species and subspecies. *Science* 231(4998):1187-1188.
- PACKARD, J.M., and MECH, L.D. 1983. Population regulation in wolves. In: Bunnell, F.L., Eastman, D.S., and Peek, J.M., eds. *Symposium on Natural Regulation of Wild Populations*. Proceedings No. 14, Forest, Wildlife and Range Experimental Station, University of Idaho, Moscow, Idaho. 151-174.
- PALSSON, H., and VERGES, J.B. 1952. Effect of plane of nutrition on growth and development of carcass quality in lambs. *Journal of Agricultural Science* 42:1-149.
- PEDEN, D.G., and KRAAY, G.J. 1979. Comparison of blood characteristics in plains bison, wood bison and their hybrids. *Canadian Journal of Zoology* 57:1778-1784.
- REIMERS, E. 1972. Growth in domestic and wild reindeer in Norway. *Journal of Wildlife Management* 36(2):612-619.
- RENECKER, L.A., BLYTH, C.B., and GATES, C.C. 1989. Game production in western Canada. In: *Wildlife production systems: Economic utilisation of wild ungulates*. Cambridge: Cambridge University Press. 248-267.
- RHOADS, S.N. 1897. Notes on living and extinct species of American bovidae. *Proceedings of the Academy of Natural Sciences of Philadelphia* 49:483-502.
- RISENFELD, A. 1969. The adaptive mandible: An experimental study. *Acta Anatomica* 72:246-262.
- ROBBINS, R.L., REDFEARN, D.E., and STONE, C.P. 1981. Refuges and elk management. In: Thomas, J.W., and Toweill, D.E., eds. *Elk of North America*. Harrisburg: Stackpole Books. 479-507.
- ROE, F.G. 1970. *The North American buffalo*. 2nd ed. Toronto: University of Toronto Press.
- ROWAN, W. 1929. Canada's buffalo. *Country Life (London)* 66:358-360.
- RYDER, M.L. 1983. *Sheep and man*. London: Duckworth.
- SETON, E.T. 1906. The whitetailed (Virginia) deer and its kin *Odocoileus americanus* (Erxleben, 1777). In: Opper, F., and Meisel, T., eds. *Hunting in North America 1885-1911*. Secaucus, NJ: Castle, Book Sales Inc. 451-471.
- \_\_\_\_\_. 1909. *Life-histories of northern mammals*. Vol. 1. Grass-eaters. New York: Charles Scribner's Sons.
- \_\_\_\_\_. 1911. *The arctic prairies*. New York: Charles Scribner's Sons.
- \_\_\_\_\_. 1929. *Lives of game animals*. Vol. 3, Part 2. New York: Doubleday Doran.
- SHACKLETON, D.M. 1973. Population quality and bighorn sheep (*Ovis canadensis*). Ph.D. thesis, University of Calgary, Calgary, Alberta. 227 p.
- SINCLAIR, R.A. 1977. *The African buffalo*. Chicago: University of Chicago Press.
- SKINNER, M.F., and KAISEN, O.C. 1947. The fossil bison of Alaska and preliminary revision of the genus. *Bulletin of the American Museum of Natural History* 89:126-256.
- SLIJPER, E.J. 1942. Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without forelegs. I & II. *Proc. Koninkl. Ned. Akad. Wetensch.* 45:288-295; 407-415.
- STUBBE, C., and PASSARGE, H. 1979. *Rehwild*. Berlin: Verlag Neumann-Neudamm.
- STUBBLEFIELD, S.S., WARREN, R.J., and MURPHY, B.R. 1986. Hybridisation of free-ranging white-tailed and mule deer in Texas. *Journal of Wildlife Management* 50:688-690.
- THOMAS, J.W., and TOWEILL D.E., eds. 1982. *Elk of North America*. Harrisburg: Stackpole Books.
- TURCEK, F.J. 1951. Effect of introductions on two game populations in Czechoslovakia. *Journal of Wildlife Management* 15:113-114.
- VAN CAMP, J.D. 1989. A surviving herd of endangered wood bison at Hook Lake, N.W.T. ? *Arctic* 42(4):314-322.
- VAN ZYLL DE JONG, C.G. 1986. A systematic study of recent bison with particular consideration of the wood bison. *National Museum of Canada, Publications in Natural Sciences* No. 6.
- VOGT, F. 1936. *Neue Wege der Hege*. Neudamm: Neumann-Neudamm.
- \_\_\_\_\_. 1948. *Das Rotwild*. Vienna: Osterreichischer Jagd und Fischerei Verlag.
- WADDINGTON, C.H. 1957. *The strategy of the gene*. London: Allan and Unwin.
- WALLMO, O.C. 1981. Mule and black-tailed deer distribution and habitats. In: Wallmo, O.C., ed. *Mule and black-tailed deer of North America*. Harrisburg: Stackpole Books. 1-25.
- WATSON, A., and MOSS, R. 1972. A current model of population dynamics in red grouse. *Proceedings of the 15th International Ornithological Congress*. Leiden: Brill. 134-149.
- WELLINGTON, W.G. 1960. Qualitative changes in natural populations during changes of abundance. *Canadian Journal of Zoology* 38:239-314.
- WILSON, M. 1980. Morphological dating of late Quaternary bison on the northern plains. *Canadian Journal of Anthropology* 1:81-85.
- WILSON, M.C., and CHURCHER, C.S. 1984. The late Pleistocene Bighill Creek Formation and its equivalent in Alberta: Correlative potential and vertebrate palaeofauna. In: Mahaney, W.C., ed. *Correlation of quaternary chronologies*. Norwich: Geo Books. 159-175.
- WILSON, P.N. 1952. Growth analysis of domestic fowl. I. Effect of plane of nutrition and sex on live-weights and external measurements. *Journal of Agricultural Science* 42:396-381.
- \_\_\_\_\_. 1958. The effect of plane of nutrition on the growth and development of the East African dwarf goat. Part I. *Journal of Agricultural Science* 50:198-210.
- WOOD, A.J., McTAGGART-COWAN, I., and NORDAN, H.C. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. *Canadian Journal of Zoology* 40:594-603.
- YING, K.L., and PEDEN, D.G. 1977. Chromosomal homology of wood bison and plains bison. *Canadian Journal of Zoology* 55:1859-1862.
- ZEUNER, F.E. 1967. *Geschichte der Haustiere*. Ross-Rath, R., trans., and Bosseneck, J., and Halthenorth, T., eds. Munich: Bayerischer Landwirtschaftsverlag.