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Bison

Bison bison

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NOMENCLATURE

COMMON NAMES. American bison, plains bison, prairie bison, bison, buffalo, wood bison, or woodland bison

SCIENTIFIC NAME. *Bison bison*

SUBSPECIES. *B. b. bison*, *B. b. athabascae*

The bison is a member of the family Bovidae, to which domestic cattle, muskox (*Ovibos moschatus*), sheep, and goats belong. Both sexes of bovids possess true horns, which are never shed. These horns are composed of a bony core and a hard, outer sheath of epidermis. Fossil bovids date to the Lower Miocene (Feldhamer et al. 1999). Bovids are grazers primarily and browsers secondarily, and they possess a four-chambered, ruminating stomach. They inhabit major grassland, shrubland, forest, and tundra ecosystems. They feed by biting off forage with forward-projecting incisors, which are present only in the lower jaw.

The genus *Bison* is characterized by a short, broad forehead with a narrowed muzzle and pointed nasal bones (Hall 1981). Bison are particularly noted for a massive head, short neck, a high hump at the shoulders, and short, curved, rounded horns, which exhibit annual growth patterns (Soper 1964). The moderate-length tail is haired, with a terminal tassel of long hair (Banfield 1974). There is a distinct beard formed by long, woolly hair on the chin. The hair on the head, neck, and shoulders is brownish black. Body pelage is generally brown, varying moderately with season to light brown. Although technically a misnomer, the popular name *buffalo* has been used interchangeably for North American bison since early European explorers first encountered the species on the continent. True buffalo, while they are bovids, belong to genera distinctly different from bison and do not possess the shoulder hump characteristic of bison. The African cape buffalo (*Syncerus caffer*) is native only to Africa, whereas the water buffalo (*Bubalus bubalis*) is native to Asia.

TAXONOMY

Bison taxonomy has been controversial for many years, and classification to the subspecies level continues to be a subject of debate. Mayr (1963:348) defined a subspecies as “an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species,” noting that differing taxonomically means “by diagnostic morphological characters.” Avise and Ball (1990:59–60) established the following subspecies definitional guidelines: “Subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits.” In 1991, a subcommittee of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) prepared guidelines for listing populations below the species level. It recommended the following criteria for including infraspecies groups, such as subspecies on the COSEWIC list: “Geographical distinctiveness as indicated by barriers, distribution gaps, behavioural isolating

mechanisms, different modes of relating to the environment, or other compelling evidence.” Furthermore, the Canadian Species at Risk Act (SARA), (Proclamation into law June 5, 2003), provides the following definition of a wildlife species: “Wildlife species means a species, subspecies, variety or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus, that is wild by nature.”

Bison Subspecies. Currently, two subspecies of North American bison have been scientifically described the plains bison (*Bison bison bison* Linnaeus, 1758) and the wood bison (*Bison bison athabascae* Rhoads, 1897). Allen (1876), Seton (1886), and Ogilvie (1893) were among the first to describe wood bison as distinct from plains bison by their larger size and darker color. Hornaday (1889) failed to recognize a subspecific status for wood bison. Rhoads (1897) was the first to scientifically describe wood bison as a separate subspecies. Many other authors (Raup 1933; Soper 1941; Skinner and Kaisen 1947; Banfield and Novakowski 1960; Flerov 1965; Karsten 1975; Geist and Karsten 1977; Cook and Muir 1984; van Zyll de Jong 1986, 1993; Wood Bison Recovery Team 1987; Gates et al. 1992a, 2001b; van Zyll de Jong et al. 1995) have since acknowledged subspecific status for wood bison in agreement with Rhoads. However, Graham (1923), Seibert (1925), Garretson (1927), and Geist (1991) recognized the larger size and darker color of wood bison, but attributed this to environmental influences and not to genetics. In addition, conflicting evidence about the size and color of wood bison has been reported (Peden and Kraay 1979).

Skinner and Kaisen (1947) made a preliminary revision of the genus *Bison*, based on skull characteristics, measurements, and identifiable patterns of horn core growth. They classified mountain bison as a southern extension of the woodland race into mountainous habitat along the Rockies. However, Skinner and Kaisen (1947:165) apparently recognized an important shortcoming in their work when they wrote, “The population sample of true *athabascae* skulls is too small to present a comprehensive understanding of the amount of variation possible within this mountain or woodland race.” Further work with cranial characteristics of plains bison suggested that a revision of the genus may be necessary (Shackleton et al. 1975). Furthermore, Peden and Kraay (1979) questioned the taxonomy of bison on the basis of their research on blood characteristics. An osteological study to clarify systematics of extant forms of *Bison*, evolutionary trends in late Pleistocene and postglacial fossil *Bison*, and possible origins of extant forms, in particular the wood bison, was completed by van Zyll de Jong (1986).

Morphological studies of plains bison and wood bison showed significant differences in cranial and skeletal characteristics (van Zyll de Jong 1986) as well as in the anterior slope of the hump, location of the highest point on the hump, angle of the hump, cape variegation and demarcation, upper front leg hair, frontal display hair, ventral neck mane, and beard. However, Geist (1991) suggested that the subspecific status is not warranted and that those observed differences are environmentally induced. A study by van Zyll de Jong et al. (1995) showed that these traits are not affected by geographic location, suggesting that phenotypic differences are genetically controlled. In an osteological study of the genus *Bison*, van Zyll de Jong (1986) concluded that subspecific

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status for wood bison was warranted, based on the differing cranial and morphological characteristics. Of 19 cranial variables measured, wood bison differed significantly from plains bison in seventeen of those measurements (van Zyll de Jong 1986). Similarly, of 23 post cranial variables measured, wood bison differed significantly from plains bison in twenty-two of those measurements (van Zyll de Jong 1986). In a DNA microsatellite study, Wilson and Strobeck (1999) reported that the distinctness of wood bison is supported because between-subspecies distances were in most cases, larger than within-subspecies distances. This suggests that genetic differences exist between wood and plains bison, which can be maintained by continuing to manage them as separate entities.

Wood bison appear to meet accepted criteria for their classification as a valid subspecies, and they have been a key component in the diversity of natural life forms in northern Canada and Alaska. Free-ranging wood bison populations in northern Canada are particularly important because they are the only herds existing in relatively unaltered and intact ecosystems. The Wood Bison Recovery Team recognizes wood bison as a distinct subspecies based on morphological characteristics and molecular genetics and strongly supports the position that publicly owned wood bison continue to be maintained and managed separately from plains bison (Gates et al. 2001b). Furthermore, the cooperating management jurisdictions within the national Wood Bison Recovery Program have accepted wood bison as a separate subspecies, in spite of some still controversial aspects of bison phylogeny and taxonomy. Currently, there is an option to manage the most representative wood bison available as a separate subspecies and/or as distinct subpopulations of a common species. If a decision to withdraw subspecific status is made and genetic mixing is permitted, then that decision becomes irreversible. Considerable thought, research, and confirmatory scientific data are prerequisite to a decision of that significance.

Bos Versus Bison. The wood bison has been documented as a valid subspecies of North American bison (Cook and Muir 1984; van Zyll de Jong 1986). However, some taxonomists believe that, because of the close morphological and genetic similarity of *Bos* and *Bison*, they should be united in a single genus (Simpson 1961; Van Gelden 1977). Morphological (Groves 1981) and genetic evidence (Miyamoto et al. 1989; Wall et al. 1992; Janeczek et al. 1996) support this view, in addition to the incomplete fertility of cattle \times bison hybrids (Van Gelden 1977). Furthermore, Jones et al. (1997:5) included bison and cattle in a single genus in their checklist of North American mammals, as they followed up on the "somewhat unpopular decision to use the name combination of *Bos bison* for the American bison." However, under the auspices of the American Society of Mammalogists, a checklist of the mammal species of the world (available online at <http://www.nmnh.si.edu/msw/>) was compiled and lists the American bison (*Bison bison*) and the European bison or wisent (*Bison bonasus*) as a separate genus from *Bos*, following the taxonomy of Wilson and Reeder (1993). Because of the lack of consensus on the taxonomy of *Bos* and *Bison*, the Canadian Wood Bison Recovery Team has favored recognition of separate genera and continues to refer to wood bison as *Bison bison athabascae* and to American or plains bison as *Bison bison bison* (Gates et al. 2001b).

External Morphology. Geist (1991) argued that extant North American subspecies are "ecotypes" with morphological differences reflecting local environmental influences rather than heritable traits. Mayr (1963:354) defined an ecotype as "the product arising as a result of the genotypical response of an ecospecies to a particular habitat." A recent study of external morphological characteristics in 11 bison populations in North America revealed three significantly different groups: plains bison (6 populations), wood bison (4 populations), and an intermediate form, the Pine Lake subpopulation in central Wood Buffalo National Park, Alberta (van Zyll de Jong et al. 1995). The Peace-Athabasca Delta in Wood Buffalo National Park, the Slave River Lowlands, the Mackenzie, and the southern Elk Island National Park bison populations were the four herds classified as wood bison. Furthermore, plains bison transferred from the National Bison Range, Montana, to Delta Junction, Alaska, in the 1940s maintained their plains bison pelage and

body confirmation characteristics for more than 60 years within the known range distribution and habitat of wood bison. This phenotypic study indicated that the shape of the hump and the pelage characters are independent and, in addition, four of the five differentiating pelage characteristics showed significant associations, which suggests that they may be genetically linked (van Zyll de Jong et al. 1995). The persistence of wood and plains bison external morphological characteristics in varying environments demonstrates that phenotypic characteristics of wood and plains bison are genetically controlled and not induced by environmental factors (van Zyll de Jong et al. 1995).

Skeletal Morphology. Skeletal material from a number of wood and plains bison populations has been analyzed in considerable detail (McDonald 1981; van Zyll de Jong 1986). These studies indicated that geographic variation in historical populations of North American plains bison was mainly continuous (clinal) through a series of overlapping populations, manifested along a north-south axis. In general, bison in the eastern and southern United States tended to be smaller than those found in the north-central United States or on the Canadian prairies. However, a continuous gradation of intermediate types between the extremes makes meaningful delineation of northern and southern plains bison types impossible. In contrast to the clinal variation observed in plains bison, phenotypic discontinuity was evident between wood bison and plains bison populations. This discontinuity was reflected not only in size, but also in morphological differences (van Zyll de Jong 1986).

Morphometric analysis of bison from the northwest area of Wood Buffalo National Park (Nyarling River) demonstrated that they are similar to the original *B. b. athabascae*, although some evidence of interbreeding with *B. b. bison* is apparent (van Zyll de Jong 1986). Because Nyarling River bison are much closer to *athabascae* morphometrically than they are to *bison*, they should be assigned to the former taxon as a valid subspecies. van Zyll de Jong (1986) concluded that wood bison differed demonstrably from plains bison in cranial and morphological characters.

Blood Characteristics. Several researchers have used serological characteristics (blood groups and other proteins) of bison to elucidate phylogenetic relationships (Stormont et al. 1960; Braend 1963; Naik and Anderson 1970; Ying and Peden 1977; Buckland and Evans 1978a, 1978b; Fulton et al. 1978; Peden and Kraay 1979). Peden and Kraay (1979) examined 10 blood characteristics from each of five herds of North American bison by using 13 cattle bloodtyping reagents and carbonic anhydrase electrophoresis. They failed to differentiate between the two subspecies and concluded that further tests for red cell antigens and blood enzymes were required. However, Peden and Kraay (1979) reported a significant variation in blood characteristics of six bison herds, including four plains bison and two wood bison herds. They were able to distinguish plains bison in Canada from those in the United States. In another study, Zamora (1983) was unable to distinguish subspecies of bison based on analysis of erythrocyte antigens and blood proteins. Based on 15 blood protein and enzyme systems, the genetic distance between *B. b. bison* and *B. bonasus* was comparable to that between local populations of a species (Hartl and Reimoser 1988).

Conservation Status. Like the plains bison, wood bison were nearly eliminated during the late 1800s. The history of their near extinction and subsequent conservation effort is thoroughly documented in the 1987 status report on wood bison prepared for COSEWIC (Wood Bison Recovery Team 1987). Wood bison were first designated as "endangered" in 1978, but progress toward their recovery during the subsequent decade resulted in them being downlisted to "threatened" status in 1988, based on the 1987 status report. Wood bison also are recognized as a threatened subspecies in Appendix II in the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). By definition, Appendix II species are not necessarily threatened with extinction, but do require some control of trade to avoid commercial uses that are incompatible with their survival. Further recovery of wood bison is required before they can be downlisted from threatened status and removed from the list of species at risk.

The American bison is listed in the Lower Risk, Conservation Dependent category in the Red List of Threatened Species (2000) maintained by the World Conservation Union (IUCN), formally known as the International Union for the Conservation of Nature and Natural Resources (Hilton-Taylor 2000). The status of plains bison in Canada has not been officially determined by COSEWIC, but a Conservation Status Survey project to review the conservation status of bison in North America and to develop recommendations for enhancing bison conservation has commenced (Boyd and Gates 2001). This will be done in conjunction with the development of an action plan for North American bison by the Bison Specialist Group, North America, which operates under the Species Survival Commission (SSC) of the IUCN. The Bison Specialist Group will evaluate the status of North American bison using the IUCN Red List Criteria and will recommend a listing designation for each subspecies of bison to the IUCN/SSC (Boyd and Gates 2001).

Application of subspecies definitional guidelines established by Avise and Ball (1990) and O'Brien and Mayr (1991) leads to the following conclusions regarding the status of North American bison subspecies. Historically, wood bison differed from other bison populations with regard to multiple morphological and genetic characteristics; intrusion of plains bison into the range of wood bison in 1925–1928 was entirely human caused; the two North American bison subspecies continue to be morphologically and genetically distinct, despite some hybridization in the 1920s, thus modern-day wood bison and their descendants continue to constitute populations of a valid subspecies of bison.

DISTRIBUTION

Historical. Various forms of the genus *Bison* have been important elements in the fauna of northwestern North America and Siberia for a period exceeding 400,000 years (Gates et al. 2001d). Bison were one of the most common large herbivores during much of the last 100,000 years and, until recently, the Bering Land Bridge linked these regions. Therefore, it is not surprising that the last types of bison to exist in these regions were similar, small-horned forms represented by the surviving wood bison. Various human societies interacted with bison and other large herbivores in Eurasia for tens of thousands of years, and in North America before and after the glacial recession some 10,000–15,000 years ago (Gates et al. 2001d). It is clear that humans were responsible for the near extinction of plains bison on the Great Plains of North America (Roe 1970; Isenberg 2000) and wood bison from northern Alberta, British Columbia, and the southwestern Northwest Territories (Gates et al. 1992a). Humans likely played a role in the extirpation of bison from Alaska and Yukon between 200 and 400 years ago (Stephenson et al. 2001).

The earliest known fossil records of the genus *Bison* appeared in the Villafranchian deposits of India and China (Geist 1971). These late Pliocene forms eventually gave rise to the present-day bison. It is believed that bison first immigrated to North America over the Bering Land Bridge (Beringia) during the early and middle Pleistocene near the time of the Illinoian glacial and Sangamon interglacial (mid-Pleistocene) periods and then again with the recession of the Wisconsin glaciation during the late Pleistocene. This latter glaciation is believed to have mediated much of bison evolution and zoogeography. Fossil bison have been found throughout northeastern Asia, Alaska, Yukon, and most of western and central North America, and show evidence of considerable variation in body size, conformation, and horn growth. Controversial theories have been presented to elucidate the evolutionary history of bison. Definitive work on the evolution and zoogeography of the genus has been done by Flerov and Zablotski (1961), Guthrie (1970, 1980, 1990), Geist (1971), Geist and Karsten (1977), Harington (1980), Hillerud (1980), and Wilson (1980). Others have reported findings on fossil bison, theories on evolution of bison, and relationships of bison and humans in North America (Fuller and Bayrock 1965; Schultz and Hillerud 1977; Frison 1980; Stephenson et al. 2001).

Fossil evidence indicates there was a single species of bison in Eurasia and North America during the middle and late Pleistocene

(Guthrie 1990). During the last (Wisconsin) glaciation, there were two separate populations of bison in North America (Guthrie 1990; van Zyll de Jong 1993). The steppe bison (*B. priscus*: McDonald 1981; Guthrie 1990; or *B. b. priscus*: van Zyll de Jong 1986), a relative newcomer from Eurasia, occupied Beringia and was adapted to the rigors of the cold steppe. *Bison antiquus*, a descendant of an invasion of bison from Eurasia during the preceding Illinoian glaciation, was adapted to a temperate climate and open woodlands, and persisted south of the continental ice sheet (Gates et al. 2001d). By about 14,000 years ago, Eurasia and Alaska were separated by rising sea levels resulting from climatic warming. Subsequently, bison on both sides of the Bering Isthmus appear to have undergone parallel evolution from large-horned to small-horned forms (van Zyll de Jong 1993). Three bison taxa (wood bison, plains bison, and European bison) continue to exist. The two North American subspecies, wood and plains bison, represent the most recent variants on this continent, and the European bison, which survived only in the forests of eastern Europe, represents the only extant bison on the Eurasian continent (Gates et al. 2001d). A northern form of small-horned bison, similar to wood bison, became extinct in eastern Siberia by the late Holocene (van Zyll de Jong 1993); however, the taxonomy of this form is not well defined.

A corridor in the ice sheet separating Beringia from central North America began to form about 13,000 years ago toward the late Pleistocene, after which northern and southern forms of bison apparently dispersed and intermingled (McDonald 1981). Existing North American bison are descendants of these two Pleistocene lines. However, the contribution of the southern *antiquus* and the northern *priscus* in the evolution of modern North American bison is not well understood (Gates et al. 2001d). The southern *antiquus* was more widely distributed and abundant than *priscus*, and may have played a larger role in the evolution of modern North American bison in the southern part of their range (van Zyll de Jong 1993).

At the end of the last glaciation and the beginning of the Holocene about 10,000 years ago, the barriers separating the two populations disappeared and a shorter horned bison (*B. occidentalis*) appeared (van Zyll de Jong 1993). Thus, the fusion of northern and southern forms produced the early Holocene form, *B. occidentalis* (van Zyll de Jong 1986), which underwent rapid evolutionary change and gave rise to the two modern North American subspecies by about 5000 years ago (Gates et al. 2001d). The living North American bison occupy an intermediate position relative to *priscus* and *antiquus*, indicating that they descended from a mixed *priscus-antiquus* line evidenced by skull and vertebrae data (van Zyll de Jong 1993). Mixing of northern and southern stocks coupled with the profound environmental changes occurring then created selection pressures that led to modern-day North American bison (van Zyll de Jong 1993). Adapted to northern woodlands and meadows, the nonmigratory wood bison evolved in the northwestern section of the species's range, whereas the migratory plains bison evolved in the extensive grasslands of central and southern North America. Radiometric data spanning much of the past 10,000 years, together with archaeological data, demonstrate that the mid- to late Holocene distribution of wood bison included much of eastern Alaska, southern Yukon, the western Northwest Territories, and possibly western Alaska (Stephenson et al. 2001).

The taxonomic status of Holocene bison in eastern Siberia is less clear, but evidence suggests they were morphologically similar, and ecologically equivalent, to wood bison (Gates et al. 2001d). A well-preserved skull from the Kolyma River lowlands, believed to be of late Pleistocene or early Holocene age, is taxonomically intermediate between *B. b. occidentalis* and *B. b. athabascae*, demonstrating a close affinity with these forms (van Zyll de Jong 1986, 1993). Bison remains also have been recorded at archaeological sites dating to as late as 900 A.D. in southern Yakutia (Lazarev et al. 1998).

Disappearance of bison and some other large herbivores from northern areas on either side of the Bering Strait during the mid- to late Holocene likely involved the combined effects of changes in habitat distribution and hunting by humans (Ward 1997; Stephenson et al. 2001). Disappearance of bison and other large herbivores may have

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had important consequences for the structure and function of northern ecosystems (Zimov et al. 1995).

Over millennia, the "Great Bison Belt" that extended across Eurasia into Beringia and southward across North America diminished in size (Guthrie 1980, 1990:51). Evidence suggests that hunting by humans played a central role in the history of northern bison, first in Siberia, where bison were extirpated during the past 2000 years, then in North America, where only remnant populations remained by the end of the nineteenth century (Gates et al. 2001d). Although bison likely disappeared from Siberia by the late Holocene, they were still widely distributed in North America, including the Great Plains, in eastern woodlands, and in northwestern Canada and Alaska (Soper 1941; Dary 1989; Stephenson et al. 2001). Bison in northern habitats were not as numerous as bison on the Great Plains. The phenomenon of a large migratory population was unique to the Holocene Great Plains, with its huge expanse of contiguous grasslands (Guthrie 1980, 1982, 1990). Beginning in the 1700s, the availability of horses altered the mobility and hunting strategies of Native groups (Isenberg 2000). Horses eventually became sufficiently abundant and widespread to compete with bison for forage (Flores 1996; Fisher and Roll 1998). A number of studies describe the importance of hunting by humans in the dynamics of late Holocene plains bison populations (Roe 1970; Guthrie 1980; Speth 1983; Flores 1991, 1996; Belue 1996; Dobak 1996; Fisher and Roll 1998; Haynes 1998; Morgan 1998; Martin and Szuter 1999; Isenberg 2000).

Written records document the occurrence of bison in the late eighteenth and early nineteenth centuries in the southern Yukon, western Northwest Territories, Alberta, and British Columbia (Gates et al. 1992a, 2001d; Lotenberg 1996). Bison were apparently scarce or had disappeared from Alaska and western Yukon before their presence was recorded in written records. However, oral narratives provide insight into the early historical distribution, human use, and disappearance of wood bison in Alaska and adjacent Yukon (Gates et al. 2001d). Historical accounts from Native elders in interior Alaska describe how bison were a source of food and raw materials, which suggests that substantial populations of wood bison declined or disappeared from Alaska by the early to mid-1800s, with small numbers occurring in the eastern interior as late as the early 1900s (Stephenson et al. 2001). These accounts are in general agreement with oral narratives obtained from First Nation elders in the Yukon (Lotenberg 1996), which suggested a decline in bison numbers during the last 400 years and the eventual extirpation of wood bison by the early twentieth century.

Historical accounts and paleontological and archaeological data indicate that humans hunted wood bison until their disappearance from Alaska and Yukon during the last few hundred years (Gates et al. 2001d). Wood bison apparently had become scarce shortly before early Euroamerican explorers, naturalists, and entrepreneurs entered the region from the east and before firearms became widely available (Jennings 1968; Holmes and Bacon 1982; Guthrie 1990). Wood bison were extirpated from most of their original range in North America by the late nineteenth or early twentieth century, persisting only in the area south of Great Slave Lake, where the Canadian Government eventually afforded some protection. This decline coincided with the historical period during which plains bison were extirpated from the woodlands east of the Mississippi River (Dary 1989; Belue 1996).

Plains Bison. The American bison ranged throughout much of North America (Fig. 48.1). They were formerly widespread from western and northern Canada across the United States and into northern Mexico (Meagher 1986). Ernest Thompson Seton estimated that 75 million were in North America before White settlers arrived (Dary 1989). However, McHugh (1972) estimated that 30 million bison was the maximum number that available range could support. Although millions of bison once roamed this region, few free-ranging herds of North American bison remain. Descriptions of historical distribution patterns for plains bison are provided by Allen (1876), Hornaday (1889), Skinner and Kaisen (1947), Roe (1970), and Meagher (1986). The original distribution of the American bison included most of central North America,

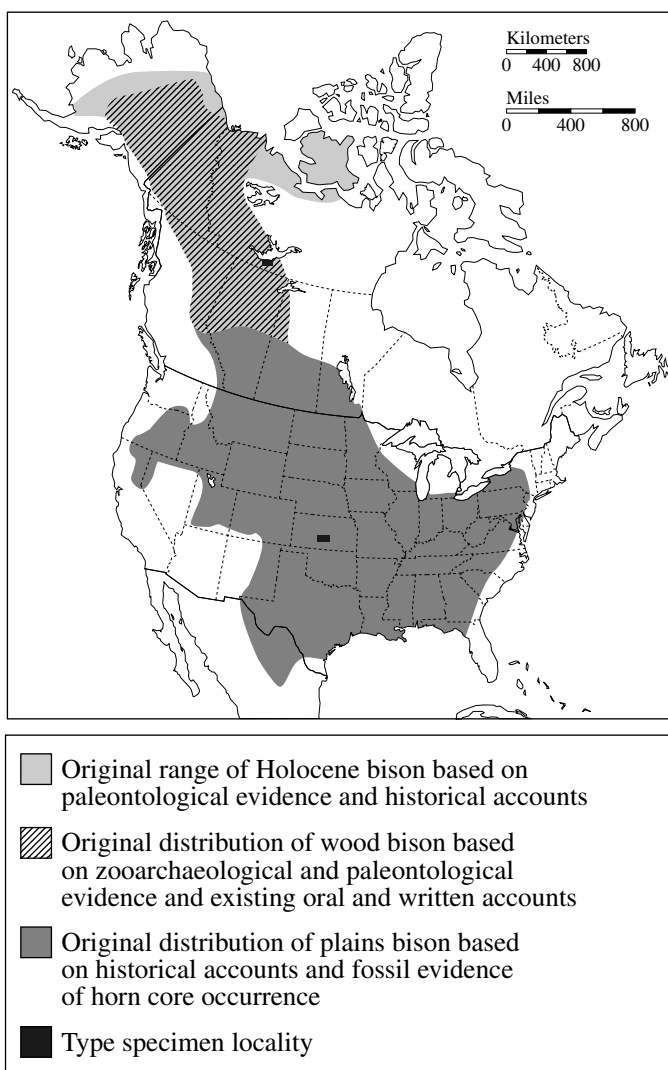


FIGURE 48.1. Original distribution of plains bison (*Bison bison bison*) and wood bison (*Bison bison athabasca*) in North America, based on available zooarchaeological, paleontological, oral, and written historical accounts. SOURCE: Data from van Zyll de Jong (1986) and Stephenson et al. (2001).

from northern Mexico to Great Slave Lake and from Washington to the Rocky Mountain states (Banfield 1974).

In Canada, the northeastern boundary for the original range of plains bison is roughly outlined by a line extending from north-central Saskatchewan in a southeastward direction to the southern shore of the Great Lakes. The northern boundary for bison in central Canada is also approximated by this line (Fig. 48.1).

In the United States, the eastern boundary was that of the Allegheny Mountains extending south through the states of Maryland, Virginia, North Carolina, and South Carolina. The southern boundary for plains bison extended from Alabama across southern Mississippi and Louisiana and continued westward along the southeastern coast of Texas and into Mexico. It was in southeastern Texas near present-day Houston that the American bison was first seen by a European, Cabeza de Vaca, in 1530 (Hornaday 1889).

The western boundary of North American plains bison distribution generally extended northward from north-central Mexico, merging with the original range for wood bison in northeastern British Columbia near the central western border of Alberta, Canada (Fig. 48.1). Here, the western and northern limits of plains bison range approximated the boundary of the ecotone between grassland, aspen parkland, and boreal forest habitat. To the north of this interface is boreal forest habitat, which is the beginning of the original range of wood bison.

Wood Bison. Based on additional information since 1987, the original range of wood bison in North America has been expanded to include a large area northwest of what was previously designated “historic range” (Gates et al. 2001b), including much of Alaska, the Yukon, and the western portion of the Northwest Territories (Fig. 48.1). Oral narratives obtained from aboriginal people and radiometric data of bison bones from archaeological and paleontological locations (van Zyll de Jong 1986; Harington 1990) indicate that bison were present in the Yukon and Alaska during the last few hundred years and persisted in small numbers into the early twentieth century (Lotenberg 1996; Stephenson et al. 2001), similar to areas in northeastern British Columbia and the southwestern Northwest Territories (Gates et al. 1992a). In view of the historical documentation and physical evidence demonstrating that wood bison inhabited this region for several thousand years, the area properly constitutes “historic” range. Therefore, in the absence of objective and biologically meaningful criteria, the dichotomy between “historic” and “prehistoric” range is not useful for the purposes of conservation and recovery, and the continuum of history should be recognized to avoid this artificial distinction (Stephenson et al. 2001). The descriptive term “original range” better represents this concept (Gates et al. 2001b).

The original range of wood bison included most of the boreal regions of northern Alberta, northeastern British Columbia, a small portion of northwestern Saskatchewan, the western Northwest Territories, most of the Yukon, and much of Alaska (Fig. 48.1) (Harington 1977; van Zyll de Jong 1986; Wood Bison Recovery Team 1987; Guthrie 1990; Gates et al. 2001b; Stephenson et al. 2001). Populations persisted in the area south of Great Slave Lake in Canada, but wood bison were extirpated in other parts of their range. The coniferous forests and aspen (*Populus*) parkland with interspersed grass and sedge (*Carex* sp.) meadows and prairies, typical of this area, constituted the main habitat for the wood bison throughout this expansive region.

DESCRIPTION

Plains Bison. The unmistakable appearance of plains bison is characterized by a massive, heavy head with a short, broad nasal area. The large head appears to be carried low because of the high shoulder hump and massive forequarters (Pattie and Fisher 1999). A short, thick neck and a high shoulder hump leave the impression that the forequarters are out of proportion to the much smaller appearing hindquarters. The hindquarters of plains bison are lighter than the forequarters, a disproportion that is further accentuated by differing pelages between front and rear. Pelage is long over the forehead, neck, hump, and forequarters, but short over the rear and tail (Meagher 1986). There is a tufted tail of moderate length (Banfield 1974). The short, round, black horns rise laterally from the side of the head and curve inward over the head. Horns of the female are more slender and tend to curve inward to a greater degree than those of the male. The eyes are located anterolaterally on the head, and the ears are nearly invisible as they are buried under the long thick pelage of the head (Meagher 1986). Plains bison have rather

short legs and large, rounded hooves, which leave tracks similar to those of domestic cattle. Sexual dimorphism is evident among adults, with females being smaller and slighter. In general, however, females resemble males in color, body configuration, and presence of permanent horns. Males have larger, more evenly curving horns, with bases that are buried in head hair; a larger hump and thicker neck; longer pelage on the forehead, chin (beard), ventral mane, and chaps of the forelegs; and a better defined, demarcated cape of longer hair on the forequarters ending abruptly with shorter hair on the flanks and rear (Meagher 1986).

Wood Bison. Wood bison possess the same general characteristics as plains bison except for some minor differences in body morphology, general conformation, pelage, and skeletal measurements. For example, wood bison have larger horn cores and exhibit differences in other cranial elements. Karsten (1975) reported that wood bison possess denser fur than plains bison, they are larger and heavier (within similar age and sex classes as verified by greater mass), more elongated in the forequarters, and darker in color, and they have a squarish hump with a more gently sloping back contour than the plains bison. Geist and Karsten (1977) described how the wood bison bull and cow differ significantly in external morphological characteristics from their prairie counterparts. There is less sexual dimorphism in wood bison compared with plains bison in respect to body size, horn structure, pelage characteristics, and body proportions. A summary of these differing characteristics follows.

1. Hair on top of the head, around the horns, in the beard, and in the midventral neck area is significantly shorter and less dense in wood bison bulls than in their plains counterparts of the same age. Plains bison generally exhibit a dense, woolly bonnet of hair between the horns, whereas in wood bison, the dark forelock of hair tends to hang in strands over the forehead. Thus, the head of the wood bison appears smaller, the horns longer, and the ears more noticeable. The beard of the wood bison is thinner and more pointed (Fig. 48.2), and the long, full throat mane, which extends from the beard to the brisket on the plains bison, is rudimentary or absent in the wood bison. The head and neck of the wood bison generally are darker in color than those of the plains bison.
2. Long hair in the area of the “chaps” on the front legs is well developed, forming a skirt on the plains bison, but is reduced or absent on the wood bison (Fig. 48.2). This most striking difference in pelage between wood and plains bison partly accounts for the more massive appearance of the plains bison in the front quarters.
3. The “robe” or cape of the shoulders, hump, and neck region of the plains bison is more distinct and lighter (golden) colored than that of the wood bison. The well-demarcated cape of the plains bison is composed of longer hair, which forms an obvious boundary with the rest of the body fur just posterior to the shoulders and is generally lighter in color than that of the wood bison. There is no clear cape demarcation in the wood bison (Fig. 48.2) and the hair is usually darker than that of the plains bison.
4. The tail of the wood bison is usually longer and more heavily haired than that of the plains bison.

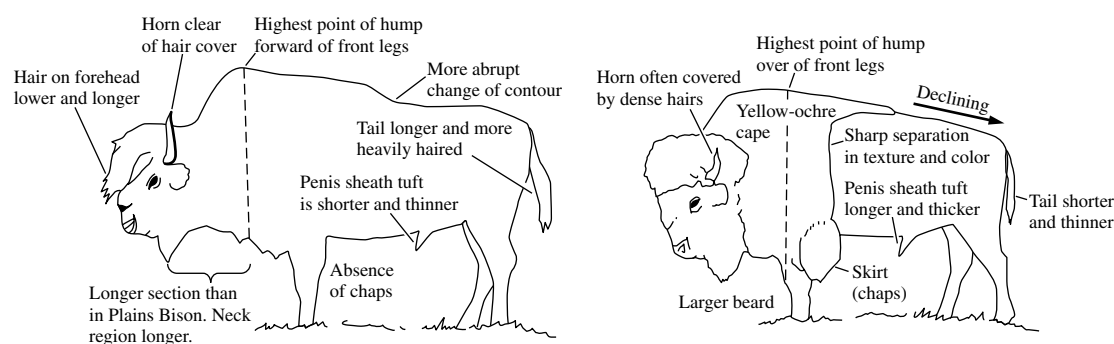


FIGURE 48.2. Basic pelage and morphological difference between (left) a male wood bison (*Bison bison athabascae*) and (right) a male plains bison (*Bison bison bison*). SOURCE: Based on character states after van Zyll de Jong et al. (1995).

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5. The penis sheath tuft of the wood bison is usually shorter and thinner than that of the plains bison.
6. Wood bison tend to be taller at the hump, which is squarer than the hump of the plains bison. The highest point of the hump is more forward in the wood bison, just ahead of the front legs, whereas in the plains bison, it is farther back and centered over the front legs (Fig. 48.2). The back contour of the wood bison has a more abrupt change at the hump, but is more gently sloping or flat overall (Fig. 48.2).

Roe (1970) cited observations of two early frontiersmen that contradicted numerous claims that wood bison were larger than plains bison. Nonetheless, most biologists who have had the opportunity to view wood and plains bison at Elk Island National Park, Alberta, agree with the descriptions presented by Karsten (1975) and Geist and Karsten (1977). Historical physical description accounts of wood bison, most

of which related to size and color, were usually compiled by explorers. Therefore, one can expect some degree of controversy in reports from these untrained (biological) observers, especially when describing characteristics that are quite variable. Still, the contradictory reports are in the minority, whereas the majority of historical accounts agree with more recent physical descriptions of living wood bison.

Morphology. Overall, the body of the bison is massive, tall, but proportionately narrow in transverse profile, where its massiveness and height are accentuated by the shoulder hump (Fig. 48.2). The hump is supported by tall, elongated spines on the thoracic vertebrae and musculature of the shoulder and pectoral girdle (Banfield 1974; Meagher 1986). The head is massive and appears to be carried low because of the high shoulder hump, massive forequarters, and the short, thick neck.

TABLE 48.1. Body measurements and weights of plains bison from several locations in North America and wood bison weights from Elk Island National Park, Alberta

Sex	Age Class (years)	Body Measurement (cm)				Weight (kg)	Reference
		Total Length	Tail Length	Hind Foot	Height at Shoulder		
M and F	Calf-birth	—	—	—	—	15–25	Rutberg 1984
M and F	Calf-birth	—	—	—	—	18	Pattie and Fisher 1999
M; F	Calves	—	—	—	—	140; 138 ^a	Rothstein and Griswold 1991
M and F	Yearling	—	—	—	—	227–318	Meagher 1973
M; F	Yearlings	—	—	—	—	233; 235 ^a	Rothstein and Griswold 1991
F	>2	—	—	—	—	413 ^a	Rothstein and Griswold 1991
M; F	2	—	—	—	—	407; 376 ^a	Rothstein and Griswold 1991
M	Adult (12.5)	318	—	—	186	814 ^b	Halloran 1961
F	Adult (6.5)	—	—	—	157 ^c	488 ^b	Halloran 1961
M	Adult	340	43	61	178	816–998	Soper 1964
F	Adult	^d	^d	^d	^d	363–544	Soper 1964
M and F	Adult	210–350	50–60	—	260–280	450–1350	Walker et al. 1975
M	Adult	304–380	33–91	58–68	167–186	544–907	Meagher 1986
F	Adult	213–318	30–51	50–53	152–157	318–545	Meagher 1986
M	Adult	304–380	43–48	56–68	167–182	460–720	Banfield 1974
F	Adult	213	45	53	152	360–460	Banfield 1974
Mixed	Mixed	—	—	—	—	450 ^e	Telfer and Scotter 1975
M	Adult	—	—	—	—	600–860	Rutberg 1984
F	Adult	—	—	—	—	350–550	Rutberg 1984
F	Adult (5+)	—	—	—	—	255–410 ^f	Lott and Galland 1987
M	Adult (4+)	—	—	—	—	615–682 ^g	Berger and Peacock 1988
F	Adult (4+)	—	—	—	—	410–470 ^g	Berger and Peacock 1988
F	Adult (6+)	—	—	—	—	352–605 ^h	Green and Rothstein 1991
F	Adult (6+)	—	—	—	—	424 ⁱ	Green and Rothstein 1991
F	Adult (6+)	—	—	—	—	518 ^j	Green and Rothstein 1991
M	Adult (≥7)	—	—	—	—	750–945 ^k	Wolff 1998
M and F	Adult	240–390	28–39	—	130–180	360–1090	Pattie and Fisher 1999
M	Adult (7.5)	—	—	—	—	727 ^l	Towne 1999
F	Adult (7.5)	—	—	—	—	455 ^l	Towne 1999
M	Adult (9.5)	—	—	—	—	858 ^m	Towne 1999
F	Adult (8.5)	—	—	—	—	542 ⁿ	Towne 1999
M, plains	Adult	—	—	—	—	591–769 ^o	Olson 2002
F, plains	Adult	—	—	—	—	417–454 ^o	Olson 2002
M, wood	Adult	—	—	—	—	642–910 ^o	Olson 2002
F, wood	Adult	—	—	—	—	493–567 ^o	Olson 2002

^aMean weight by sex and age class in November 1983, Wind Cave National Park, South Dakota.
^bHeaviest in sample of 510, Wichita Mountains Wildlife Refuge, Oklahoma.
^c5.5-year-old female.
^dFemales were 25–30% smaller than males.
^eMajority of animals in sample were adult females, Elk Island National Park, Alberta.
^fWeight range of 11 adult (5+ years) cows, Santa Catalina Island, California.
^gMean seasonal plains bison (4+ years) weights for winter and fall, Badlands National Park, South Dakota.
^hBody weight range in females aged 6 years and older (over 8 years), Wind Cave National Park, South Dakota.
ⁱMean weight of paturient females aged 6 years and older (over 8 years), Wind Cave National Park, South Dakota.
^jMean weight of nonreproductive females aged 6 years and older (over 8 years), Wind Cave National Park, South Dakota.
^kWeight range of ≥7-year-old bulls in September at the Fort Niobrara National Wildlife Refuge, Valentine, Nebraska.
^lAverage weight for age class, Konza Prairie Research Natural Area, northeastern Kansas.
^mHeaviest bull in herd, Konza Prairie Research Natural Area, northeastern Kansas.
ⁿHeaviest cow in herd, Konza Prairie Research Natural Area, northeastern Kansas.
^oMean weight range from age class 4+ years to a maximum mean weight by age class, Elk Island National Park, Alberta.

The forequarters appear out of proportion to the slim hindquarters, a disproportion that is also accentuated by pelage differences between the front and the rear (Fig. 48.2). The legs are short, stout, clothed in shaggy hair, and end with large, rounded hooves (Banfield 1974; Meagher 1986; Pattie and Fisher 1999). Morphological studies of plains bison and wood bison show differences in cranial and skeletal characteristics (van Zyll de Jong 1986). Furthermore, phenotypic differences exist between plains bison and wood bison in the anterior slope of the hump, location of the highest point on the hump, angle of the hump, cape variegation and demarcation, chap hair on the front legs, frontal display hair on the head, and ventral neck mane and beard hair. These differences occur regardless of geographic location and environmental conditions, indicating that they are genetically controlled and not environmentally induced (van Zyll de Jong et al. 1995).

Size and Weight. Bison are the largest native terrestrial mammal in North America. Plains bison are smaller than wood bison, based on body mass. However, bison weights and measurements differ considerably by age and sex among different localities (Table 48.1). In studying the relationship of weight to chest girth, Kelsall et al. (1978) discovered that males were 9.1% heavier than females of equal chest girth in an approximately linear relationship. However, the maximum amount of variation for weight explained by chest girth in a study of live male and female bison in Badlands National Park, South Dakota, was only 64% and 33%, respectively (Berger and Peacock 1988). Although chest girth may be a good measure for approximating relative weight within a population, such information is difficult to collect, therefore, an alternative method for estimating weights is to rely on differences in head length or width or body length (Berger and Peacock 1988).

McHugh (1958) reported that plains bison bulls approach maximum size by 5–6 years of age, with small yearly increments for a few years thereafter. Banfield (1974) stated that male plains bison reached adult size at 6 years of age, whereas females attained maximum size at about 4 years. Weight data for plains and wood bison herds at Elk Island National Park, Alberta, have been sporadically collected over a 30-year period since 1962 and annually since the early 1980s providing data by which growth could be compared between the two subspecies and between males and females (Fig. 48.3). Male bison continued to grow until they were 8–10 years of age (Fig. 48.3A), whereas females reached mature weight at between 5 and 6 years (Fig. 48.3B). Wood bison females became markedly heavier than plains bison females after 3 years of age; male weights diverged after about 6 years, when wood bison males became markedly heavier than their plains counterparts, based on mean weights by age category.

During the routine, midwinter weighing of bison at Elk Island National Park, mean weights of wood bison were greater than those for plains bison (Table 48.1) for each sex and age category (Olson 2002). The asymptotic mean weight for mature plains bison males was 739 ± 10.0 kg, which was attained at age 8–9 years (Fig. 48.3A). The greatest overall mean weight for plains bison males of 769 kg was reached at 13 years of age. The asymptotic mature mean weight for wood bison males was 880 ± 15.1 kg and this was attained at age 8 years, similar to the plains bison (Fig. 48.3A). The greatest overall mean weight for wood bison males of 910 kg was reached at age 13 years. The asymptotic mean weight for mature plains bison females was 440 ± 2.1 kg and this was attained at 6 years (Fig. 48.3B). The greatest overall mean weight for wood bison females of 567 kg was reached at 12 years of age, 2 years older than when plains bison females reached their maximum weight.

A wide range of intrapopulation and interpopulation variability in body weight and growth occurs in bison (Berger and Peacock 1988). Although some studies have implicated age, sex, and season as variables (Halloran 1961; Lott 1979; Rutberg 1983; Olson 2002), other factors such as population density, nutrition, weather, reproductive effort, and inbreeding should be considered as possible influences at the individual and the population levels (Berger and Peacock 1988). Food

as a limiting factor may lead to smaller animals in poorer condition. On Santa Catalina Island, California, where bison forage is limited, the largest plains bison mature cow weighed only 410 kg and was lighter than the smallest (427 kg) of 18 mature cows studied by Rutberg (1983) in the National Bison Range, Montana (Lott and Galland 1987). The average cow in the National Bison Range weighed 482 kg, compared to only 362 kg for an average Santa Catalina cow, a difference attributed to poorer nutrition on Santa Catalina Island (Lott and Galland 1987).

Pelage. The pelage of bison is composed of long, coarse guard hairs with a thick, woolly undercoat (Banfield 1974). The hair on the head, shoulders, and forequarters is long, shaggy, manelike, and dark brown to black, and abruptly becomes shorter and lighter brown behind the shoulders and on the hindquarters (Pattie and Fisher 1999). Chin hair usually resembles the shape of a goatee-type beard. The head is very dark, almost black, with little or no color contrast. There are usually two seasonal molts: one in early spring and one in late summer (Banfield 1974). Albino and gray hair colors are rarely observed in bison, with a speculated proportion varying from 1 in 100,000 to 1 in millions (McHugh 1972). Historically, the former type was held in great reverence by the Plains Indians. Newborn calves are reddish to orange brown, but this changes to the typical dark brown at about 2.5 months of age (Meagher 1978, 1986).

Skull. Skulls of male bison are larger and more massive and have longer, more pronounced horn cores and burrs than those of females (Skinner and Kaisen 1947). The muzzle is narrow with long, pointed nasal bones, which do not reach the premaxillae (Fig. 48.4, top right).

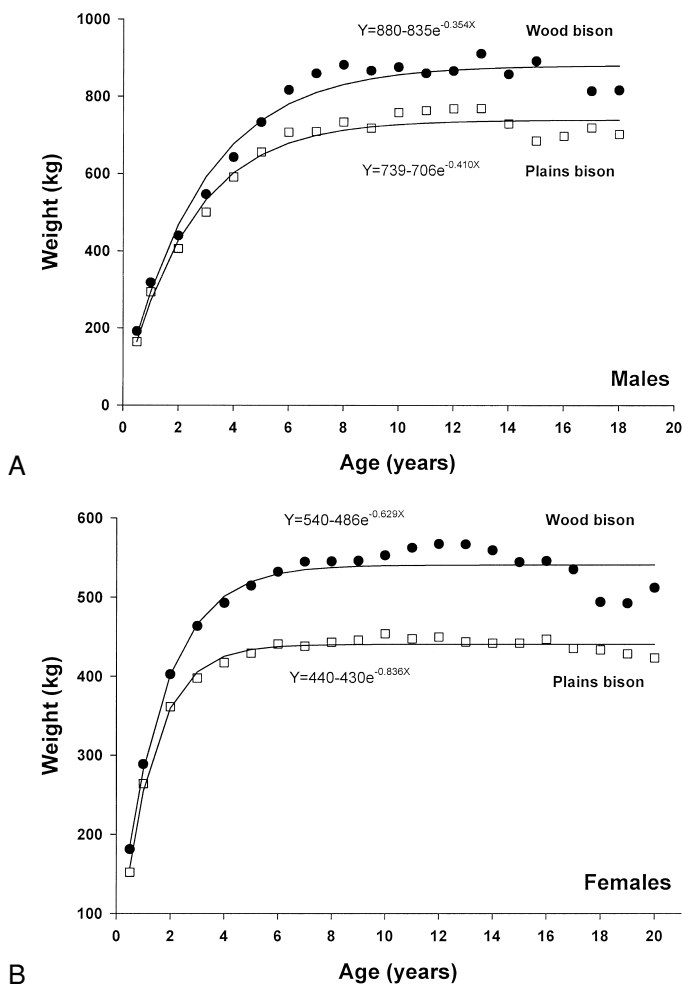


FIGURE 48.3. Growth of wood and plains bison (A) males and (B) females at Elk Island National Park. SOURCE: Average weight for age-specific data from Olson (2002).

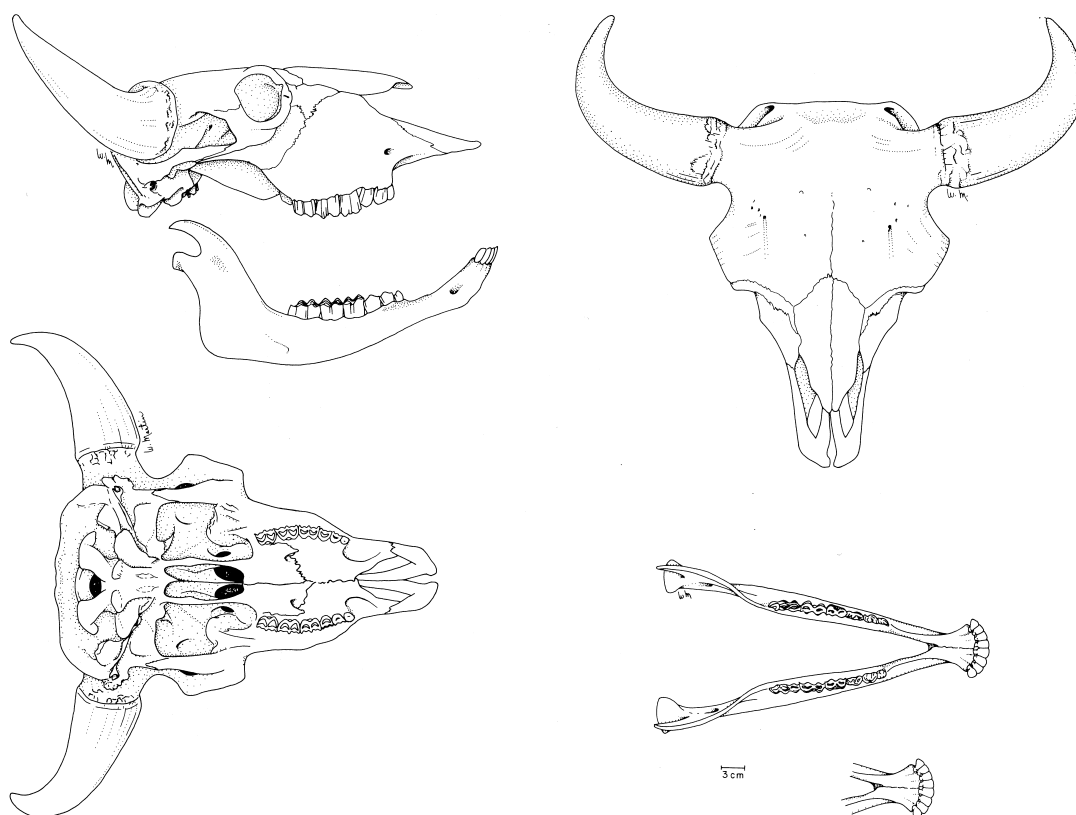


FIGURE 48.4. Skull of the bison (*Bison bison*). Top: (left) lateral view of cranium and mandible and (right) dorsal view of cranium; Bottom: (left) ventral view of cranium and (right) dorsal view of mandible and incisor bar.

Unlike cervids and antilocaprids, bison do not have preorbital vacuities in the skull. The length of 12 male bison skulls ranged from 500 to 600 mm and the width varied from 240 to 280 mm (Allen 1876). Overall length of 29 plains bison skulls varied from 491 to 570 mm, and the greatest postorbital width ranged from 271 to 343 mm (Skinner and Kaisen 1947). Hall (1981) reported that the greatest skull length of male plains bison ranged between 491 and 595 mm. Length for 81 specimens of adult male plains bison from Elk Island National Park, Alberta, ranged from 476 to 570 mm, and the greatest postorbital width ranged between 282 and 352 mm (Shackleton et al. 1975). The overall length for 33 adult female skulls from the park population varied from 425 to 500 mm, and the greatest postorbital width for 35 specimens ranged from 237 to 275 mm (Shackleton et al. 1975). Wood bison and plains bison skulls resemble each other, however wood bison, generally, are larger (Meagher 1986). A few sets of measurements of male skulls for wood and plains bison, respectively, are as follows: maximum length, 562–604 and 500–583 mm; spread of horn cores, 542–848 and 510–778 mm; and least width at frontals between horn cores and orbits, 273–313 and 237–318 mm (McDonald 1981). Some mean measurements of male skulls for original wood bison (pre-1925), modern-day wood bison, and plains bison, respectively are as follows: basilar length, 531, 518, and 486 mm; spread of horns tip to tip, 701, 653, and 594 mm; and width of cranium between horn cores and orbits, 295, 285, and 265 mm (van Zyll de Jong 1986). Of 19 cranial variables measure by van Zyll de Jong, the single measurements that best discriminate between wood and plains bison skulls are basilar length, width of the cranium between horn cores and orbits, vertical diameter of the horn core at right angles to the longitudinal axis and circumference of horn-core at right angle to longitudinal axis (van Zyll de Jong 1986).

Bayrock and Hillerud (1964) used the standard skull measurements of Skinner and Kaisen (1947) to describe three *Bison bison athabasca* skulls that had been collected in Wood Buffalo National Park, Alberta, in 1925. Two of these skulls exhibited measurements

exceeding the maximum and the minimum for the subspecies, thereby appreciably extending the range of variation for cranial measurements of wood bison. Skinner and Kaisen (1947) concluded that horn cores of fossil bison appeared to provide the best distinguishing criterion once growth, age, and individual variation were taken into consideration. In contrast, horn core dimensions were the most variable of the cranio-metric measurements taken from 157 known-age skulls of plains bison (Shackleton et al. 1975). This suggested that further studies were required to determine intraspecific and interspecific variability of these and other skull characteristics (Shackleton et al. 1975).

Selected mean measurements for 6 of 23 postcranial variables for male bison for original wood bison (pre-1925), modern-day wood bison, and plains bison are, respectively: metacarpal length, 228, 226, and 208 mm; radius length, 361, 370, and 337 mm; proximal width of radius, 109, 111, and 98 mm; tibia length, 452, 447, and 411 mm; humerus length, 404, 404, and 368 mm; and femur length, 483, 476, and 430 mm (van Zyll de Jong 1986). These six measurements were the best univariate discriminators of the 23 postcranial variables to distinguish between wood and plains bison. The mean size of different postcranial elements between male and female wood and plains bison both averaged about 12.5%, indicating that sexual dimorphism of size of postcranial elements is quite similar in both subspecies (van Zyll de Jong 1986).

Dentition. Bovids have hypsodont premolars and no upper incisors (Fig. 48.4). The upper canines are reduced or absent (Fig. 48.4, top left). The selenodont molars of bison have a median style or enamel fold between the anterior and posterior lobes (Fig. 48.4, bottom right), which tends to disappear with age and wear (Skinner and Kaisen 1947). These molars are used to section and finely grind vegetation (Feldhamer et al. 1999). The dentition of bovids is phylogenetically advanced and probably developed in association with grazing habits. The dental formula for bison and all other bovids is I 0/3, C 0/1, P 3/3, M 3/3 (Soper 1964, Hall 1981).

Abnormal dentition, such as supernumerary teeth or missing teeth, is generally infrequent in bison. In five reported cases of dental anomalies, four from the Henry Mountains, Utah, and one from Delta Junction, Alaska, these herds were founded with few individuals, suggesting the influence of in-breeding and genetic drift (Van Vuren 1984a). The rate of tooth wear in northern wood bison was much lower than that from northern plains archaeological sites. This was attributed to a grittier diet and possible mineral deficiencies that may cause increased tooth wear in bison from southern, more arid habitats (Haynes 1984).

Horns. In bison, both sexes possess short, round, curved black horns, which rise laterally on the side of the head (Fig. 48.4, top left and right; bottom left), and with inward-curving tips, which taper to circular, relatively sharp tips (Banfield 1974; Meagher 1986; Pattie and Fisher 1999). The female's horns are more slender, whereas males have proportionately stouter, more evenly curving horns, which have cores that are burred at the base (Meagher 1986). Based on horn growth, Fuller (1959) recognized four age classes for female bison and five age classes for male bison: (1) calf, <1 year; (2) yearling, <2 years; (3) spikehorn, 2 to <4 years; (4) young adult, 4 to 7 or 8 years; and (5) adult and aged, greater than 7 or 8 years. The spikehorn stage was not recognized in classification of females. Counting annual growth rings on horns was not a useful criterion for age estimation. Only gross age classification is possible for free-roaming bison as determined by horn development and body conformation.

GENETICS

Cronin (1986) examined mitochondrial DNA (mtDNA) restriction fragments in Nyarling River wood bison and plains bison and concluded they could not be distinguished. With the notable exception of mule deer (*Odocoileus hemionus hemionus*) and black-tailed deer (*O. h. columbianus*), Cronin (1991) also was unable to distinguish between other subspecies within several cervid and bovid taxa. Strobeck et al. (1993) compared sequence divergence in a section of the D-loop in mtDNA of a small number of Nyarling River wood bison and plains bison. They found that differences between wood bison and plains bison are approximately the same as or less than those within the plains bison group. Their gene tree did not reveal monophyletic separation between wood and plains bison alleles. However, separate groups are not expected to have monophyletic mtDNA trees until $4N$ generations have passed (where N represents population size), assuming constant and equal population sizes. Thus, there is no reason to expect a monophyletic tree for bison mtDNA unless N is less than 250, assuming a generation time of 5 years and that wood and plains bison existed separately for the last 5000 years.

MtDNA is maternally inherited and therefore reflects the contribution of the maternal population that gave rise to Nyarling River bison and other bison populations in the vicinity of Wood Buffalo National Park. Because plains bison cows greatly outnumbered wood bison cows following the introduction of plains bison from 1925 to 1928 (Lothian 1981), it is not surprising that mtDNA in extant bison populations in this area is similar to that of plains bison. Furthermore, the rate of sequence divergence in mtDNA is 1–2%/million years (Wilson et al. 1985). Because divergence of wood and plains bison occurred only during the last 5000–10,000 years, there has been little evolutionary time for development of significant differences in bison mtDNA.

Molecular studies that have examined restriction fragment length polymorphisms (RFLP) of various nuclear genes have provided additional insights regarding the phylogeny of bison subspecies (Bork et al. 1991; Cronin and Crockett 1993; Morris et al. 1994). Bork et al. (1991) found significant differences in RFLP frequencies in 2 of 28 fragments in wood and plains bison. The low number of net nucleotide substitutions in these two populations suggests recent divergence, a finding that supports the idea that wood and plains bison existed as reproductively isolated populations during the last 5000–10,000 years, which is a relatively short time in evolutionary terms. However, protein-level methods detect little or no variation and usually only few differences

when determining taxonomic differentiation of bison (Bork et al. 1991; Cronin and Crockett 1993; Stormont 1993).

A system more able to detect genetic variation uses DNA microsatellites, which are highly polymorphic nuclear markers. These have been employed to analyze genetic relationships among bison populations to address conservation genetics (Wilson 2001). Wilson and Strobeck (1999) investigated genetic variability, diversity, and heterogeneity in 11 microsatellite loci of genomic DNA in 11 public herds of North American bison. Wood bison herds originating in Wood Buffalo National Park formed a single group, although some subpopulations showed significant differences in allele frequencies. In particular, allele frequencies in the Pine Lake subpopulation were significantly different from those in the other subpopulations. This subpopulation also was identified by van Zyll de Jong et al. (1995) as being intermediate between wood bison and plains bison based on external morphology. Genetic distances between wood bison and plains bison populations were larger than those within either of the two subspecies populations. Wilson and Strobeck (1999) and Wilson (2001) concluded that genetic clustering of the three wood bison populations implies that they are functioning as a genetic entity, distinct from plains bison, and that wood and plains bison populations should continue to be managed separately.

Low levels of genetic variability have been reported in many bison herds (McClenaghan et al. 1990; Wilson and Strobeck 1999). The near extinction of both subspecies in the late 1800s may be the initial factor causing reduced variability. However, subsequent establishment of numerous populations from few individuals and prevention of gene flow among populations has resulted in further reduced genetic variation and diversity from founder effects and genetic drift. There is a positive correlation between the number of founders for a population and the genetic diversity within that population (Wilson 2001). Reduced variability resulting from the effects of small number of founders and genetic drift are present in many public herds. For example, the Elk Island National Park and the Mackenzie wood bison populations showed less genetic variation than their parent population in Wood Buffalo National Park, reflecting the small number of founders used to establish the former two populations. The most genetically diverse bison populations in North America are the Greater Wood Buffalo National Park Ecosystem and the Greater Yellowstone Ecosystem herds (Wilson and Strobeck 1999).

The karyotype of wood bison and plains bison is characterized by the same number of chromosomes ($2n = 60$) which resembles that of domestic cattle in that the diploid complement comprises 60 chromosomes (Bhambhani and Kuspira 1969; Ying and Peden 1977). Bison and cattle differ only in that the Y chromosome is telocentric in bison and metacentric in domestic cattle (Bhambhani and Kuspira 1969). This karyotype is nearly identical to that of the European bison or wisent, which is indigenous to Europe (Orlov and Chudinovokaya 1979). When G-banding patterns were compared for wood bison and plains bison, 20 pairs plus the sex chromosomes were found to be homologous and patterns for the 9 remaining pairs of chromosomes could not be distinguished (Ying and Peden 1977).

All living forms of bison are completely interfertile and lack intrinsic isolating mechanisms, which suggests that they are members of one species. Similarity of the karyotypes of bison and cattle justifies the grouping of bison and domestic cattle within a single genus (Bhambhani and Kuspira 1969). However, because bison and cattle are not completely interfertile, they should be considered as separate species (Gates et al. 2001b). For a more detailed explanation, see the section *Bos Versus Bison*. In conclusion, karyotype comparison suggests that these two members of the family *Bovidae*, domestic cattle and plains bison, are closely related species (Bhambhani and Kuspira 1969).

PHYSIOLOGY

Metabolism. Like other northern wild ruminants, bison exhibit seasonal variation in energy metabolism. Rutley and Hudson (2000) found that metabolizable energy intake was lower in pen and field trials with yearling bison during the winter than in the summer. In field trials,

estimated metabolizable energy requirements varied from 146 ± 22 kJ $W^{-0.75}$ /day in December to 478 ± 45 kJ $W^{-0.75}$ /day in June, where W is weight in kilograms.

Bison and cattle respond differently to cold. Christopherson et al. (1979) observed that in winter at -30°C , the metabolic rate of bison (718 kJ kg^{-1} metabolic body weight/day) was less than that of cattle (830 kJ kg^{-1} metabolic body weight/day). At 10°C , the metabolic rate of bison (934 kJ kg^{-1} metabolic body weight/day) was greater than that of cattle (659 kJ kg^{-1} of metabolic body weight/day), indicating that in winter a temperature of 10°C exceeds the upper critical temperature of bison. An increase in metabolic rate is considered a normal response to cold exposure, although this response may be reduced by cold acclimation (Slee 1972). However, Christopherson et al. (1979) found that yearling bison decreased their metabolic rate from 748 kJ kg^{-1} metabolic body weight/day at 10°C to 584 kJ kg^{-1} metabolic body weight/day at -30°C . They attributed the reduced metabolic rate largely to a reduction in activity.

Bison calves are as cold tolerant at 6 months of age as Hereford yearlings are between 13 and 17 months of age (Christopherson et al. 1979). Yearling Herefords that were acclimatized to ambient spring temperatures increased their metabolic rate from 760 kJ kg^{-1} metabolic body weight/day at 10°C to 938 kJ kg^{-1} metabolic body weight/day at -30°C . The greater cold tolerance of bison compared to cattle can be attributed primarily to greater insulating pelage. Peters and Slen (1964) observed that in winter, bison had a greater weight of hair per unit area, a greater density of hair, and a greater fineness of hair than Hereford, Angus, or Shorthorn cattle. Dziurdzik (1978) observed a similar contrast between the hair of European bison and cattle. Cattle \times bison hybrids (cattalo) were intermediate in these pelage characteristics and were more cold tolerant than cattle, resulting in a greater capacity for foraging on open range in the winter (Smoliak and Peters 1955).

Growth and Performance. Plains bison weigh 14–18 kg at birth (McHugh 1972). By 6 months of age, male bison calves are heavier than female calves (Towne 1999). At Konza Prairie (tallgrass prairie in Kansas), by 7.5 years of age, female plains bison weighed an average of 455 kg and males averaged 727 kg (Towne 1999). Male and female calves gained an average of 2.6% of their body mass over their first winter, but older bison lost an average of 11.3% of their body mass over winter. Winters were relatively mild during the study.

Bison have a lower rate of weight gain than cattle under conditions favorable for growth of cattle. When fed a complete finishing ration under feedlot conditions, male and female bison calves gained 0.64 and 0.50 kg/day, respectively, whereas Hereford calves gained 0.91 and 0.82 kg/day, respectively (Peters 1958). Cattalo calves were intermediate in performance, gaining 0.86 and 0.68 kg/day for males and females, respectively. Feed conversion efficiencies are higher for cattle (Young et al. 1977). The average gain from November to October of Hereford calves was 215 kg, compared to 160 kg in a female bison calf and 163 kg in a male bison calf. The ration was an alfalfa–brome grass mixture. Christopherson et al. (1979) fed one male and one female bison calf and two male and two female Hereford calves a ration comprised of 40% alfalfa–brome hay and 60% concentrate at a rate of 100 g of feed/unit metabolic weight/day. Average daily gain over 1 year of the bison calves, approximated from graphically presented data, was 0.5 kg/day, whereas that of cattle calves was 0.9 kg/day.

Peters and Slen (1966) reported birth weights of calves surviving to weaning as 32.7 kg for Herefords, 31.5 kg for cattalo from dams less than one-fourth bison, 30.5 kg for cattalo from bison dams, and 26.4 kg for cattalo from F_1 hybrid dams. Thus, birth weight decreased with an increased proportion of bison in the dam. The rate of gain of calves was inversely correlated with the birth weight. Average daily gain of calves was 0.69 kg from Hereford dams, 0.74 kg from bison dams, and 0.77 kg for calves from F_1 hybrid dams. Keller (1980) calculated that the effect of percentage bison parentage of the dam on calf daily gain was negligible, despite the fact that it had a negative effect on total milk yield. Total milk yield decreased by over 10 kg for each 1% increase in bison parentage.

Reynolds et al. (1982) reported that the rate of gain of Hereford steers exceeded that of bison steers from approximately 4 months to 31 months under feedlot conditions. The average growth rate of six bison steer calves from September 1975 to November 1977 was 0.4 kg/day. The greatest rate of gain in the bison was 0.5 kg/day from March to June. Feed intake and feed conversion were 5.5 kg/day and 9.8%, respectively. The ration, fed ad libitum, contained 12.4% crude protein (CP), 68% total digestible nutrients (TDN), 0.7% calcium, and 0.4% phosphorus. The rate of gain, feed intake, and feed conversion of eight Hereford steer calves during this period that received the same ration were 1.1 kg/day, 9.9 kg/day, and 10.9%, respectively. When receiving a finishing ration of 13.4% CP and 72% TDN at approximately 20 months of age, cattle gained 1.1 kg/day and bison 0.4 kg/day. These data may not have been representative of maximum animal performance, because of the intensive handling of animals and the interspersed experiments involving different rations. Hawley et al. (1981b) observed that bison steers gained 0.4 kg/day on sedge hay in the summer, whereas Hereford steers did not show any appreciable growth. When ration composition and intake only marginally met the nutrient requirements for growth of cattle, the rate of gain of bison exceeded that in cattle. Dry matter (DM) intake rates on a body weight basis were similar. Intake of digestible energy on a metabolic body weight basis was slightly greater for bison because of their greater ability to digest sedge hay.

Hawley et al. (1981b) observed a significantly ($p < .05$) lower DM intake of sedge hay and a numerically lower gain in bison steers than in cattle steers during winter. Inappetence, reduced metabolism, and reduced growth in the winter are common in wild ungulates (Wood et al. 1962; Silver et al. 1969; Ozoga and Verme 1970; Kirkpatrick et al. 1975; Westra and Hudson 1979), and are viewed as adaptive strategies developed to reduce nutritional requirements. Seasonal inappetence and reduced growth rate may depend on age and ration quality. Bison calves that were fed high-quality rations grew considerably in their first winter (Christopherson et al. 1979). Richmond et al. (1977) suggested that seasonal changes in growth and the stress of handling and confinement could have contributed to the relatively poor performance they observed in bison fed sedge and grass hays and the good performance of bison relative to cattle when fed alfalfa.

Carcass Characteristics. Bison have similar hot carcass weight as a proportion of liveweight (dressing percentage), slightly higher cooler shrink, and a higher proportion of saleable yield compared to beef (Aalhus et al. 1992). Bison dress from 55.7% to 61.9% of liveweight (Aalhus and Janz 2001). The range reported for beef carcasses is 58.6–61.8% for cattle raised on diverse feeding regimes (Aalhus et al. 1992). Shrinkage in bison carcasses during cooling ranges from 0.98% to 2.25% (Aalhus and Janz 2001), whereas shrinkage in beef carcasses ranges from 1.14% to 1.62% (Aalhus et al. 1992). The distribution of fat cover (finish) on bison carcasses tends to be uneven and is located mainly over the shoulders and loins (Hawley 1986; Koch et al. 1995). This provides less protection from evaporation for lean tissue than in beef carcasses, which have a more evenly distributed cover of fat. Aalhus and Janz (2001) reported that total bison carcass saleable yield was 78%. Similarly, Hawley (1986) reported a mean saleable yield of 77% from six bison 2.5 years of age at slaughter with an average liveweight of 444 kg. Aalhus and Janz (2001) and Koch et al. (1995) reported that total saleable yield from bison was greater than that from beef. Koch et al. (1995) found that bison had less fat trim in all cuts except in the rib section, where subcutaneous fat accumulates in bison.

The massive front shoulder of bison gives the impression that a large proportion of the body weight is in the forequarter. Peters (1958) compared carcass proportions between yearling bison and Hereford bulls, and reported a similar weight distribution in the forequarters (54% in bison and 52.5% in Hereford bulls). In contrast, Berg and Butterfield (1976) observed that the proportion of body muscle in the proximal pelvic limb area of a bison bull was greater than that in domestic cattle bulls, and attributed the difference to muscles connecting the neck to the forelimbs and in the hump. Koch et al. (1995) explained that the large dorsal spinous processes in the bison hump result in more meat

in the shoulder region in bison than in beef. The exaggerated size of the forequarter in bison creates the appearance of a disproportionately small hindquarter. However, there is little difference between bison and beef hindquarter cuts (Berg and Butterfield 1976; Koch et al. 1995).

The flavor and texture of meat from identically finished bison and cattle is similar. Meat from carcasses of 2.5-year-old bison was compared to meat from A2, C1, and D1 grade cattle carcasses (Cox 1978); panelists could not tell the difference between bison and cattle meat. Bison meat has a similar shear force (tenderness), darker meat color, similar moisture and protein content, and lower intramuscular fat compared to beef (Aalhus and Janz 2001). In a controlled comparison of bison and beef, Koch et al. (1995) reported bison meat had a lower mean shear force and a greater acceptability rating for tenderness.

Digestion and Nutrition. Much of what is known about bison digestion and nutrition has been extrapolated from beef cattle requirements and digestive physiology. Applied information is generally available in books and government reports published for the commercial bison production industry (Feist 2000). Specific energy, protein, mineral, and vitamin requirements have not been developed for bison.

Characteristic of grazing ruminants, bison have a four-compartment stomach designed for efficient processing and digesting of a roughage diet made up mostly of grass and grasslike plants. The first two stomach chambers are the rumen and reticulum, which together form the forestomachs or reticulorumen. A bison's rumen is structured into broadly connected compartments or sacs, which retain forage for long periods of time for more complete microbial digestion. Rumination, or rechewing of food returned to the mouth as a bolus by facultative muscular contractions of the esophagus, reduces the size of food particles. As microbial fermentation proceeds in the rumen, forage is further reduced to smaller and smaller particles. Contraction of the muscular rumen wall constantly flushes suspended solids back into the rumen. Small, dense material is flushed into the cranial sac of the rumen and then into the reticulum.

The highly liquefied, microbe-rich fluid in the reticulum flows through the reticulo-omasal orifice into the omasum, or third stomach. The omasum absorbs residual volatile fatty acids and bicarbonate. Fluids pass rapidly through the omasal canal, but particulate matter is trapped. Material passes from the omasum into the fourth stomach—the abomasum. The abomasum is the glandular stomach, which secretes acid and digestive enzymes similar to the stomach of a monogastric. One important functional specialization of this organ that differentiates it from a monogastric stomach is the requirement to digest large masses of microbes produced in the reticulorumen. In a ruminant, the abomasum secretes lysozyme, an enzyme that efficiently digests bacterial cell walls.

The rate of passage of forage through the digestive system of a bison is constrained by digestion in the reticulorumen. Poor-quality feeds are broken down into small particles by microbes more slowly than high-quality forage, reducing the rate of passage from the forestomach. As a result, bison only feed four to nine times a day, consuming large quantities of forage per feeding, then resting and ruminating until the mass of ingesta in the reticulorumen is reduced.

Bison retain low-quality, high-fiber, low-protein forage in their digestive system longer and are more efficient in digesting it than are cattle (Hawley et al. 1981a; Hawley 1987). However, differences between bison and cattle are not as great for high-quality, high-protein feeds like alfalfa or alfalfa brome hay (Hawley et al. 1981b). The fiber level in alfalfa-based forages is typically lower than in grasses and sedges. The poorest quality ration used in comparative trials by Hawley et al. (1981a, 1981b) was native winter forages from northern Canada containing 6% CP content. The highest quality ration was alfalfa hay (18.7% CP). The weighted average DM digestibility values for native forages reported by Hawley et al. (1981a) were 52% and 39% for bison and cattle, respectively.

Digestion of slough sedge (*Carex atherodes*) also was compared in bison and cattle through total fecal collection (Hawley et al. 1981b). The CP and acid-detergent fiber (ADF) contents of the sedge were about

8% and 46%, respectively. All nutrients tested were digested to a greater extent by bison than by cattle; organic matter digestibilities averaged 55% and 49% for bison and cattle, respectively.

Hawley et al. (1981a) compared the digestion of five native forages in bison using a nylon bag technique. The forage samples ranged from 36.4% crude fiber (CF) to 70.1% CF. The mean DM digestibilities of forages for bison were as follows: willow (*Salix* spp.), 58%; slough sedge, 59%; baltic rush (*Juncus balticus*), 55%; aleppo avens (*Geum aleppicum*), 45%; and northern reed grass (*Calamagrostis inexpansa*), 46%.

Peden et al. (1974) used a nylon bag technique to measure the digestion of native forages grazed by bison and cattle on shortgrass prairie. Digestibilities were greater in bison than in cattle for fall and winter forages in which the CF content was high and the CP content was <7%. For spring and winter forage, in which the CP content exceeded 7% and the CF content was low, differences in digestibilities between bison and cattle were not evident.

Richmond et al. (1977) used acid-insoluble ash as an indicator to compare the digestion of alfalfa, grass, and sedge hays in bison, Hereford, and yak (*Bos grunniens*) yearlings. The CP and ADF contents of the alfalfa, sedge, and grass hays were, respectively, 18.7% and 30.5%, 8.3% and 39.2%, and 6.6% and 40.3%. Grass and sedge hays were digested more efficiently by bison than by cattle, but there was little difference in digestion of alfalfa.

Young et al. (1977) used chromic oxide as an indicator to compare the digestibility of a pelleted alfalfa-brome grass mixture (15.1% CP, 25.1% ADF) in pairs of bison, yak, and three breeds of cattle. The greatest digestibility was observed in Holstein cattle, whereas Hereford cattle, Highland cattle, and bison displayed similar digestibilities.

Differences in nitrogen recycling or passage rate could explain differences in forage digestion between bison and cattle (Reynolds et al. 1982). When nitrogen in the rumen is limiting, greater recycling of nitrogen to the rumen may enhance microbial fermentation and hence forage digestion (Peden et al. 1974; Church 1988). Crude protein levels below about 6% appear to limit rumen metabolism in domestic ruminants (Gilchrist and Clark 1957; Glover and Dougall 1960). Peden et al. (1974) observed greater forage digestibilities in bison than in cattle only when CP levels were less than about 7% and suggested that these differences might be attributable to animal species differences in nitrogen recycling. This hypothesis has not been tested. The research of el Shazly et al. (1961) suggested that the availability of nitrogen markedly affects digestion of fibrous substances within the rumen.

Differences in nitrogen recycling presumably would produce different rumen environments and therefore different rumen microbial populations. Pearson (1967) observed that the rumen bacteria and ciliated protozoa from range-fed bison killed in fall were similar in kind and number to those found in domestic livestock. Reynolds et al. (1982) reported the results of an unpublished study in which only small differences existed in the number of rumen protozoa in bison and cattle receiving a high-quality finishing ration under feedlot conditions.

A lower rumen passage rate generally increases the digestion of fibrous feedstuffs (Church 1988) because feed is maintained in the presence of gastrointestinal microflora for a longer period of time. Young et al. (1977) observed forestomach retention times of 38.7 hr in bison and an average of 30.6 hr in three breeds of cattle. However, the longer retention time in bison was not manifested by greater forage digestion on good-quality ration. Dziuk (1965) concluded, based on sampling periods of 2–3 hr, that reticulorumen motility in bison was similar to that in domestic cattle. During in situ nylon bag experiments (Peden et al. 1974; Hawley et al. 1981a), samples remained within the rumen for equal lengths of time, thereby obviating the direct effect of the rate at which material leaves the rumen on the digestion of that material, and all forages tested were better digested by bison than by cattle.

In general, reducing DM intake increases the digestibility of fibrous foods (Schneider and Flatt 1975). In some instances, intake has been observed to be less in bison than in cattle (Peters 1958; Christopherson et al. 1976, 1978; Hawley et al. 1981b). Thus, greater forage digestion in bison might be associated with lower rates of intake.

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However, greater digestibility coefficients were observed in bison than in cattle when intake rates did not differ significantly (Richmond et al. 1977; Hawley et al. 1981b).

Rice et al. (1974) estimated greater intake rates for bison than for cattle or sheep on native range. Forage grazed by bison was less digestible than that grazed by cattle, which, in turn, was less digestible than forage grazed by sheep. They suggested that intake was greater to compensate for a poorer quality ration. Because bison were less selective grazers (Peden et al. 1974; Rice et al. 1974), availability of acceptable forage may have been greater for bison than for the other, more selective grazers.

Galbraith et al. (1998) measured the digestibility of alfalfa pellets and methane and heat production in bison, wapiti (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*) in February–March and April–May. No difference in heat production or estimated energy requirements for maintenance could be detected between species, although animals numerically produced 40% more heat in April–May when feed intakes were higher than in February–March. Voluntary dry matter intake of native ungulates was higher in spring than winter. Methane emissions per unit feed consumed were highest with bison and least with white-tailed deer.

Bergman et al. (2001) developed a forage intake model for bison in which the two constraints were forage quality and availability. They tested the predictions of the model on wood bison grazing on naturally occurring slough sedge. In penned trials, digestibility and intake rate decreased with sedge biomass, which varied with phenology. However, short-term intake increased with biomass. The model predicted that daily energy gain should be maximized by grazing patches with a biomass of 10 g/m², whereas the minimum daily foraging time needed to fulfill energy requirements could be achieved by cropping patches with a biomass of 279 g/m². Observations of bison grazing mosaics of sedge patches varying in quality and quantity indicated that patches with a biomass < 120 g/m² were avoided, whereas patches with a biomass of 156 and 219 g/m² were highly preferred, with the greatest preference for the latter. The results of the study indicated that bison behaved as time minimizers rather than energy maximizers when grazing sedge.

Post et al. (2001) observed differences in content and quality of the diet between age and sex classes of plains bison. They found that bulls had a significantly higher proportion of C₄ (warm season) grasses in their diet than cows, juveniles, or calves. Diets of calves were of higher quality than diets of bulls, cows, or juveniles. These results support the hypothesis that sexual dimorphism in body size allows for nutritional and habitat segregation between the sexes in large ungulates.

As with metabolism, digestion varies seasonally in bison. Rutley and Hudson (2000) reported that total digesta turnover time was longer in December (46.4 ± 1.4 hr) than in June (24.9 ± 2.7 hr). The difference was related to seasonal variation in transit time (18.2 ± 1.2 and 4.0 ± 0.8 hr, respectively) rather than differences in reticulorumen and lower gastrointestinal tract turnover time.

Blood and Urine Chemistry and Hematology. Marler (1975) analyzed jugular and tail vein blood samples from 77 bison in two herds in Kansas. No differences in chemistry or hematology were noted between sexes, but there were differences between bison < 2 years old and those ≥ 2 years old. Most blood components measured were at levels comparable to those of domestic cattle, but hematologic values were generally greater in bison. The mean packed cell volume for all bison was 50% and the mean hemoglobin (Hgb) concentration was 17 g/100 ml, compared with values of approximately 35% and 11 g/100 ml for domestic cattle (Schalm et al. 1975). Mehrer (1976) observed a mean hematocrit of 47% and a Hgb concentration of 17 g/100 ml for 163 bison ranging in age from 1 to 5 years and sampled from five different herds in five states. The density of red blood cells, packed cell volume, and Hgb can increase with excitement (Searcy 1969; Swenson 1970). Because wild animals are likely to be more excited than domestic animals during sampling, the higher erythrocytic values of bison might be attributable in part to excitement. Haines et al. (1977) recorded an oxygen-carrying capacity for adult bison of 22.2 ml/100 ml blood and a Hgb concentration of 17.1 g/100 ml blood. These values were

equivalent to values reported for some cervids and exceeded values reported for several domestic ungulates.

Blood urea nitrogen (BUN) was higher in bison than in cattle under a variety of ration and season conditions (Hawley 1978). Nitrogen recycling may be related to the level of BUN over a wide range of concentrations (Haupt 1970). A greater level of BUN could thereby contribute to greater recycling of nitrogen, and this has been suggested as one reason for the greater digestive capacity of bison on low-protein rations (Peden et al. 1974). However, BUN is not the only parameter influencing nitrogen recycling. Keith (1977) reported that rumen ammonia levels and salivary urea concentrations were more strongly influenced by factors other than BUN.

As in other ungulates (DelGiudice et al. 1989, 1991; Saltz and White 1991), urine chemistry has been used as an index of nutritional status in free-roaming bison, particularly for monitoring increases in endogenous protein catabolism during the winter (DelGiudice et al. 1994). Chemical analysis of urine suspended in snow provides the opportunity to collect large sample sizes necessary to study free-ranging populations in natural environments. In bison, urinary urea:creatinine ratios of 4 mg:mg or higher indicate either an unnaturally high protein, high energy diet or accelerated body protein catabolism in response to severe dietary energy restriction (Keith et al. 1981; DelGiudice et al. 1989, 1994). In Yellowstone National Park, urea:creatinine ratios increased over the winter on most bison ranges (DelGiudice et al. 1994). Urinary potassium:creatinine and phosphorus:creatinine ratios declined under nutritional deprivation. Low dietary sodium in winter forage was reflected by low sodium:creatinine values.

Means and standard deviations of serum glutamate oxaloacetate transaminase (GOT) levels reported by Marler (1975) for bison were 99 ± 8 mU/ml in adults and 128 ± 31 mU/ml in animals < 2 years old. Keith et al. (1978) observed levels of 57 ± 25 to 121 ± 63 IU/L in adults. These values are somewhat higher than the normal range for cattle (Kaneko and Cornelius 1970). Serum GOT levels can increase markedly with rough handling of untractable animals, which could explain higher GOT levels in bison. Alkaline phosphatase was higher in young bison than in adults (Marler 1975). Higher levels in young animals also have been observed in pronghorn antelope (*Antilocapra americana*) by Barrett and Chalmers (1977) and in cattle and sheep by Kaneko and Cornelius (1970).

BEHAVIOR

Reproductive Behavior. During the rut (breeding season), there is a marked increase in herd size and activity. Activities of rutting bulls may include sexual investigation, exhibiting flehmen, tending cows, incomplete and fertile mountings, threat posturing, fighting, horning, wallowing, and loud vocalizations.

Mature bulls tend to form their own groups apart from the cow-calf herd. However, during the rut, they often enter the cow-calf herd to investigate cows sexually, and temporarily stay within the herd to tend a cow approaching or in estrus (McHugh 1958; Fuller 1960; Egerton 1962; Shackleton 1968; Shult 1972; Meagher 1973). Bulls methodically check herd cows by sniffing their vulvas and often prod resting females to stand for a more thorough examination (McHugh 1958). It has been suggested that stimulation by bulls may induce estrus in cows (Petropavlovskii and Rykova 1958).

Flehmen refers to a reflexive facial expression manifest by bison and many other ungulates (Egerton 1962; Geist 1963; Alexander et al. 1974; Mahan et al. 1978). It often occurs during the rut when a bull sniffs and/or licks the vulva or urine of a cow; however, bulls, females, and immature animals will initiate flehmen over other odors. During flehmen, the upper lip is curled upward and the neck is extended, an expression that may last several seconds. It is believed that flehmen makes the vomeronasal organ more effective (Estes 1972). A cow's urine on the ground, a bloody wound, amniotic fluid, rotted skeletons, bison hair, new calves, and human urine may also stimulate flehmen (Egerton 1962; Herrig and Haugen 1969; Shult 1972; Lott 1974).

Tending is defined as a temporary bond between a cow and a bull (McHugh 1958), which can last from a few minutes to several days. In

consideration of the short-term nature of the tending bond, Seton (1929) and Soper (1941) described the mating system in bison as polygamous, whereas McHugh (1958:24) referred to it as "temporary monogamous mateship." Atypical tending bonds, where bulls tended cows for short time periods or tended calves or young bulls, also have been observed. In the latter case, McHugh (1958) observed a bull tend a yearling for approximately 4 hr and attempt mounting with penis unsheathed.

While tending, the bull usually tries to keep the tended cow peripheral to the main herd by keeping himself between the herd and the cow. A bull will occasionally use considerable force to keep the cow sexually isolated (Lott 1974). Close proximity of other males is not tolerated. Female bison appear to actively participate in mate selection. Wolff (1998) reported that cows often approach high-ranking bulls, but attempt to run away from low-ranking bulls. Tending by adult males appears to be a more reliable indicator of estrus in females than when subadult males are observed tending females (Komers et al. 1994). Wolff (1998) noted that bulls attempted to mate with any female in estrus.

Immediately before copulation, bison pairs may engage in amatory behavior such as mutual licking and butting. The cow may also attempt to mount the bull. A cow mounting another cow or mounting the tending bull is often a sign of estrus in domestic cattle (Dukes 1937; Schein and Fohrman 1955). The bull indicates his intention to mount by swinging his head up onto the rump of the cow. He next rears up to embrace the lower ribcage of the cow with his forelimbs and follows with penetration. The cow and bull may start to run while copulating. Insemination is usually achieved on the first few thrusts, after which the cow often displays "servicing symptoms" (Jaczewski 1958), which may last up to several hours (McHugh 1958; Shult 1972). Typically, the cow arches her back and holds her tail at some angle to the body. Urine and/or semen are often voided. Most breeding is done by "prime bulls," generally those animals between 6 and 9 years old (Egerton 1962; Lott 1974). Copulation is usually a crepuscular or nocturnal activity, a behavioral phenomenon that may enhance physiological performance, such as increased semen viability, or coincide with a time when the animals are less conspicuous to predators.

Wood bison herds tend to form smaller groups than plains bison and herd size declines during the rut as opposed to large herd sizes observed for plains bison (Soper 1941; Melton et al. 1989). In this manner, smaller herd sizes are more controllable by fewer dominant males which may result in a different mating system between wood and plains bison (Calef and Van Camp 1987). It is not evident whether there is a genetic basis for these differences in group size between wood and plains bison or whether it is a response to environmental influences of differing habitats (Melton et al. 1989). Small habitat patches in northern boreal forest areas are less likely to be grazed by larger herds of bison. Furthermore, wood bison appear to be more solitary during the rut than plains bison and the greatest interactions occur when a new lone male wanders into a cow herd and clashes with the existing dominant male (Melton et al. 1989). Wood bison may use a harem formation system, whereby a small harem is formed which is defended against intruders, versus the dominance hierarchy system employed by plains bison (larger groups which are more difficult to defend) indicating that a smaller proportion of wood bison males should be reproductively successful each year (Wilson et al. 2002). However, dominant males within harems do change throughout the breeding season (Komers et al. 1992b).

Calving Season. Immediately before parturition, the behavior of the cow and nearby members of the herd often changes. McHugh (1958) observed that cows close to parturition became restless and excitable as well as exhibited marked physical changes such as viscous, mucous discharge from the vagina, swelling of the vulva into a heart-shaped flaccid mass, and filling of the udder. Before calving, cows often wander away from the herd for 1 or more days, although calving may occur within the herd (Audubon and Bachman 1849; McHugh 1958; Egerton 1962). Lott (1991) reported that cows in open country choose to calve within close proximity to other herd members, whereas in habitat with more tree and shrub growth, cows generally give birth away from the herd and take advantage of the available cover.

Bison usually give birth while lying down. The amniotic membranes, portions of the umbilical cord, and the placenta often are eaten by the cow following birth of the calf (McHugh 1958; Egerton 1962; Mahan 1978). Egerton (1962) noted that cows licked their calves frequently for several hours postpartum and that such licking seemed to stimulate activity in the calf. Licking also may serve to dry and warm the calf and thus lessen the stress imposed by harsh climatic conditions. Calves have been observed standing within a few minutes (Egerton 1962) to 85 min (Mahan 1978) following birth.

Suckling behavior appears to be the first directed action of the newborn calf (Egerton 1962; Mahan 1978), and may motivate the calf to stand and gain mobility. First suckling may take anywhere from 12 to 95 min to be initiated (Mahan 1978).

Calves usually nurse by standing parallel to the cow and facing her posterior. Suckling periods last an average of 6.3 min (Mahan 1978) and range up to 10 min (McHugh 1958). Suckling periods are usually short and erratic in newborn calves and are similar for those older than 3 months (McHugh 1958; Egerton 1962; Mahan 1978). Disturbance near a calf often induces suckling behavior (Egerton 1962). Yearlings may suckle occasionally (Hornaday 1889; McHugh 1958; Egerton 1962; Mahan 1978), although most bison are weaned before this stage. McHugh (1958) reported weaning within 7–8 months, whereas Mahan (1978) believed it occurred within 9–12 months. Green et al. (1993) reported that nursing may last between 12 and 24 months. Mature bison cows do not force wean their calves. Older cows tend to nurse their young longer and are less likely to terminate nursing bouts than are young cows despite the probability that young cows likely produce less milk during their first few lactations (Green 1986).

Cow–calf pairs maintain their closest contact during the first week after parturition, a pattern that tends to be reduced in subsequent weeks. Calf independence and distance separation from the maternal cow increase with age and are accelerated by the presence of other conspecifics and herd members (Green 1992). This independence may potentially increase the feeding efficiency of the cow and the resting time for the calf, the former being particularly important where range productivity may be limited (Green 1992). Lott (2002) noted that cohesion between bull calves and their mothers was less than that for heifer calves and that the mother–daughter bond or close association appeared to last longer on higher quality range. McHugh (1958) believed that, during the first year of life, cohesion between the calf and the cow was sufficiently evident to identify them during most periods of the day. Recognition between the cow and the calf may include the use of scent, sight, and/or sound, although calves occasionally may follow the wrong cow.

Herd members may focus considerable interest on new cow–calf pairs shortly after parturition and occasionally will come to sniff and lick the newborn calf (Egerton 1962; Engelhard 1970). However, cows will not hesitate to defend their calves against intruding bison or other animals. Egerton (1962) and Mahan (1978) observed that cows usually try to keep themselves between their calf and other herd members. The ability of a cow to defend its calf from investigation by other bison may depend on the position of the cow in the dominance hierarchy (Egerton 1962).

McHugh (1958) observed cows defending their calves by quick charges or slow advances when confronted by other species. Similar defensive behavior was reported by Hornaday (1889) and Garretson (1938). Carbyn and Trottier (1987) observed that calves tended to gather around cows when under attack. They also noted that when groups of bison with calves were being pursued by wolves, the calves tended to be positioned in a group more toward the front half of the herd than the rear. This behavior was suggested as reducing the likelihood of calf mortality. A cow occasionally will abandon its calf when the calf drops behind after a long chase. When the precipitating disturbance has stopped, the cow usually returns in search of its calf (Seton 1929; Soper 1941; McHugh 1958).

Protection of calves may be shared by other herd members. At Wood Buffalo National Park, Alberta, a small, mixed herd of bison defended a calf against a wolf attack for 36 hr; however, defensive response to wolf predation overall was observed to be quite variable

(Carbyn 1998). Although he never observed a bull conspicuously defend a calf, McHugh (1958) did observe one incident where a mixed herd, including two older bulls, had clustered around a corral housing a lone calf and could not be chased away. Several instances have been reported where calves as young as 2 days old tried to defend themselves (Hornaday 1889; Inman 1899; McHugh 1958). Bison calves also occasionally hide in foliage as a defensive behavior (Allen 1876; Grinnell 1904; McHugh 1958).

Play in bison, as in other mammals, appears to occur with a frequency inversely proportional to age. It is manifest by seemingly purposeless frolicking, including chasing, battling, butting, mounting, kicking, and racing. To the casual observer, the motivation to engage in play appears to be "for the sake of the activity itself"; however, its inverse relationship with age would, for example, also hasten muscle development and coordination essential in later life.

Agonistic and Dominance Relations. Both sexes and all age groups of bison may engage in threat displays and fighting. The most frequent and dramatic participants are usually bulls 4 years of age (McHugh 1958; Fuller 1960; Lott 1974). Although agonistic behavior may occur at any time of year, it is much more common during the rut when herds are larger.

Threat postures may be the prelude to fighting, although they are usually sufficient to terminate an encounter before serious physical contact. Such postures include elevation of the tail, broadside threats, pawing and wallowing, aggressive advances and lunges, and the nod threat (McHugh 1958; Lott 1974; Komers et al. 1992a). During the broadside threat, one or both animals stand broadside to each other, presumably to display their size, disposition, and intent. Aggressive advances involve one or both animals approaching the other using a slow foot-by-foot walk, which may, if they do not result in displacement, lead to physical exchange. Following such advances and between fights, the pair of combatants may bob their heads up and down in what Lott (1974) described as the nod threat.

Fighting may involve butting, horn locking, shoving, and hooking. The thick cushion of hair on the head helps to reduce the impact from butting (McHugh 1958). Hooking can result in serious injury. In this respect, bison differ somewhat from other North American bovines and cervids. The frequency with which serious injury occurs suggests that bison have better perfected offensive strategies than defensive ones. Bison occasionally take advantage of exposure of the flanks of an opponent and, rather than resume head-to-head combat, follow through to gore the animal in the side and belly. Such goring may result in broken bones, lacerations, punctured organs, general trauma, and death (McHugh 1958; Lott 1974). Approximately 50% of the bison carcasses examined at a herd-reduction slaughter at Elk Island National Park during the winter of 1971 showed evidence of healed previously broken ribs. The majority of these were assumed to be a direct result of fighting.

Fighting between sexes or involving more than two animals may also occur (McHugh 1958; Lott 1974). Bulls may temporarily stop tending a cow to cross the herd and fight. Disturbance by an external source such as an approaching vehicle or placing animals in confinement may also provide the stimulus for fighting.

Submissive display can include turning and/or running away, backing up with head swinging side to side, and sudden resumption of grazing and tail wagging. The victor also may attempt to mount the loser (Lott 1974; Meagher 1978; Komers et al. 1992a).

Agonistic behavior was observed by Coppedge et al. (1997) following the release of 43 bison calves without their mothers into a 288-member resident bison population. They reported significantly more aggression against these calves than between any other age class in the resident population, with most aggression attributable to the resident yearling bison.

Rothstein and Griswold (1991) observed that yearlings, but not calves, overtly differentiated between sexes. Yearlings showed more aggression toward male conspecifics and initiated more olfactory investigation of females than did calves. They suggested that the experiences gained during this period provide important social training for bison as they mature.

Expression of intraspecific dominance in bison appears after the first few weeks of life (McHugh 1958; Mahan 1978). McHugh (1958) found no correlation between the position of dominance of the calf and its seniority in the calf group, morphological differences, or the mother's position in the dominance hierarchy (derived dominance). Male calves tend to dominate female calves, as is the norm for older animals.

It appears that dominance among calves is primarily a function of inherent disposition. Early disposition may predispose an individual bison to develop specific physical and behavioral attributes significant in maintaining or advancing dominance position later in life. In a 9-year study at Wind Cave National Park, Green and Rothstein (1993a) observed that an individual bison's subsequent dominance, growth, and reproductive success typically was enhanced for earlier-born individuals. At the National Bison Range in Montana, neither age nor weight was correlated with dominance in mature bison bulls; however, among females, age was positively correlated with dominance (Lott 1979; Rutberg 1983). Similar findings were reported by Wolff (1998) at Fort Niobrara Wildlife Refuge in Nebraska, where dominance was not correlated with age for bulls in the 7- to 13-year-old age classes nor was it correlated with size for bulls > 750 kg.

McHugh (1958) observed that dominance expressions by bison at Jackson Hole Wildlife Park were either "passive" or "aggressive." Passive dominance did not involve the use of force, whereas aggressiveness involved the use of force or threat. Of the 1027 dominance interactions observed, 73% were passive and 27% were aggressive.

After 3 years of studying a herd of 14 bison, McHugh (1958) did not observe any permanent reversals in hierarchical position between the herd's two mature bulls and among the seven most dominant cows. At the National Bison Range, Lott (1974) observed that 12% of aggressive interactions resulted in hierarchical reversals in a breeding herd containing 35 mature bulls. A number of dominance triangles also were observed. Instability in dominance relationships may be a function of habitat attributes, size of age class, and fatigue (Lott 1974). Expression of dominance tends to be more intense between animals whose positions are close together in dominance hierarchy.

Bulls, and cows with calves, are the most prone to be involved in intraspecific interaction (Egerton 1962). Almost any desired resource can elicit expression of dominance. The expression of dominance may occur as a result of competition for some obvious resource or may be precipitated by sudden disturbance. Bull groups at Elk Island National Park, Alberta, have been observed to initiate fighting, mounting, and horning when vehicles stopped near them. Similar occurrences have been observed in Wyoming (McHugh 1958) and Wood Buffalo National Park (Fuller 1960).

Horning and Wallowing. During the rut, bulls frequently horn trees including pine (*Pinus* spp.) or spruce (*Picea* spp.) (McHugh 1958). Rutting bulls at Elk Island National Park thrash and horn shrubs and saplings of several species. Following horning, the trees may be used for rubbing and/or simply uprooted. Rubbing posts are frequently sought by both sexes throughout the year. Horning also has been observed in cows just before parturition (McHugh 1958). Although the activity is not restricted to calving and rutting seasons, the increased frequency at those times suggests that it could be important in physically conditioning the animal for particularly stressful periods.

Wallowing is practiced by both sexes and all age classes of bison. Wallows are usually in dry sites, although wet, muddy wallows may be used. Wallowing may have a role in grooming, sensory stimulation, alleviating skin irritations, and reproductive behavior. As with horning, wallowing may help precondition the animal for periods of physical stress. Dust, which packs into the hair as a result of wallowing, appears to minimize the effect of biting insects (Lott 1974). Bulls wallow more frequently during the rut and occasionally urinate in the wallow before engaging in the activity (McHugh 1958). Studies in Alaska have indicated that such behavior is linked to priming of estrus in females (Bowyer et al. 1998). Urine odor may advertise the physical condition of the rutting bull. Lott (1974) suggested that the odor of urine from a bull may permit it to use preestablished dominance relations more effectively in the dark, a tenable hypothesis, considering

the crepuscular nature of rutting activity and the highly developed olfactory sense of bison.

Vocalization. The repertoire of sounds made by bison includes soft to loud grunts, bleats, roars, snorts, sneezes, foot stamping, and tooth grinding (McHugh 1958; Fuller 1960; Lott 1974; Gunderson and Mahan 1980). Calves bleat and issue piglike grunts in response to grunting by or separation from the dam, when playing, and in response to other stimuli. When searching for a calf, cows often snort or give a loud grunt similar to their "threat grunt." Bulls are prone to giving loud, lion-like roars or bellows, particularly during the rut (Shult 1972; Lott 1974; Meagher 1978; Gunderson and Mahan 1980). Such roars may be audible from 5 km (McHugh 1958) to 16 km (Audubon and Bachman 1849). Bison bulls at Badlands National Park in South Dakota bellowed less frequently following copulation and more frequently on days when females were in estrus (Berger and Cunningham 1991). In this same study, bulls did not bellow unless other bulls were present, and smaller bulls tended to bellow more frequently than large bulls. Berger and Cunningham (1991) concluded that bellowing is more likely an intrasexual display than a display to attract females.

The roar produced by bison is the result of a single forceful exhalation over the vocal cords, in contrast to the two-way system in domestic cattle (Gunderson and Mahan 1980). Bulls often roar while tending cows, before fighting, while moving through or approaching bull subgroups or mixed herds, in answer to a roar from another bull, and less commonly at other times, for example, when loafing, when disturbed by vehicles, and in response to imitated roars or distant thunder. Occasionally, cows with newborn calves will roar when approached. Bulls also use snorts and foot stamping as part of their agonistic behavior. McHugh (1958) observed bison producing a squeaking noise by grinding their teeth. Bison are usually more vocal during herd movements, as are domestic cattle.

Tail Posture. Bison tail posture appears to reflect their social state and likely forms part of bison "body language" used to convey information to other herd members. Tail postures of free-ranging wood bison vary from tail wagging during grazing to holding the tail horizontally or vertically during periods of sexual behavior, aggression, or danger (Komers et al. 1992a). During fights between bulls, "tail up" was associated with dominance, whereas tail wagging was associated with submission. Cows more often held their tail up when disturbed by predators; bulls more often held their tail up during sexual encounters. As previously discussed, cows hold their tail out at some angle to the body for up to several hours following copulation.

Disposition. The disposition and approachability of individual bison and of herds are a function of the many environmental, genetic, and sociological conditions impinging on the individual. Bison have been described as having personalities (Shinn 1978). Although bison have been trained to do tricks and pull carts, they become more aggressive and intolerant with maturity and should be treated with considerable respect. "Pet" bison, once mature, have been known to kill their owners (Garretson 1927). At Elk Island National Park during the late 1970s, a park warden, who was experienced in working with bison, was gored severely by a bull bison after releasing it from a squeeze chute. The attack came without any warning and minimal threat posturing. Many similar attacks have been reported (McHugh 1958, 1972). During handling, bison can become enraged and can inflict serious damage on other animals, on themselves, and on property. At other times, these animals can be docile and shy.

Movements and Migration. Bison often undertake annual migrations that may be elevational or directional. In the American Northwest, Garretson (1927) noted that there was a definite movement of herds from the plains region in the east to the foothill areas of the Rockies in the winter. The reverse occurred in spring. Regarding these migrations, Hornaday (1889:423-24) stated that "the buffalo had settled migratory habits. . . . At the approach of winter the whole great system of herds which ranged from the Peace River to the Indian Territory moved south a few hundred miles, and wintered under more favorable circumstances than each band would have experienced at its farthest north."

In mountainous areas of Wyoming (Aune et al. 1998) and in north-eastern British Columbia, seasonal movements from higher elevation habitats in summer and fall to lower elevation habitats in winter and spring are common. Snipe flies (*Symphoromyia* sp.) may be responsible for some elevational movements in Yellowstone bison herds during the summer (Meagher 1973). Large, wind-swept prairies also may be chosen in summer for similar relief. Directional movements occur annually at Wood Buffalo National Park (Reynolds 1976) and at Yellowstone National Park (Meagher 1978). Bison, particularly cows, show strong affinity to return to traditional winter range (Meagher 1973).

In studies of bison home range size in northern Canada, the median home range size varied with age, sex, and forage availability (Larter and Gates 1994). Median home range size for young of the year (712 km²), immature males (706 km²), and adult females (1240 km²) on lower productivity range was significantly larger than median home range size for two age classes of mature bulls (younger, 434 km²; and older, 170 km²) and as well as for adult females on more productive range (398 km²). This difference may relate to differing energy requirements or other behavioral adaptations. In Yellowstone National Park, adult female home range size averaged 541 km² (Aune et al. 1998). In an unconfined setting, the home range of wild bison varies with habitat productivity. Temporal and spatial variations in range use are likely related to such factors as tradition, forage availability and nutritional quality, macroclimatic and microclimatic variations, open water, shelter, and insect harassment. An unusually severe winter in 1975/76 in Yellowstone National Park appeared to provide the impetus that led to the major westward movements or stress dispersal of bison on the northern winter range (Meagher 1989b).

Bison usually travel via the most practical direct route and will rapidly establish trails to do so (Garretson 1927; McHugh 1958). Forest and shrub areas often are used as daily and seasonal travel corridors in northern Canada (Reynolds 1976). When crossing rivers, bison usually take shallow fords with gradual approaches. However, they will not hesitate to cross large, swift-flowing rivers in northern Canada, such as the Peace, Liard, and Nahanni. Distance traveled on a daily basis can vary from <1 km to considerably more. Carbyn (1997) documented a herd of bison in Wood Buffalo National Park moving 81.5 km in a 24-hr period following wolf predation on a calf. In Yellowstone National Park, use of a plowed road in winter for easier and energy-efficient travel as well as acquired knowledge of areas having less snow appeared to be a stimulus that strongly influenced bison movements (Meagher 1989b). The attraction of bison to road corridors in northern Canada has led to animal-vehicle collisions in some instances and likely has affected dispersal and movement patterns.

During inclement weather, bison often head into the wind, unlike domestic cattle, a behavior perhaps related to the greater amount of hair insulating their head and forequarters. If unable to avoid traveling in deep snow, bison will form a line, with the lead animals plunging to create deep trenches (Meagher 1973).

Older cows tend to be the most wary and often take the lead in sudden herd movements (McHugh 1958; Fuller 1960). In the family group, the cow is usually the leader (Walker et al. 1975). At Elk Island National Park and Wood Buffalo National Park, cows generally are the leaders during herd movements, although some observers have ascribed this role to bulls (Seibert 1925; Soper 1941).

Disturbance of a wary group of bison within or near a herd may precipitate sudden movements or stampedes. Bison are capable of fleeing at speeds up to 60 km/hr (McHugh 1958; Fuller 1960). The initiating stimulus can be seemingly insignificant, making the stampede appear spontaneous. Stimulus to stampede may be caused by the sudden running of one animal toward the herd after being alarmed or by any other sudden external stimulus.

Encounters with fences can act as a deterrent to the movement of bison. Buck-and-pole style fencing virtually stops bison and elk movement while being much less of a barrier to pronghorn antelope and mule deer (Scott 1992). In general, efforts, such as hazing or herding, physical barriers (short fences and cattleguards), and scare devices, made over a 12-year period to contain bison within the boundaries of Yellowstone National Park proved to be ineffective (Meagher 1989a).

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TABLE 48.2. Size and composition of matriarchal and breeding groups at Lamar and Hayden valleys in Yellowstone National Park, Wyoming, and at Wind Cave National Park, South Dakota

Item	Group Location and Season			
	Lamar (Jan–Mar)	Lamar (May; Calving)	Wind Cave (Calving)	Hayden (Rut)
Group size				
Number of groups	18	15	17	36
Mean number/group	23	23.6	21.9	175.3
Standard deviation	11.4	18.4	21.2	108
Range	10–50	4–63	3–76	19–480
Group composition				
Number of groups censused	12	10	14	3
Mean number/group	20.3	17.3	16.8	115.2
Mean grouping tendency				
Cows ≥2 years old	12.1 ^a	8.6 ^b	7.4	39.3
Yearlings	4.4	4.8	4.0	20.0
Calves	0	3.9	3.9	25.3
Bulls 2–3 years old	3.8	3.7	1.1	16.3
Bulls ≥4 years old	0	0.2	0.4	14.3
Percentage of bulls 4 years old	0	1.0	2.1	9.2 ^c

SOURCE: After McHugh (1958).

^a19.3% 2-year-olds.

^b19.5% 2-year-olds.

^cComputed from census of eight groups.

The conclusion was that hazing and herding techniques served to move bison only where they wanted to go and may treat immediate problems at specific locations, but did not change the overall direction of bison movement through the river corridor (Meagher 1989a). When primary routes were blocked by human activities, the bison moved around barriers by crossing steeper terrain or traveling along tributary drainages (Meagher 1989b). Page wire game fencing is used routinely in the bison farming industry to contain captive bison herds. Commercial bison ranches have also had success with five-strand barbed wire fences and electric high-tensile fences (Deshano 2002). Animals that have learned to break fences, often bulls, can subsequently become much more difficult to restrain (Grandin 1999).

Aggregation. Bison are gregarious animals, but group size varies. Over the course of a year, three types of groups can be observed: matriarchal groups (cows, calves, yearlings, and sometimes a few older bulls), bull groups (including solitary bulls), and breeding groups (a combination of the first two groups).

Individual matriarchal groups vary little in size for most of the year. During the rut, they are joined by breeding bulls and other matriarchal groups to form breeding groups (Table 48.2). In Wood Buffalo National Park, Fuller (1960) suggested that the average group size for matriarchal groups ranged from 11 to 20 individuals among years and that there was considerable flexibility in the size of groups. In a study of bison group dynamics on a predator-free, forested summer range in southern Utah, Van Vuren (1983) noted that group size tended to be small, similar to what was seen for bison in other forested locations, but found no evidence of a basic social unit of the size reported by Fuller (1960). Van Vuren (1983) observed that group size varied with habitat openness, with larger groups associated with more-open habitats. He noted that bison usually grazed 3 m or more apart and that this behavioral phenomenon could be associated with smaller group size in small open habitats. Social groups include nursery groups composed of cow–calf pairs, calf groups, bull groups, barren cows, and yearlings, accompanied by some 2-year-olds (McHugh 1958). Nursery groups with 100–200 individuals have been reported in Yellowstone National Park (Aune et al. 1998). There is some controversy over whether matriarchal groups are consanguineous; Seton (1929) and Soper (1941) suggested that they are, whereas Garretson (1938), McHugh (1958), and Fuller (1960) believed otherwise. Green et al. (1989) showed a more prolonged association of cows with older daughters, which lends

some support to the suggestion of Soper (1941) and Seton (1929). Aune et al. (1998) noted that, in general, group fidelity was temporal and that associations between marked bison suggested a very fluid and dynamic group structure.

Mature bulls seldom form groups of more than a few animals and seem to become less gregarious with increasing age. Solitary bulls are common even during the rut. Occasionally, one or two cows are found with bull groups.

McHugh (1958) reported that breeding herds in Yellowstone ranged in size from 19 to 480 and averaged 175 animals (Table 48.2). Egerton (1962) reported that the size of herds in Wood Buffalo National Park varied from 11 to 30 animals. At the National Bison Range, Lott (1974) observed an average group size during the rut of 57 with a maximum of 174, whereas on Catalina Island, California, he found an average breeding group size of 17. Shackleton (1968) observed smaller breeding groups at Elk Island National Park than on the National Bison Range.

Bison herds often show a remarkable degree of herd fidelity even after temporarily mixing with other herds (Fuller 1960). Fences separating groups of animals will not discourage their attempts to form a single herd. McHugh (1958) and Meagher (1973) observed that disturbance by aircraft and certain physical phenomena such as shade and rain would increase herd cohesiveness.

Foraging Behavior. McHugh (1958) observed that feeding activity was mostly a diurnal occurrence, with the night spent loafing or occasionally feeding and traveling. Similar behavior has been reported in cattle (Hancock 1953). The amount of time spent foraging appears to be seasonally influenced. Hudson and Frank (1987) observed that during summer, a greater proportion of grazing occurred at night. Study of bison foraging ecology and behavior in the aspen boreal habitat of the Beaver Hills in central Alberta documented an increase in the amount of time bison spent grazing from 9 hr/day to 11 hr/day from summer through fall (Hudson and Frank 1987). On the Slave River Lowlands, Reynolds (1976) observed that foraging was done in open meadows, whereas loafing and ruminating occurred in forest habitat. During winter, bison in that area foraged in small, sheltered meadows and along river and creek beds. Such areas offered less-severe snow conditions and supported preferred forages.

Melton et al. (1990) concluded that wood bison foraging behavior was affected by sex, season/rut, biting flies, social status, and forage

biomass/habitat type. Presence of moderate to heavy concentrations of biting flies on northern bison ranges results in a shift from foraging to simply standing (Melton et al. 1989).

When lakeshores are free of ice and emergent vegetation is available, bison often forage in chest-deep water, similar to feeding behavior in moose (*Alces alces*). Bison usually prefer to seek open waters or break through thin ice to get water rather than eat snow (McHugh 1958). Unlike all other North American bovids and cervids, bison prefer to use their massive heads to sweep snow away from forage rather than to paw. For additional information on feeding patterns, refer to the FEEDING HABITS and ECOLOGY, Forage and Habitat Requirements sections.

REPRODUCTION

Breeding Season. In most regions, the breeding season, or rut, for bison generally occurs from July to October with the peak occurring between late July and mid-August (Garretson 1927; Soper 1941; Fuller 1966; Halloran 1968; Lott 1972; Meagher 1973; Banfield 1974; Haugen 1974). Temporal variability in onset and duration of the rut may be related to variation in climate, photoperiod, habitat, population density, and genetic expression. Female bison tend to be seasonally polyestrous, with a cycle of approximately 3 weeks duration (Fuller 1966; Banfield 1974; Kirkpatrick et al. 1993); however, unseasonal matings sometimes occur (Soper 1941; McHugh 1958; Banfield 1974). If conception does not occur with the first mating, the female may breed again 19–21 days later (Wolff 1998).

The rutting season varies in length depending on herd location. Rut has been observed to last from 15 June to 30 September at Hayden Valley, Yellowstone National Park, Wyoming (McHugh 1958), but generally it occurs in Yellowstone between mid-July and early September (Meagher 1978; Kirkpatrick et al. 1993); from 23 June to 14 September at Wind Cave National Park, South Dakota (McHugh 1958); from 21 July to 15 August for peak breeding activity and from 25 August to 3 September for a second, smaller peak of activity in Wind Cave National Park and Custer State Park, South Dakota (Haugen 1974); is confined to a 4- to 6-week period centering around early August at the Fort Niobrara National Wildlife Refuge, Nebraska (Mahan 1978; Wolff 1998); from 1 June to 30 July at the Wichita Mountains Wildlife Refuge,

Oklahoma (Halloran and Glass 1959); and from 1 July to 30 September in Wood Buffalo National Park, Alberta (Fuller 1960; Banfield 1974).

Calving and Pregnancy Rates. Calving rate is determined by dividing the total number of calves produced by the total number of mature females ≥ 3 years old in the herd (Rutberg 1986; Shaw and Carter 1989; Towne 1999). Pregnancy rate can be determined by necropsy of culled animals, rectal palpation in live, restrained animals (Wolfe et al. 1999), serum assay for pregnancy-specific protein B of blood samples drawn from immobilized live animals (Gates and Larter 1990), and urinary estrone conjugates measured by enzyme immunoassay of urine samples and fecal total estrogens measured by radioimmunoassay of fecal samples (Kirkpatrick et al. 1993). Urinary and fecal steroids or their metabolites can be used to detect pregnancy and ovulation in free-ranging bison with a reasonable level of accuracy (Kirkpatrick et al. 1992). Similarly, wood bison estrous cycles and synchronization can be monitored using either urine or feces (Matsuda et al. 1996). Calving and pregnancy rates for mature female bison vary considerably in free-ranging and semiwild herds throughout North America, ranging from a low of 35% to a high of 88% (Table 48.3). Calving and pregnancy rates for bison vary according to age, with reproductive vigor highest in animals between age 3 years and the onset of old age, presumed to commence at about 12–13 years of age, after which calving rates decline (Fuller 1961; Shaw and Carter 1989). In a reproductive success study of wood bison at Elk Island National Park, Alberta, Wilson et al. (2002) reported that the peak reproductive age of wood bison females was from 5 to 14 years indicating a decline in calving rates at age 15–16 years. Within this age span of 9–10 years, calving rates for young and older adults did not differ appreciably (Shaw and Carter 1989). Wild bison normally produce two calves every 3 years (Soper 1941; Fuller 1961, 1966; Halloran 1968; Banfield 1974).

The low reproductive rates observed in the Santa Catalina Island and Antelope Island bison herds, 35% and 46%, respectively (Table 48.3), were attributed to nutritional deficiency and poor-quality forage (Lott and Galland 1987; Wolfe et al. 1999). Nutrition likely affected productivity in the Henry Mountains bison population (Van Vuren and Bray 1986). Higher population densities may impose nutritional stresses that could explain an alternate-year pattern in calving (Shaw and Carter

TABLE 48.3. Calving and pregnancy rates of several free-ranging herds of North American bison

Herd Location	Calving Rate ^a (%)	Pregnancy Rate (%)	Reference
National Bison Range, Montana	—	78–100	McHugh 1958
National Bison Range, Montana	88.2	—	Rutberg 1986
Fort Niobrara National Wildlife Refuge, Nebraska	83.0	—	Wolff 1998
Fort Niobrara National Wildlife Refuge, Nebraska and Wind Cave National Park, South Dakota	78.4	—	Haugen 1974
Konza Prairie Research Natural Area, Kansas	74.4	—	Towne 1999
Wichita Mountains Wildlife Refuge, Oklahoma	71.8	—	Shaw and Carter 1989
Mackenzie Bison Sanctuary, Northwest Territories	—	70.0 ^b	Gates and Larter 1990
Wood Buffalo National Park, Northwest Territories	67.0	—	Fuller 1966
Wichita Mountains Wildlife Refuge, Oklahoma	66.9	—	Halloran 1968
Badlands National Park, South Dakota	64.3	—	Berger and Cunningham 1994
Henry Mountains, Utah	62.0	—	Van Vuren and Bray 1986
Yellowstone National Park, Wyoming	—	52.0 ^c	Meagher 1973
Yellowstone National Park, Wyoming	—	48.2 ^d	Kirkpatrick et al. 1993
Antelope Island State Park, Utah	—	46.2 ^e	Wolfe et al. 1999
Slave River Lowlands, Northwest Territories	<50.0 ^f	—	Van Camp and Calef 1987
Santa Catalina Island, California	35.0	—	Lott and Galland 1987

^aNumber of calves produced based on females ≥ 3 years old.

^bBased on necropsies of 28 adult females and serum pregnancy-specific protein B testing of 16 adult females in March 1987 and 1988 from an increasing herd of wood bison.

^cNecropsies of animals from herd reductions.

^dBased on measurements of urinary estrone conjugates (E₁C) and fecal total estrogens from 255 random urine and fecal samples collected from two subpopulations of lactating and nonlactating bison in 1989 and 1990.

^eMean annual pregnancy rate based on rectal palpation examination of live animals for the period 1987–1997 (range = 32.5–66.6%).

^fDeclining herd of diseased wood bison based on herd segregation counts in 1978.

1989). Environmental factors can have direct effects on reproductive success in bison and other large ungulates (Kirkpatrick et al. 1993) and may contribute to prolonged lactation and delayed ovulation the following season, especially in younger cows (Kirkpatrick et al. 1996). Population age structure differences may also account for some of the variation in pregnancy rates among herds. In Yellowstone National Park, overall reproductive performance was influenced by three variables: environmental conditions, which appear to have the most impact; age; and lactational status (Kirkpatrick et al. 1996). In Wind Cave National Park, reproductive strategies appeared to change with age, whereby older females trade offspring quantity for quality and are more likely to reproduce in alternate years (Green and Rothstein 1991). Furthermore, earlier-born females at Wind Cave had higher fecundity during their first 9 years and birth date not only was important to survival, but likely had positive fitness consequences for the survivors (Green and Rothstein 1993a). In areas where there are severe winters, calving and pregnancy rates often may be <50% (Van Camp and Calef 1987; Kirkpatrick et al. 1993). At Elk Island National Park, female wood bison reproductive success depended on age, mass, and prior success and was also affected by environmental differences between years (Wilson et al. 2002).

At the Wichita Mountains Wildlife Refuge, Oklahoma, Halloran (1968) attributed the low overall reproductive rate (52%) to high calf survival. In this herd, calves were observed nursing into their second year of life. This prolonged the physiological stress on the cows, which could adversely affect pregnancy and reproductive rates. Lactating cows at Wood Buffalo National Park carried smaller midwinter fetuses than did nonlactating cows, which suggested that bison cows with calves bred later in the year than did dry cows (Fuller 1961). Loss of a calf before the end of the breeding season probably increases the chances of breeding for the cow (Fuller 1966). Loss of a calf at any time before weaning may enhance the vigor of a calf in utero by improving the energy balance of the cow during the critical winter period. In Yellowstone National Park, during the 1960s, pregnancy rates averaged 52% (Meagher 1973). Visual observations in 1989–1990 indicated a calving rate that varied between 35% and 55%, implying an every-other-year or every 3-year pattern of calving in two subpopulations of bison at Yellowstone National Park (Kirkpatrick et al. 1993). The 2-year combined pregnancy rate, based on endocrine evidence of ovulation and pregnancy, was 48.2%, which was consistent with the visual observations and suggested that lactating cows with calves have significantly reduced fertility. Lactational suppression of ovarian activity likely is the primary mechanism by which fecundity is reduced (Kirkpatrick et al. 1993).

Diseases such as brucellosis and tuberculosis can influence pregnancy rate. Brucellosis causes abortion of calves and temporary sterility in cattle (Choquette et al. 1978). This disease in bison, in most aspects, is similar to that in cattle, where it also causes abortion in adults, and it can be associated with death in bison calves at least 2 weeks of age (Rhyan et al. 2001). From 1959 to 1974 in Wood Buffalo National Park, brucellosis infection rates averaged 30.2% (Broughton 1987), and from 1997 to 1999, 30.9% of bison tested were seropositive for brucellosis (Joly and Messier 2001a). From 1950 to 1967, the rate of tuberculosis infection in bison in Wood Buffalo National Park, based on postmortem examination, averaged 38.8% (Broughton 1987), and from 1997 to 1999, 49% of bison tested were positive for tuberculosis (Joly and Messier 2001a). The presence of bovine tuberculosis and brucellosis affected late-winter pregnancy rates in Wood Buffalo National Park bison. Animals that tested positive for tuberculosis and also had a high titer for brucellosis had a reduced pregnancy rate compared to bison with only one or neither disease (Joly and Messier 2001a). Furthermore, bison that tested positive for tuberculosis were significantly less likely to be pregnant than bison that tested negative (Joly and Messier 2001a). Based on population simulations using field data, Joly and Messier (2001b) described a “disease–predation” hypothesis where the presence of tuberculosis and brucellosis reduces bison survival and reproduction, thereby shifting bison abundance from a high-density equilibrium where food competition is regulatory to a low-density equilibrium where predation by wolves is regulatory. These data suggest that

tuberculosis and brucellosis are responsible for the sustained decline of bison abundance in Wood Buffalo National Park during the last 30 years (Joly and Messier 2001b). In Yellowstone National Park, abortions have occurred in bison since 1917 (Meagher 1973). Because the population continues to increase, the impact of this disease on fecundity appears to be minimal (Dobson and Meagher 1996). Although interpopulation variation in birth synchrony occurs in Yellowstone, evidence suggests that bison exposed to brucellosis failed to deviate significantly from two nondiseased populations (Badlands National Park and Wind Cave National Park), suggesting that food plays a greater role in the timing of reproduction in bison than does brucellosis exposure alone (Berger and Cain 1999). However, prudent conservation planning demands that disease transmission risks be minimized and ideally eliminated by rendering bison disease-free (Berger and Cain 1999).

Sexual Maturity. The age at which bison cows first conceive varies considerably among locations and often within herds from the same region (Fuller 1961, 1966; Halloran 1968; Meagher 1973; Haugen 1974). In Fort Niobrara National Wildlife Refuge, Nebraska, 79% of 2-year-olds breed (Wolff 1998). Few bison cows conceive as yearlings, giving birth to a calf at 2 years of age, varying from 5% in Wood Buffalo National Park (Fuller 1966), to 6% in Nebraska and South Dakota (Haugen 1974), to 12–13% in the Wichita Mountains Wildlife Refuge (Halloran 1968; Shaw and Carter 1989). Sexual maturity was attained earlier in bison cows at the Wichita Mountains Wildlife Refuge and in herds from Nebraska and South Dakota than in herds from Wood Buffalo National Park. In the Wichita Mountains Wildlife Refuge and in Nebraska and South Dakota bison herds, 73% and 87%, respectively, conceived as 2-year olds, producing first calves at age 3 years (Halloran 1968; Haugen 1974), whereas in Wood Buffalo National Park, only 52% of the cows conceived for the first time as 3-year-olds (Fuller 1966). During a 5-year study at Wind Cave National Park in the 1980s, 5% of the females began calving at age 2 years, 79% at age 3 years, and 17% at age 4 years (Green and Rothstein 1991). In general, bison cows usually breed when they are 2 years old and give birth to their first calf when they are 3 years of age (McHugh 1958; Fuller 1961; Shaw and Carter 1989; Green and Rothstein 1991). However, at Elk Island National Park over a 4-year reproductive study on wood bison, only two 2-year-olds successfully produced offspring and the mean age at first reproduction for females was 3.7 years suggesting that younger female wood bison in Elk Island National Park were not as fecund as plains bison in other populations (Wilson et al. 2002). Reduced range nutrition resulting from environmental influences and competition with an increasing elk population may have been a factor.

Attainment of sexual maturity in male bison was similar to that for female bison in Wood Buffalo National Park, varying from a low percentage of yearlings, to approximately 33% of 2-year-olds, to the majority of bison ≥ 3 years old (Fuller 1961). In the Wichita Mountains Wildlife Refuge, two experimental bulls were not effective herd sires as yearlings, but were effective at 2 years of age (Halloran 1968). In Nebraska and South Dakota, three of six yearling males and >75% in subsequent age classes were in breeding condition (Haugen 1974). In a 1985 study at the Fort Niobrara National Wildlife Refuge, the curve depicting male reproductive effort is flat from age 0 to 6 years, increases to age 8 years, flattens out again to about age 10 years, and then gradually decreases (Maher and Byers 1987). Because reproductive effort begins about age 6 years, contrasted with sexual maturation, which occurs at age 3 years (Maher and Byers 1987), this confirms that male bison attain sexual maturity well in advance of becoming part of the active breeding population (Fuller 1960; Meagher 1973; Rothstein and Griswold 1991). In Elk Island National Park over a 4-year study, only two 5-year-old male wood bison were reproductively successful as most of the successful males were in the 7- to 14-years age classes; however, the range of reproductively successful males was from 5 to 14 years (Wilson et al. 2002). In Fort Niobrara, reproductive success of 6+-year-old bulls ranged from 0 to 16 calves sired per bull over 3 years and was positively correlated with dominance rank (Wolff 1998). At Elk Island National Park, mature wood bison males produced

a mean of 3.8 offspring over the 4-year reproductive study period with a range of 0–24 (Wilson et al. 2002). In Badlands National Park, South Dakota, Berger (1989) demonstrated that bison males were capable of discrimination among females based on the reproductive potential of the females, whereby males ≥ 6 years outnumber younger males early in the rut, and older males actively select and copulate with females that have higher probabilities of bearing calves in the next season. At Elk Island National Park, only mass and prior success were useful in predicting male wood bison reproductive success (Wilson et al. 2002).

Number of Young. One calf is usual, as twinning in bison is rare (Garretson 1927; McHugh 1958; Fuller 1961, 1966; Halloran 1968; Banfield 1974; Van Vuren and Bray 1986; Rutberg 1986; Dary 1989; Green and Rothstein 1991). One instance of twin bison calves was reported by McHugh (1958) in the Lamar herd in Yellowstone and one set of twins was recorded in the plains bison herd at Wichita Mountains Wildlife Refuge in 1965 (Halloran 1968). In Wood Buffalo National Park from 1952 to 1956, no twins were observed in 481 gravid uteri examined (Fuller 1966), nor were twins observed in the 1964–1968 productivity study at Yellowstone National Park (Meagher 1973). In Elk Island National Park, Alberta, during the period 1945–1960, three sets of plains bison twins were observed. Between 1947 and 1971, examination of herd-reduction slaughter records of 4500 plains bison at Elk Island yielded only one case of twin fetuses (Wes Olson, Elk Island National Park, pers. commun., 2002). During round-ups of plains and wood bison at the park from 1984 to 2002, there was only one case of suspected twins where a cow with two calves was observed; however, the calves were never seen nursing (Wes Olson, Elk Island National Park, pers. commun., 2002). There was an extremely rare case of triplets reported from a farmed bison herd in Alberta in 2000, but two of the three calves were abandoned by the cow and had to be bottle-raised (Wes Olson, Elk Island National Park, pers. commun., 2002).

Calving Season. Most calves are born in a 3- to 4-week period from late April to early June, with an occasional calf being born as late as July (Rutberg 1984). However, conception and therefore parturition can occur at any time of year. From 1937 to 1950, calving at Yellowstone National Park had commenced by mid-April, whereas more recent studies indicated a later calving season, with most calves being born in the first half of May (Meagher 1973). McHugh (1958) noted that a few late calves were born from June through October in herds at Yellowstone National Park, the Crow Reservation, Wind Cave National Park, and the National Bison Range. Calving season became prolonged as the size of the population increased (Meagher 1973).

In the Wichita Mountains Wildlife Refuge herd, the first bison calf was always recorded within the period from 10 March to 7 April (Halloran 1968). In Wood Buffalo National Park, calving was observed from mid-April until the beginning of June (Egerton 1962; Banfield 1974). Soper (1941) noted that most calving in this park occurred around mid-May. Egerton (1962) observed that the calving period in a captive herd at Waterton Lakes National Park, Alberta, occurred from April through July. In the National Bison Range, the mean length of the calving season, the minimum period during which 80% of the young are born, was 23 days (Rutberg 1984), compared with 54 days, from early April to late May, in Wind Cave National Park (Green and Rothstein 1993b). In the National Bison Range, births were concentrated into the last week of April and the first 2 weeks of May, where 97% of the calves were born in the 6 weeks between 20 April and 2 June (Rutberg 1984). In Fort Niobrara National Wildlife Refuge, Nebraska, the first calves were born about 20 April each year and the last calves born by 24 August, with about 90% born between 20 April and 1 June each year (Wolff 1998). The high degree of synchrony of breeding, exhibited by the short calving season, at the National Bison Range appears to be the result of climatic and energetic factors rather than antipredator adaptations and is not limited by nutrition (Rutberg 1984). Bison breed less synchronously than previously reported, as indicated by the longer birth season (54 days) at Wind Cave National Park, a longer than expected time frame for an ungulate species with follower young (Green and Rothstein 1993b).

In Elk Island National Park, the calving period for wood bison commences during the latter part of April and lasts through mid-August, whereas for plains bison it usually begins by the first week in May and lasts until late August, with occasional late calves born in September and sometimes October. The calving season for plains bison became prolonged as herd size increased. The peak calving season for wood and plains bison is from 1 May to 15 June at Elk Island National Park. Calving season in northern bison occurs about 2 weeks later than in more southern herds, a phenomenon likely related to variations in climate and photoperiod between regions (Egerton 1962).

Gestation. Gestation for bison is usually 9–9.5 months and is similar to that for domestic cattle (Garretson 1927; Soper 1941; Walker et al. 1975; Halloran 1968; Rutberg 1986). Haugen (1974) reported that gestation was about 285 days for bison herds in South Dakota and Nebraska, and Banfield (1974) indicated that, in general, gestation is between 270 and 300 days. The length of gestation in bison approximates 262–272 days (Towne 1999).

POPULATION DYNAMICS

Longevity. Longevity of bison is not well documented. However, reports exist of bison living beyond 20 years of age (Halloran 1968; Meagher 1973; Berger and Peacock 1988) and even up to age 41 years (Dary 1989). In wild populations, by the time a bison has reached age 15 years it can be considered to have entered old age (Fuller 1966); in captivity, life span increases.

Calf and Adult Survival. In the Henry Mountains, Utah, calf survival was high at 93% and when hunting mortality was excluded, average survival rates for bulls (95%) and cows (96%) were similarly high (Van Vuren and Bray 1986). In Wood Buffalo National Park, calf (through 6 months of age) mortality was estimated at 50% and survival to the yearling category ranged from 5% to 8% of the herd per year (Fuller 1966). Wolf predation in the northern herd was considered to be the primary cause for the differential mortality rate in calves. During the peak growth period for the increasing Mackenzie wood bison population near Fort Providence, Northwest Territories, between 1970 and 1980, survival must have been greater than 95% among both calves and adults to achieve the observed population increase (Calef 1984). The adult survival rate in the Mackenzie wood bison herd during 1986–1987 was 97%, whereas the calf survival rate was 55% (Gates and Larter 1990).

Calf Percentage. In Yellowstone National Park, spring calf percentages (expressed as percentages of mixed herds) are normally 18–20% (Meagher 1973). In the spring of 1965, after herd reductions had removed large numbers of cows, the lowest calf percentages of the study (7–14%) were recorded for three herds. Calf percentages for these populations increased after 1965. Pooled percentages for the three herds in 1967 (20%) and 1968 (19%) suggested that the calf-producing segment of the population was leveling off and if so, then the proportion of newborn calves in mixed bison herds in Yellowstone approximated 20% (Meagher 1973). Nonselective herd reductions may alter calf percentages by taking an imbalanced harvest from the more easily slaughtered mixed herd groups rather than over the entire population. In Wood Buffalo National Park, a potential calf crop of 20–25% of the herd is expected during the latter part of June and early July. The calf crop declines by approximately 2%/month until December, when calves make up <10% of the herd (Fuller 1966). In the Mackenzie wood bison population during its peak growth years between 1970 and 1980, calves accounted for approximately 20% of the total number of animals, yearlings were 16%, 2- to 3-year olds were 13%, and ≥ 4 -year olds were about 50% of the population (Calef 1984).

The reproductive rate (calf crop expressed as a percentage of all herd females less calves and yearlings) for the bison herd in the Wichita Mountains Wildlife Refuge varied from 47% to 60% between 1960 and 1966, with an average of 52% (Halloran 1968). In that study, the rate for 198 experimental animals from six age classes was 67%. The higher value for the experimental animals compared with the entire herd was

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likely attributable to the higher percentages of younger animals (prime breeding age) in the former group (Halloran 1968).

Based on observations at Lake One in Wood Buffalo National Park in 1980, the recorded calf/cow ratio was extremely low at 0.12 (12 calves/100 cows) and was deemed not to be representative of the rest of the park population (Carbyn and Trotter 1987). The mean spring calf/cow ratio for bison herds south of the Peace River in Wood Buffalo National Park from 1989 to 1996 was 0.30, indicating an overall low rate of reproduction in the Park bison population (Carbyn et al. 1998). The low calf production and extremely low yearling survival may have been caused by a combination of factors such as disease, an aging population because of low recruitment, wolf predation, and variable habitat conditions (Carbyn et al. 1998). In contrast, over a 35-year period from 1960 to 2001, the annual calf/cow ratio for plains bison at Elk Island National Park varied from a high of 1.04 to a low of 0.28 and showed a significant ($p < .001$) inverse relationship with the number of breeding-age females (≥ 3 years) in the population (Fig. 48.5A). Likewise, over a 35-year period from 1967 to 2001 the annual calf/cow ratio for wood bison at Elk Island National Park varied from a high of 1.12 to a low of 0.47 and also showed a significant inverse relationship with the number of breeding-age females in the population (Fig. 48.5B).

The yearling-to-cow ratio for the increasing Mackenzie wood bison population near Fort Providence, Northwest Territories, during 1984 to 1988 averaged 0.30 (Gates and Larter 1990). The average ratio of males to females in the adult population (≥ 2 years old) was 0.76 (Gates and Larter 1990).

The mean exponential growth rate of the Mackenzie wood bison herd was 0.21, a rate that exceeded that of most other North American bison populations and is considered to be close to the maximum rate of increase for bison under natural conditions in the Northwest Territories (Calef 1984; Gates and Larter 1990). For example, the Henry Mountains herd grew at the exponential rate of 0.09 between 1977 and 1983 (Van Vuren and Bray 1986).

Sex Ratio. At Yellowstone National Park during the 1930s, Rush (1932) reported that primary (*in utero*) sex ratios for bison ranged from 108 to 163 males:100 females. The average in a sample of 294 fetuses was 56% males. In bison herds in Nebraska and South Dakota, of 101 embryos examined, 54.5% were males (Haugen 1974). Between 1952 and 1956 in Wood Buffalo National Park, the primary sex ratio for 472 fetuses examined was 112 males:100 females (Fuller 1966). Palmer (1916) reported 119 males:100 females in a sample of 460 plains bison fetuses. The fetal sex ratio in 82 culled pregnant females from the National Bison Range herd from 1964 to 1967 was 51:31 (Rutberg 1986). The reported primary sex ratios from four of these five herds are similar. With the exception of the National Bison Range sample, the different herd fetal sex ratios vary only within a 6% range. A slight excess in favor of males in the primary sex ratio is common among mammals (Fuller 1961, 1966; Halloran 1968; Haugen 1974; Feldhamer et al. 1999).

At the Wichita Mountains Wildlife Refuge between 1908 and 1966, 51% of the 5633 bison born at the Refuge were males (Halloran 1968). In the National Bison Range during fall round-ups from 1965 to 1968, the number of calves born to the herd showed a sex ratio of 162 males:184 females or 47% males, which differed substantially from the fetal proportion of 62% males from the culled sample (Rutberg 1986). Selective culling of nonlactating females may distort estimates of natural sex ratios *in utero* and at birth (Rutberg 1986). On the Konza Prairie in northeastern Kansas between 1991 and 1997, out of 317 calves born, 47% were male and 53% were female, and the number of male and female calves born each year did not deviate from an expected 50:50 ratio, with only one exception in 1997 (Towne 1999). In the Fort Niobrara National Wildlife Refuge, Nebraska, the sex ratio of calves did not deviate from 50:50 in any year, but the 3-year overall sex ratio slightly favored females (Wolff 1998). The sex ratio of bison calves at birth is not dependent on maternal condition and generally does not deviate from parity (Shaw and Carter 1989; Towne 1999). Sex ratio adjustment is more closely correlated with previous reproductive effort than it is to food source competition (Wolff 1998).

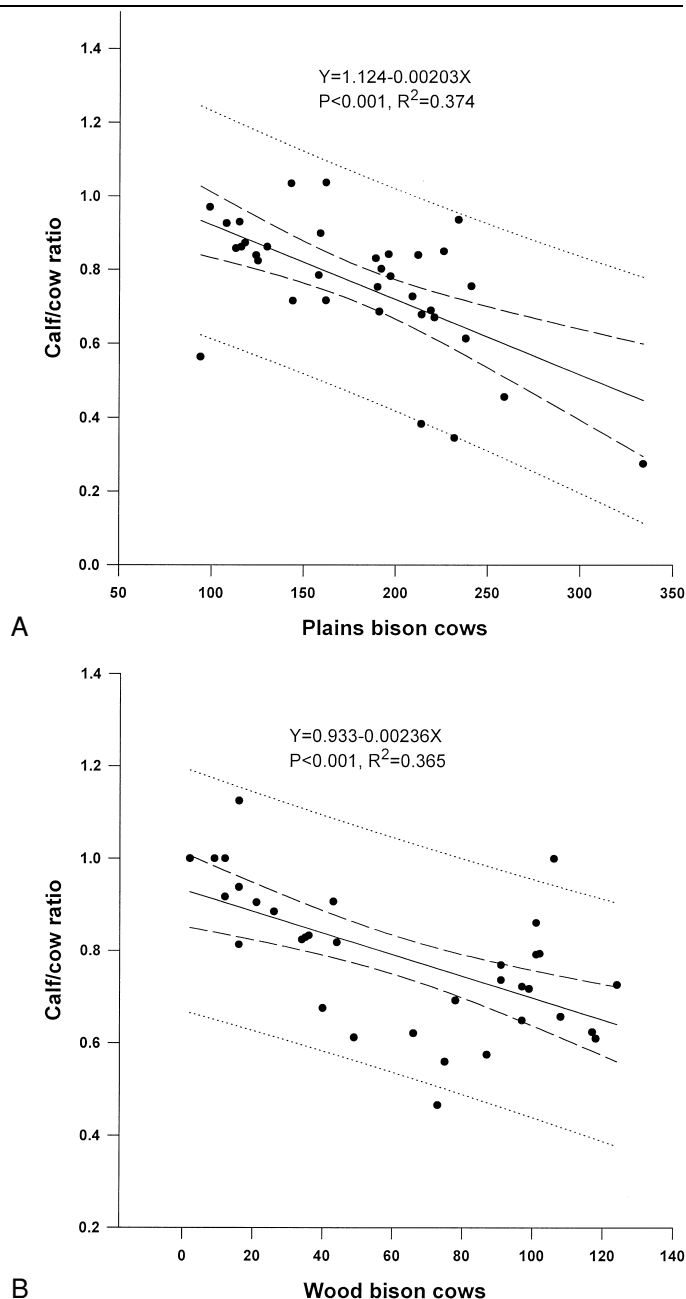


FIGURE 48.5. Relationship between the calf/cow ratio and the number of (A) plains bison (*Bison bison bison*) cows and (B) wood bison (*Bison bison athabasca*) cows aged 3 years and older at Elk Island National Park. SOURCE: Data from Olson (2002).

MORTALITY

Predation. A few circumstances have suggested occasional predation by the grizzly bear (*Ursus arctos*) on bison calves and adults in Yellowstone National Park, Wyoming (McHugh 1958; Meagher 1973). In the past, predation on bison by wolves in Yellowstone has not been a problem, as evidenced by the long survival time of injured and solitary animals and by the fact that wolves were rare and never observed in packs (Meagher 1973). However, with the reintroduction of 31 Canadian wolves into Yellowstone National Park in 1995–1996, this situation is expected to change with an increasing number of wolf–bison interactions and kills made during spring (Smith et al. 2000). Between April 1995 and March 1999, 14 bison kills by wolves were documented; however, the first wolf-killed bison was not observed until 25 months after the release (Smith et al. 2000). Furthermore, all kills were made

during late winter when bison were more vulnerable because of poor condition, injuries, or young age (Smith et al. 2000).

Wolf predation on bison is an important mortality factor in Wood Buffalo National Park, Alberta, (Fuller 1961, 1966; Oosenbrug and Carbyn 1982; Carbyn and Trottier 1987, 1988; Carbyn et al. 1993, 1998; Carbyn 1997). Fuller (1961) concluded that bison form the staple diet of Wood Buffalo National Park wolves during summer and winter. He found that 80% of the summer wolf scats examined contained bison hair, and in an early-winter sample of 59 wolf stomachs, 65% of the contents was bison (Fuller 1966). During winter 1978/79 in Wood Buffalo National Park, a study of radio-collared wolves indicated that bison were their major prey item. The Hornaday River wolf pack, composed of 10 members, killed an average of one bison every 7.8 days from 12 February to 31 March 1979. This equaled an estimated consumption rate of 5.3 kg/wolf/day and an estimated winter predation of 19 bison or 9.9% of the study area population (Oosenbrug and Carbyn 1982). Similar consumption rates were observed in the Slave River Lowlands, Northwest Territories, where wolves killed 13 adult female bison, 2 adult males, and 4 calves during 33 pack-weeks of effort (Van Camp 1987).

In Wood Buffalo National Park during the 1950s, wolves selectively preyed on calves or old animals, but predation was not considered to be detrimental to the bison population (Fuller 1961, 1966). However, during the 1978–1979 wolf study in the park, a higher proportion of bison killed by wolves were adult males (Oosenbrug and Carbyn 1982), whereas in the Slave River Lowlands, cows and calves were killed more often (Van Camp 1987). However, packs of wolves in other areas of Wood Buffalo National Park preferentially attacked bison herds with calves (Carbyn and Trottier 1987, 1988). Similarly, wolves associated with the Mackenzie wood bison population exhibited a preference for bison calves (Gates and Larter 1990). Recently reintroduced wolves in Yellowstone National Park showed a decided preference for bison that were more vulnerable because of poor condition, injury, or young age (Smith et al. 2000). Prey species, such as bison, are more vulnerable in winter and represent a greater amount of resource per unit effort at that time than do smaller prey species.

In the Slave River Lowlands, free-ranging bison herds numbered at least 2000 animals in 1971, but had declined to an estimated 750 by March 1977. Wolf numbers in the region were estimated to be between 64 and 76 during winter 1976/77 (Van Camp 1987). During this time, six packs of wolves were observed operating in the Lowlands, of which four were radio-marked. During 1975–1977, bison was the most important of six major prey types of wolves in this region and represented 88% of prey weight of wolf diets in winter (Van Camp 1987). Based on estimates for 22 weeks of winter in 1976/77, wolf predation accounted for approximately 31% of the adult and subadult mortality and about 27% of the calf mortality. When combined with hunting mortality, it accounted for at least 70% of the adult and subadult bison lost that year (Van Camp 1987). Wolf predation was exerting a major role in the continued decline of the Slave River Lowlands bison population. A wolf control program selectively removed 72 wolves from the region during the winters of 1977–1979, but the bison population continued to decline (Van Camp 1987).

In conclusion, wolf predation is a significant limiting factor for some bison populations (Van Camp 1987; Carbyn and Trottier 1988; Carbyn et al. 1993, 1998) and may regulate diseased herds at low density (Gates 1993). The “disease–predation” hypothesis described by Gates (1993) and Joly and Messier (2001b) suggests that tuberculosis and brucellosis reduce bison survival and reproduction, thereby increasing vulnerability of some animals to predation and causing populations to decline to chronically low densities where predation by wolves can be regulatory. In contrast, disease-free bison populations may be regulated at a high-density equilibrium where interspecific food competition can be regulatory, despite the presence of wolves.

Hunting. During regulated seasons from 1968 to 1977, sport hunting of bison was permitted in the Slave River Lowlands north of Fort Smith, Northwest Territories. The reported number of bison kills from license

returns averaged 179/year from 1969 to 1974, which approximated 8.8% of the population/year (Van Camp 1987). During 1974–1976, the average annual recruitment to the bison population declined to an average of only 3%/year (Van Camp and Calef 1987), but hunters killed at least 8% of the bison population annually (Van Camp 1987). Hunting alone could have caused the bison population to enter into a period of negative annual increments. In fall 1977, the recreational hunting season was closed and general hunting license holders voluntarily agreed to reduce their harvest. However, based on kill return data, the general hunting license holders accounted for approximately 5% of the total bison herd annually since the 1970s. Therefore, hunting harvest rates exceeded the average annual recruitment rate, at least during the period of major decline (1973–1976), and a decreasing population was inevitable (Van Camp 1987). Wolf predation and human hunting were the two major mortality factors contributing to the continued decline of the Slave River Lowlands bison population and appeared to be additive rather than compensatory mortality (Van Camp 1987). In a 7-year study (1977–1983) in the Henry Mountains, Utah, hunting mortality averaged 9% of the population, but was heavily biased toward males (Van Vuren and Bray 1986).

Accidents. Accidental drowning often occurs as a result of animals falling through thin ice in spring and fall. Whole herds of bison have succumbed to such fatalities (Raup 1933; Meagher 1973). Drowning was considered an important mortality factor of the plains bison (Roe 1970). Spring flooding in the Peace–Athabasca River Delta in Wood Buffalo National Park in 1958 caused the death of about 500 bison, autumn flooding in 1959 resulted in the death of an estimated 3000, and spring floods in 1961 resulted in the death of >1100 bison (Fuller 1966). Several thousand bison also were drowned in the delta region of Wood Buffalo National Park during a nontypical spring flood in 1974. In Yellowstone National Park, a few bison from all age classes have drowned in bogs or by falling into hot pools (Meagher 1973). In Elk Island National Park, Alberta, occasionally a few bison fall through the ice and drown as a result of traveling too close to beaver (*Castor canadensis*) houses when crossing frozen lakes.

Forest fires commonly occur in northern bison ranges without causing appreciable mortality (Soper 1941; Fuller 1966). The main effect on bison is loss of cover; however, in many situations, feeding habitat is improved and sometimes created by fire. Prescribed burning has been employed as a management tool to enhance habitat in the Hook Lake and Mackenzie bison ranges in the Northwest Territories (Chowns et al. 1998). Wildfires can be catastrophic to herds of bison, although such events are rare. Roe (1970) describes two historical accounts of bison being destroyed by fire where many animals were killed, blinded, or badly burned.

A few bison fatalities from motor vehicles have occurred along access roads within Wood Buffalo National Park (Fuller 1966) and along highways through the Mackenzie Bison Sanctuary and the Liard River Valley, Northwest Territories. In the Konza Prairie Research Natural Area, northeastern Kansas, annual mortality from lightning strikes, injury, or advanced age averages approximately 4% of the plains bison herd (Towne 1999).

Climate. Above-average snowfall, long periods of subzero temperatures, and midwinter thaws followed by severe freezing conditions result in winter-caused mortality in bison. Such severe winter conditions reduce forage availability, which often leads to poor animal condition and subsequent death. Extreme snowfall, in excess of 4 m, on bison ranges in northern Canada during the early 1800s resulted in the loss of thousands of animals (Soper 1941). In 1928, an early spring thaw followed by freezing temperatures in Wood Buffalo National Park caused crushing snow conditions that forced bison to remain in forests and sheltered areas to feed (Raup 1933). In Yellowstone National Park, Meagher (1973) defined winterkill as the combined effects of climatic stress, reduced forage availability, and physiological condition of individual animals and, considered it to be the main cause of bison mortality in the park. Weather, independent of other factors, is not usually a significant cause of mortality, but is an additional physiological stress, which, when

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TABLE 48.4. Parasites reported from *Bison bison*

Parasite	Site of Infection ^a	Location ^b	Reference ^c
Arthropoda			
<i>Cochliomyia macellaria</i>	S	?	37, 38
<i>Damalinea sedecimdecembrii</i>	S	WBNP	14, 37
<i>Demodex</i> spp.	S	—	32
<i>Dermacentor albipictus</i>	S	EINP	26, 36
<i>D. andersoni</i>	S, NV (neurotoxin)	M	17
<i>D. nigrolineatus</i> (= <i>D. albipictus</i>)	S	WMWR	24
<i>Hypoderma bovis</i>	S, SC	MI	33
<i>Hypoderma lineatum</i>	S, E	WMWR, NY, OK, YNP	24, 27
<i>Hypoderma</i> sp. ^d	S, E, D	WBP, NBR	5, 6, 18
<i>Speleognathus australis</i>	NS	WMWR	11, 38
Cestoda			
<i>Echinococcus granulosus</i> (suspected)	LV	WBP	5
<i>Moniezia benedeni</i>	SI	SD, M, YNP, NBR, WMWR, EINP	3, 9, 10, 12, 15, 18, 24, 26
<i>M. planissima</i> (probably)	SI	WBP	5
Protozoa and rickettsia			
<i>Anaplasma marginale</i>	B	NBR	28
<i>Babesia bigemina</i>	B	Experimental infection	29, 30
<i>B. major</i>	B	Experimental infection	29, 30
<i>Eimeria</i> sp.	I	LZ	22
<i>E. auburnensis</i>	I	EINP, W	20, 25, 31
<i>E. bovis</i>	I	EINP, M	20, 31
<i>E. brasiliensis</i>	I	W	25, 31
<i>E. bukidnonensis</i>	I	—	21
<i>E. canadensis</i>	I	W	25, 31
<i>E. ellipsoidalis</i>	I	W	25, 31
<i>E. zurnii</i>	I	W, M	31
<i>Sarcocystis</i> sp.	HM	WBP, NY	5, 6, 27
<i>Toxoplasma gondii</i>	Serology	M	42
Nematoda			
<i>Chabertia ovina</i>	C/CO	SD, ZGP	3, 16
<i>Cooperia bisonis</i> ^e	SI	WBP, EINP	5, 10, 15
<i>C. oncophora</i>	AB, SI	SD, EINP, NY	3, 4, 12, 26, 27
<i>C. surnabada</i> (= <i>C. mcmasteri</i>)	AB, SI	SD, EINP	3, 4, 12, 26
<i>Cooperia</i> sp.	SI	WBP	6
<i>Dictyocaulus filaria</i>	LG	WBP	5
<i>D. viviparus</i> (<i>hadweni</i> syn.)	LG	SD, WBP, K, NBR, EINP, NY, WMWR	3, 7, 8, 10, 12, 13, 15, 18, 24, 26, 27
<i>Dictyocaulus</i> sp.	LG	WBNP, YNP	14, 19

(Continues)

combined with predation and disease, can increase the rate of mortality (Fuller 1961).

Parasites and Diseases. Bison carry many parasites (Table 48.4) and diseases that also occur in their close relative, domestic cattle (Tessaro 1989). Controversies have arisen over the risk of transmission of diseases between bison and domestic livestock in Utah (Popov and Low 1950; Nelson 1965), the Greater Yellowstone Ecosystem (Thorne et al. 1991), and northern Canada (Gates et al. 1992a). Despite the similarity and close genetic relatedness of bison and cattle, knowledge of disease organisms in cattle cannot necessarily be used to infer their epidemiology or pathobiology in bison (Tessaro 1989; Meagher and Meyer 1994; Meyer and Meagher 1995). For example, Van Vuren and Scott (1995) found that endoparasite prevalence differed between sympatric bison and cattle in the Henry Mountains, Utah. They suggested that host-parasite relationships may differ between bison and cattle because of genetic differences (Cronin and Crockett 1993), metabolism (Christopherson et al. 1978), digestive physiology (Schaefer et al. 1978), or different rumen microbial populations (Towne 1988). Ecological and behavioral differences between bison and cattle may affect transmission. When bison and cattle occur in the same area, they may forage in different localities because of differing responses to forage availability, slope, and distance to water (Van Vuren 1982).

ENDOPARASITES. Anaplasmosis is caused by *Anaplasma marginale*, a rickettsia that parasitizes red blood cells of host animals. Insects, like

the tick *Dermacentor andersoni*, transmit the organism between hosts (Radostits et al. 2000). Bison have been experimentally infected with *A. marginale* (Zaugg and Kuttler 1985; Zaugg 1986). In the National Bison Range, Montana, 15.7% of bison tested positive for anaplasmosis (Zaugg and Kuttler 1985). Clinical signs of anaplasmosis in cattle include anemia, jaundice, emaciation, and debility (Radostits et al. 2000). Bison may be more resistant than cattle, because experimentally infected bison calves demonstrated only mild clinical signs (Zaugg and Kuttler 1985).

Babesiosis is caused by the protozoans *Babesia bigemina* and *B. major*. These two species of *Babesia* are the only ones reported to cause disease in bison (Locker 1953; Zaugg and Kuttler 1987). *Babesia* spp. are transmitted by ticks. Babesiosis has been induced in bison by experimental infection with *B. bigemina* (Zaugg and Kuttler 1987). Natural infections of bison have not been reported. The organism causes intravascular hemolysis where clinical signs include fever, jaundice, hemoglobinuria, heavy breathing, and anorexia (Locker 1953; Zaugg and Kuttler 1987).

Coccidiosis is caused by six species of protozoans in the genus *Eimeria*, including *E. auburnensis*, *E. bovis*, *E. brasiliensis*, *E. canadensis*, *E. ellipsoidalis*, and *E. zurnii* (Ryff and Bergstrom 1975; Penzhorn et al. 1994). This disease has been reported infrequently in bison calves. Short-yearling bison in a captive herd of wood bison in the Slave River Lowlands in northern Canada experienced severe coccidiosis in March 1994 (C. Gates, pers. obs.); two calves died after experiencing bloody

TABLE 48.4—Continued

Parasite	Site of Infection ^a	Location ^b	Reference ^c
<i>Haemonchus contortus</i>	AB	SD, K, NY, WMWR	3, 10, 12, 13, 23, 24, 27
<i>Nematodirella longispiculata</i>	SI	EINP	15
<i>Nematodirus helvetianus</i>	SI	EINP, NY	15, 27
<i>Oesophagostomum radiatum</i>	CO	K, EINP, WMWR	10, 12, 13, 24, 26
<i>Oesophagostomum</i> sp.	CO	WBP	5
<i>Oesophagostomum</i> sp.	SI, LI	Y	27
<i>Ostertagia bisonis</i>	AB	SD, WBP, K, EINP	3, 7, 10, 12, 13, 26, 41
<i>O. lyrata</i> (= <i>Grosspiculugia lyrata</i>)	AB, SI	EINP	12, 26
<i>O. ostertagi</i>	AB	EINP, NY	10, 12, 26, 27
<i>O. trifurcata</i>	AB	SD	3
<i>Setaria labiatopapillosa</i>	CE	ND, M, NZP, WBP, WBNP, EINP, NY	1, 5, 12, 14, 15, 26, 27
<i>S. yehi</i>	CE	ND	1
<i>Setaria</i> sp.	CE	WBP	6, 10
<i>Strongylus</i> sp.	I	H, YNP	34, 35
<i>Trichostrongylus axei</i>	CE, SI	EINP, NY	10, 12, 26, 27
<i>T. lerouxi</i>	SI	NY	27
<i>Trichuris discolor</i>	C	NY	27
<i>T. ovis</i> [†]	C	NBR	12, 18
<i>Trichuris</i> sp. (eggs)	F	EINP	26
Trematoda			
<i>Fasciola hepatica</i>	BD/LV	NBR, W, H	12, 18, 2, 34, 35
<i>Fascioloides magna</i>	LV	WBP	5, 6, 10, 40
<i>Paramphistomum microbothrioides</i>	RU	—	39

^aAB, Abomasum; B, blood; BD, bile duct; C, cecum; CE, coelom; CO, colon; D, diaphragm; E, esophagus; F, feces; HM, heart muscle; I, intestine; LI, large intestine; LV, liver; LG, lung; M, muscle; RU, rumen; NS, nasal sinus; NV, nervous system; S, skin; SC, spinal cord; SI, small intestine.

^bEINP, Elk Island National Park; K, Kansas; H, Henry Mountains, Utah; LZ, Leningrad Zoo; M, Montana; MI, Michigan; NBR, National Bison Range; ND, North Dakota; NY, New York State; NZP, National Zoological Park (District of Columbia); OK, Oklahoma; SD, South Dakota; WBP, Wainwright Buffalo Park; WMWR, Wichita Mountains Wildlife Refuge; WBNP, Wood Buffalo National Park; W, Wyoming; YNP, Yellowstone National Park; ZGP, Zoological Garden of Prague.

^c1, Becklund and Walker 1969; 2, Bergstrom 1967; 3, Boddicker and Huggins 1969; 4, Burtner and Becklund 1971; 5, Cameron 1923; 6, Cameron 1924; 7, Chapin 1925; 8, Corner and Connell 1958; 9, Dikmans 1934; 10, Dikmans 1939; 11, Drummond and Medley 1964; 12, Dunn 1968 (literature review only); 13, Frick 1951; 14, Fuller 1966; 15, J. Holmes, 1981, pers. commun.; 16, Jaros et al. 1966; 17, Kohls and Kramis 1952; 18, Locker 1953; 19, Meagher 1973; 20, L. Morgantini, unpublished data; 21, Pellerdy 1963; 22, Pellerdy 1974; 23, Ransom 1911; 24, Roudabush 1936; 25, Ryff and Bergstrom 1975; 26, W. Samuel, University of Alberta, Edmonton, 1981, pers. commun.; 27, Wade et al. 1979; 28, Zaugg and Kuttler 1985; 29, Findlay and Begg 1977; 30, Zaugg and Kuttler 1987; 31, Penzhorn et al. 1994; 32, Vestweber et al. 1999; 33, Schillhorn van Veen et al. 1991; 34, Zaugg et al. 1993; 35, Van Vuren and Scott 1995; 36, Mooring and Samuel 1998; 37, McHugh 1972; 38, Tessaro 1989; 39, Herd and Hull 1981; 40, Swales 1936; 41, Lichtenfels and Pilit 1991; 42, Dubey 1985.

^dOther species of parasitic Diptera (e.g. those within the Culicidae, Muscidae, Rhagionidae, and Tabanidae) have been observed in association with bison (Meagher 1973).

^e*Cooperia bisonis* (Cram 1925) was reported as *Haemonchus ostertagi* by Cameron (1923).

^fIdentification suspect, since it was based on examination of female worms only (Locker 1953).

diarrhea and emaciation. Others were treated and survived. The disease is associated with overcrowding, fecal build-up in pens, fecal contamination of water sources, a build-up of coccidia oocysts in the environment, and consumption of large numbers of oocysts by calves (Radostits et al. 2000). Stress associated with weaning, transport and mixing of calves, and cold weather conditions can induce coccidiosis. Coccidiosis was diagnosed in a captive wood bison herd established in northeast Alberta during 2000, resulting from stress and overcrowding. It was believed to be a contributing factor in the death of several animals. Treatment administered in drinking water along with reduced levels of stress alleviated the problem. Although there are no reports of this disease in wild bison, *Eimeria bovis* and *E. zurnii* are common among bison in Montana (Penzhorn et al. 1994). In spite of coccidia oocysts being found in cattle grazed sympatrically with bison in Utah, no oocysts were found in bison feces (Van Vuren and Scott 1995).

Sarcocystosis is caused by protozoans in the genus *Sarcocystis*, for which bison and other ungulates serve as intermediate hosts. Oocysts or sporocysts are released in the feces of an infected wolf, coyote, or dog, which serves as the definitive host. Intermediate hosts become infected when they consume contaminated food or water. This protozoan has been reported in the muscle tissue of 94% of bison in Alberta and 13% in Montana (Pond and Speer 1979; Dubey 1980a, 1980b; Mahrt and Colwell 1980; Fayer et al. 1982). Clinical signs have not been described for bison. However, bison calves experimentally infected with large

doses of sporocysts became anemic, anorexic, and lethargic, and had elevated body temperatures (Dubey 1982).

The term *helminth* refers to a number of phyla with superficial similarities, usually grouped into three categories: tapeworms (Cestoda), flukes (Trematoda), and roundworms (Nematoda).

The tapeworms *Taenia hydatigena* and *Echinococcus granulosus* cause hydatid disease in mammals, which is expressed as fluid-filled cysts in the liver or lungs. The adults of these tapeworms live in the intestinal tracts of their primary hosts, wild and domestic carnivores. Eggs are passed in the feces. If the eggs are consumed by a secondary host, including cattle, sheep, bison, and other herbivores, they hatch in the intestinal tract and migrate to the liver, lungs, and peritoneal cavity. Within these organs, cysts, called cysticerci or hydatids, are formed. The resistance of bovids to *E. granulosus* may account for its absence in bison at Wood Buffalo National Park despite its occurrence in dogs, wolves, caribou, and moose in the region (Fuller 1966). Hydatid cysts commonly occur in cervids at Elk Island National Park, but have not been seen in the resident bison. Choudary et al. (1987) reported *E. granulosus*, in an American bison in a zoo in India; pathological changes associated with infection included hepatomegaly and hydatid cysts in the liver and the lungs.

The tapeworm *Monezia benedeni* lives as an adult in the gastrointestinal tract of its herbivore host. It is a common parasite in bison and has been reported widely in North America (Cameron 1923; Dikmans 1934; Boddicker and Huggins 1969; Wade et al. 1979). Neither clinical

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symptoms nor pathology associated with this parasite have been reported in bison.

Both the common bile duct liver fluke *Fasciola hepatica* and the deer fluke *Fascioloides magna* have been reported from bison (Table 48.4). *F. hepatica* has been isolated from bison fecal samples in Utah (Locker 1953; Van Vuren and Scott 1995) and Yellowstone National Park (Zaugg et al. 1993). The life cycle of *F. hepatica* requires the development of immature stages in snails, which are the intermediate host. Larval flukes leave the snail and encyst on vegetation. Bison, cattle, and sheep become infected when they consume infected snails or cysts. Clinical signs of liver fluke infection have not been described for bison. Bison are not considered to be a preferred host for the deer fluke (Swales 1936).

The rumen fluke (*Paramphistomum microbothrioides*) has been reported in bison (Herd and Hull 1981). In domestic cattle, severe diarrhea and weight loss have been associated with intestinal paramphistomiasis.

A variety of parasitic roundworms occurs in the gastrointestinal tracts or peritoneal cavity of bison (Table 48.4). Although reduced growth rate, loss of productivity, lack of vitality, and unthriftiness have been reported in cattle that were heavily infected with gastrointestinal nematodes, the only species reported to have caused clinical disease in bison is *Ostertagia* spp. (Wade et al. 1979). *Ostertagia* larvae can penetrate the glands of the abomasum, where they enter into a dormant, hypobiotic state. If large numbers of larvae emerge from hypobiosis, they can cause serious damage to the abomasal mucosa, which can then result in clinical disease and death. This form of ostertagiosis (Type II) was reported in three bison herds in New York State (Wade et al. 1979).

In ranches in northern Alberta, *Cooperia* spp. was the predominant parasite identified in feces, accounting for 96% of all parasites found in calves and 92% of all parasites found in cows (Dies 1998). Van Vuren and Scott (1995) reported a high prevalence of strongylida in bison feces collected from the Henry Mountains herd in Utah. This is similar to results from Yellowstone National Park, where 80% of bison examined carried *Strongylus* spp. (Zaugg et al. 1993). A low prevalence of *Fasciola hepatica* and *Trichuris* spp. was reported in several studies (Locker 1953; Zaugg et al. 1993; Van Vuren and Scott 1995).

The nematodes *Dictyocaulus hadweni*, *D. filaria*, and *D. viviparus* live and reproduce as adults in the bronchi of lungs. Eggs produced in the lungs develop into larvae, which are coughed up, swallowed, and passed in the feces. *Dictyocaulus* spp. is a direct life cycle parasite. Larvae are consumed with vegetation by grazing bison. They then migrate through the wall of the intestines, enter the venous drainage, and are transported through the circulatory system to the lungs. *Dictyocaulus* spp. have been isolated from bison in Kansas (Frick 1951), Wyoming (Bergstrom 1982), Montana (Locker 1953), Oklahoma (Roudabush 1936), Yellowstone National Park (Meagher 1973), and Wood Buffalo National Park (Fuller 1966). Clinical signs associated with lungworm in bison include increased respiratory rate, coughing, slight nasal discharge, increased heart rate, and mild fever (Berezowski n.d.). Severe infections may cause death. Postmortem findings include pulmonary edema, emphysema, and large quantities of bloody froth in the trachea and bronchi containing adult lungworms (Berezowski n.d.).

ECTOPARASITES. Demodex mange, or demodectosis, is caused by mites (*Demodex* spp.) infesting hair follicles and sebaceous glands in the skin. The disease is characterized by small, 7- to 9-mm pus-filled nodules around the eyes, perineum, and ventral surface of the tail, or as small, palpable lesions on the neck, flank, and shoulders (Vestweber et al. 1999).

The winter tick (*Dermacentor albipictus*) and the Rocky Mountain tick (*D. andersoni*) occur in bison (Table 48.4). Ticks cling to the hair and suck blood by attaching to and piercing the skin of the host. In large numbers, they can cause severe anemia and debility and negatively affect host populations (Samuel and Welch 1991). Bison are less susceptible to tick infestation than are cervids. Bison at Elk Island National Park exhibited only light infestations in the presence of moose and elk that were infested with high numbers of *D. albipictus*. This probably reflected the tick-reducing effect of the grooming behavior of bison (Mooring and Samuel 1998). The only reported clinical effect resulting

from tick infestation in bison is tick paralysis (Kohls and Kramis 1952). This condition is caused by a neurotoxin produced by some ticks. Initially, bison experiencing tick paralysis exhibit an unsteady gate and jerky movements followed by an inability to get up. Tick paralysis has only been reported in bison calves and yearlings (Kohls and Kramis 1952).

Warbles, the late larval stage of the parasitic fly *Hypoderma bovis* and *H. lineatum*, have been reported in bison from several locations (Roudabush 1936; Locker 1953; Schillhorn van Veen et al. 1991). Adult warble flies attach their eggs to the hair on the legs and lower body of the host. After hatching, the larvae penetrate the skin and migrate to the esophagus (*H. lineatum*) or the spine (*H. bovis*). The larvae grow throughout the winter in these locations, then in the spring they migrate to just under the skin on the back. They eventually make a hole in the skin, emerge, and drop to the ground, where they pupate and metamorphose into adult flies (Radostits et al. 2000). In bison from Montana and Yellowstone National Park, dead, discolored larvae were found under the skin, which suggests that they may not have been able to penetrate the thick hide (Locker 1953). Clinical signs of warble infestation in bison have not been reported.

Other ectoparasites reported from bison include the chewing louse (*Damalinea sedecimdecembrii*) recorded by Fuller (1966) in Wood Buffalo National Park, the nasal mite (*Speleognathus australis*) (Drummond and Medley 1964; McHugh 1972), and the screw worm (McHugh 1972; Tessaro 1989). Biting insects cause serious harassment of bison, including mosquitoes (*Aedes* spp.), horse and deer flies (*Tabanus* spp.), black flies (*Simulium* spp.), the face fly (*Musca autumnalis*), the stable fly (*Stomoxys calcitrans*), and snipe flies (*Symphoromyia* spp.) (Bay et al. 1968; Burger and Anderson 1970; Meagher 1973; Tessaro 1989).

BACTERIAL DISEASES. Actinobacillosis is caused by *Actinobacillus lignieresii*, which is found in the mouth of clinically normal ruminants (Radostits et al. 2000). Abrasions of the oral mucosa associated with foraging on coarse feed may allow entry into the oropharyngeal. Eruption of teeth also may create an opportunity for infection with the bacterium. Actinobacillosis has been reported in bison, but the clinical signs associated with infection have not been described (Choquette et al. 1961). In cattle, actinobacillosis is known as wooden tongue disease (Radostits et al. 2000). It is characterized by a swollen, hard tongue and excessive salivation.

Anthrax is an infectious, often fatal disease of mammals, including humans. It is caused by the endospore-forming bacterium *Bacillus anthracis* (Dragon and Rennie 1995; Gates et al. 2001a). The life history strategy of *B. anthracis* is different from that in many other co-evolved host-parasite relationships in that its persistence depends on extreme virulence, the death of its host, and the long-term survival of highly resistant endospores in the environment. Anthrax epidemics occur regularly around the world. The bacillus is endemic to many areas in Europe, Asia, Africa, Australia, and North, Central, and South America (Gates et al. 2001a). In North America, outbreaks of anthrax occur regularly in bison herds in the Slave River Lowlands, Northwest Territories, and in Wood Buffalo National Park (Tessaro 1989; Broughton 1992; Dragon and Elkin 2001). Over the period from 1962 to 1978, at least 1086 bison deaths in these populations were attributable to anthrax (Reynolds et al. 1982). An outbreak occurred in a free-ranging wood bison herd near Fort Providence west of Great Slave Lake in 1993, killing at least 172 bison (Gates et al. 1995). The disease disproportionately affects male bison and is not considered to be a significant factor in population dynamics (Gates et al. 1995). Anthrax is not treatable in free-ranging wildlife, but captive bison can be vaccinated (Gates et al. 2001a). Anthrax Emergency Response Plans, preplanned logistical frameworks for responding effectively to outbreaks to minimize spread of the disease, reduce environmental contamination, and minimize risk to public health, are now being developed by responsible jurisdictions (Nishi et al. 2002c).

Clostridium chauveii causes the disease blackleg in bison. Other bacteria may cause a similar disease in cattle (Tessaro 1989). *C. chauveii* is a soil-borne bacterium. Similar to *B. anthracis*, it can survive in the soil for many years. The bacterium enters the body when consumed

with contaminated forage. In clinically normal animals, bacteria occur in the spleen, the liver, and the intestinal tract. Disease may occur when bacterial spores that are lodged in normal tissue, typically muscle, proliferate following bruising of the tissue. The bacteria rapidly increase, producing toxins that kill tissue and cause toxemia. In cattle, blackleg leads rapidly to death of the host. The clinical signs of blackleg in bison have not been described (Tessaro 1989).

Brucella abortus is a coccobacillus that lives as a facultative intracellular parasite (Radostits et al. 2000) and causes a disease known as bovine brucellosis. It is transmitted in mammals primarily by oral contact with aborted fetuses, contaminated placentas, and uterine discharges. The organism also may be excreted in milk. *B. abortus* is thought to have been introduced to bison from cattle (Meagher and Meyer 1994). Lesions associated with brucellosis are similar in bison and cattle, including abortion (Williams et al. 1993; Rhyan et al. 1994), retained placenta, and endometritis (Tessaro 1987; Rhyan et al. 2001), although there may be some interspecies differences in tissue colonization (Rhyan et al. 2001). Brucella-induced abortion occurs in >90% of female bison during the first pregnancy following infection, depending on inoculum size (Davis et al. 1990, 1991). The abortion rate subsequently declines to near zero after the third pregnancy due to naturally acquired immunity. Some females may be lost as a result of acute metritis associated with retained placentas (Broughton 1987). Infected calves surviving to birth may be weak, with low survival rates. Pathology described in neonatal bison includes broncointerstitial pneumonia, focal splenic infarction, and purulent nephritis (Rhyan et al. 2001). In male bison, *B. abortus* causes orchitis, seminal vesiculitis, and epididymitis and sterility in advanced cases (Tessaro 1989). In Wood Buffalo National Park, localization of brucellae in joints causes chronic suppurative arthritis and lameness (Tessaro 1989). Fuller (1966) reported that arthritis occurred in 2% of adult bison slaughtered in Wood Buffalo National Park during the 1950s. Debility caused by chronic septic arthritis may increase susceptibility to predation. The disease was formerly found in public bison herds in Elk Island National Park (Corner and Connell 1958), and the National Bison Range, Montana (Creech 1930). *B. abortus*-infected public bison herds continue to exist in and near Yellowstone National Park, Grand Teton National Park, and Wood Buffalo National Park, where the disease has been the center of management controversies for many years (Gates et al. 1992a, 2001b, 2001c; Inserro 1997; Keiter 1997).

Pasteurellosis refers to a number of localized and systemic infections caused by bacteria in the genera *Pasturella* and *Mannheimia*. These organisms are nonmotile, small, pleiotropic, Gram-negative rods or coccobacilli. Three species are potentially important for bison, *P. multocida*, *P. trehalosi*, and *P. haemolytica* (reclassified as *Mannheimia haemolytica*; Angen et al. 1999). All of them are common fauna of the respiratory tract in bison (Jaworski et al. 1998) in captivity (Ward et al. 1999a) and in the wild (Taylor et al. 1996). Diseases caused by these organisms include localized abscesses arising from scratch or bite wounds and respiratory disease or septicemia. *Pasteurella* spp. can be considered as typically commensal organisms, which function as endemic, opportunistic pathogens. The organisms become pathogenic, causing respiratory or septicemic disease following exposure to predisposing factors such as severe weather, crowding, or other environmental stresses (Carter and de Alwis 1989). Three epidemics of septicemic pasteurellosis occurred in bison between 1911 and 1965 (Mohler and Eichorn 1912–1913; Gochenour 1924; Heddleston et al. 1967). The disease occurs in explosive outbreaks with a high mortality rate (Gochenour 1924; Heddleston and Gallagher 1969). Young animals are most susceptible to pneumonic pasteurellosis (Dyer and Ward 1998). Pathology associated with *P. haemolytica* pneumonia includes fibrinopurulent bronchopneumonia, with fibrinous pleuritis and pericarditis (Dyer and Ward 1998). Pasteurellosis has a sudden onset. Clinical signs can include an extremely high fever, profuse salivation, hemorrhages in mucous membranes, severe depression, and swelling of the throat, brisket, and perineum. Death is commonly the first clinical sign reported in a herd with peracute septicemic and pneumonic pasteurellosis.

Hemophilosis is a disease caused by the bacterium *Hemophilus somnus*. The organism is commonly present in the respiratory system

of cattle; in a Canadian study, 25% of cattle were serologically positive (Radostits et al. 2000). Similar to *Mannheimia haemolytica* and *Pasteurella multocida*, *H. somnus* is associated with disease in livestock and should be regarded as a potential pathogen for bison, particularly in animals stressed by management practices such as herding, crowding, and shipping (Ward et al. 1999b). Tissue analysis from 21 bison with bronchopneumonia suggested that *H. somnus* can be a respiratory pathogen in bison (Dyer 2001). Berezowski (n.d.) reported meningitis in bison caused by *H. somnus* and referred to the same disease in cattle as infectious thromboembolic meningoencephalitis or ITEME. Outbreaks in captive bison occur most commonly in the fall and winter and are associated with extremely cold weather and stressful situations such as handling.

Paratuberculosis (Johne's disease) is caused by *Mycobacterium avium paratuberculosis*. It occurs around the world in a wide range of domestic and wild mammals (Williams 2001) including bison (Buergelt et al. 2000). *M. a. paratuberculosis* primarily infects the digestive tract, which reflects its primary mode of transmission through contaminated feed and water. It has a long incubation period and exhibits prolonged clinical duration. Gross lesions reported in bison included enlarged mesenteric lymph nodes and intestinal mucosal thickening. Histology reveals noncaseating granulomatous inflammatory infiltrates and acid-fast bacilli characteristic of *M. a. paratuberculosis* (Buergelt et al. 2000). Morphological changes of subclinical Johne's disease in bison are characterized by microgranulomas composed of epithelioid macrophages and individual multinucleate giant cells of Langhans type occasionally containing individual cytoplasmic acid-fast bacilli compatible with *M. a. paratuberculosis* (Buergelt and Ginn 2000). The most common clinical signs of Johne's disease in cattle are chronic diarrhea and loss of body weight leading to emaciation and death (Radostits et al. 2000).

Bovine tuberculosis is a chronic infectious disease, which causes death in advanced cases. The etiological agent is the bacterium *Mycobacterium bovis*. Depending on the location of the infection in the host, the organism can be excreted in exhaled air, sputum, feces, milk, urine, and vaginal and uterine discharges (Radostits et al. 2000). Inhalation and consumption of contaminated feed or water are the principal modes of transmission and determine the primary locations of lesions. Consuming infected milk may infect young animals. Intrauterine infection of the fetus occurs via the umbilical vessels. Inhalation is the primary route of infection in bison (Tessaro et al. 1990). The organism may spread to any part of the body after invading the blood or lymph vessels. The pathogenesis of mammalian tuberculosis is well described (Thoen and Bloom 1995). Infection with *M. bovis* generally results in development of chronic granulomatous lesions, which sometimes become necrotic, caseous, and calcified (Radostits et al. 2000). The pathology, pathogenesis, and epidemiology of bovine tuberculosis are the same in bison and cattle (Thoen et al. 1988; Tessaro et al. 1990).

Tuberculosis was first reported in bison in 1923 at Wainwright Buffalo Park in east-central Alberta (Cameron 1924). The source of infection was probably local domestic cattle rather than bison herds in Montana from which the Wainwright bison originated (Hadwen 1942; Tessaro et al. 1990). In 1922, >6000 bison were translocated from Wainwright Buffalo Park to Wood Buffalo National Park in northern Alberta, thereby introducing *M. bovis* to a wood bison population existing in the region. Tuberculosis was first documented in Wood Buffalo National Park bison in 1952 (Fuller 1966) and was verified in subsequent postmortem examinations (Choquette et al. 1961). Bison in and around Wood Buffalo National Park remain the only public herds infected with *M. bovis* in North America. The Mackenzie wood bison herd located 100 km northeast of Wood Buffalo National Park is considered to be at a high risk of infection. Tessaro et al. (1993) found it to be free of tuberculosis when it was tested in the late 1980s. Another free-ranging population in the region, the Hay-Zama herd in northwestern Alberta, has not been tested (Gates et al. 2001c), and its tuberculosis status remains unknown. There have been occasional outbreaks among fenced herds in New Brunswick, Manitoba, Ontario, Alberta, South Dakota (Stumpff et al. 1985), and Pennsylvania (Tuckerman 1955).

The effects of tuberculosis on bison population dynamics were studied in Wood Buffalo National Park (Joly and Messier 2001a, 2001b). Considered individually, neither brucellosis nor tuberculosis had significant effects on reproduction or survival rates. However, bison that were both positive for tuberculosis and had a high titer for antibodies against *B. abortus* had lower reproductive and survival rates in the presence of wolves. A model of the tuberculosis-brucellosis/wolf-bison system demonstrated that the combined effects of these diseases and wolf predation could have caused the decline of the Wood Buffalo National Park bison population observed since the cessation of intensive management, including wolf control, during the late 1960s (Joly and Messier 2001b).

VIRAL DISEASES. Bovine virus diarrhea/mucosal disease (BVD) is caused by an RNA virus in the pestivirus group. Positive serological evidence has been found in Yellowstone National Park bison in Wyoming (Taylor et al. 1997) and in bison at Elk Island National Park in Alberta (Cool 1999; Gates et al. 2001b). In Yellowstone National Park, positive antibody titers were detected in 31% of bison tested (Taylor et al. 1997). BVD was detected in the Elk Island National Park plains bison herd in 1996, prompting a serological survey of the plains bison and wood bison herds (Cool 1999; Gates et al. 2001b). Forty-seven percent of 561 plains bison tested seropositive for BVD, with only 1 testing positive for the virus antigen. At least six plains bison deaths in the Park have been attributed to the BVD virus (Cool 1999). The type 1 virus was isolated from tissues of plains bison from Elk Island National Park that were submitted to the Animal Disease Research Institute, Lethbridge, Alberta (Tessaro and Deregt 1999). None of 352 wood bison in Elk Island National Park tested seropositive for BVD. Both populations are vaccinated for BVD during annual round-ups. However, calves to be used in translocations are not vaccinated to allow future screening for BVD in the recipient herd.

The BVD virus is highly contagious and is transmitted by direct contact between animals, in contaminated feed and water, and will cross the placenta to the fetus (Van Campen et al. 2001). In cattle, BVD virus is shed in nasal discharge, saliva, semen, feces, urine, tears, milk, and discharges following abortion of a fetus (Radostits et al. 2000). Some individuals remain persistently infected and shed large quantities of the virus for the rest of their lives. Chronically infected individuals are the main source of infection in cattle herds (Radostits et al. 2000). Little is known about the pathology of BVD in bison. Acute BVD is seen in bison and can cause mortality at any age (Berezowski n.d.). Infection of the fetus can cause abortion, stillbirths, weak calves, and fetal abnormalities. Mucosal disease in cattle may occur in animals that are persistently infected. Persistently infected calves may be unthrifty and may develop lameness associated with foot lesions. Commercial BVD vaccines are widely available for use in cattle. Modified live BVD vaccines can cause diarrhea in recently weaned bison calves (Berezowski n.d.).

Malignant catarrhal fever (MCF) is caused in North American bison by ovine herpes virus type 2. The natural host for this virus is domestic sheep, in which it does not cause disease. Li et al. (1996) found that 61% of goats and 53% of sheep in a sample in the United States were seropositive to MCF virus. Recently, MCF has become an important disease in the commercial bison industry. Infected herds have experienced up to 100% mortality (Schultheiss et al. 2001). Infected bison exhibit rapid clinical disease. With the acute fatal form of disease, they usually die within 7–10 days of infection or within 48 hr of the onset of illness. With the chronic fatal form, they may die up to 156 days after infection. Some animals recover and remain persistently infected for an unknown length of time (Schultheiss et al. 1998).

Clinical signs in bison include hemorrhagic cystitis, colitis, conjunctivitis, ocular discharge, nasal discharge, excess salivation, anorexia, diarrhea, melaena, hematuria, multifocal ulceration of the oral mucosa, fever, circling, ataxia, behaviors suggestive of blindness, lameness, and difficulty urinating (Ruth et al. 1977; Liggitt et al. 1980; Schultheiss et al. 1998). Lymphadenomegaly and corneal opacity occur in fewer than half the cases (Schultheiss et al. 2001). Direct contact with sheep is considered to be the most likely source of infection, although

it has not been demonstrated in all bison herds experiencing MCF. The common means of transmission of this disease is unknown.

Parainfluenza 3 (PI3) virus has been detected by serology in bison in Yellowstone National Park (Taylor et al. 1996), the National Bison Range in Montana (Heddleston and Wessman 1973), and the free-ranging Delta Junction herd in Alaska (Zarnke and Erickson 1990). In the latter case, a recent expansion of the cattle population in the area was considered the likely source of PI3 infection in bison. Clinical signs of PI3 infection have not been reported in bison. In cattle, infection has been associated with pneumonia (Radostits et al. 2000).

FEEDING HABITS

In the majority of situations, North American bison are grazers. Because bison are located in widely varied habitats throughout their range, it is most useful to identify their diets by association with geographic area. Seasonal diets from eight different populations of bison have been compared by forage class (Table 48.5). Grasses and sedges were the most important foods of free-roaming bison in most of these populations. Peden (1976) confirmed that bison on the shortgrass plains in northeastern Colorado consume mainly grasses during all seasons. Similarly, on semidesert range in southwestern Colorado at the Colorado National Monument, grass was the dominant forage used by bison during summer and exceeded 27% during all seasons. In a shrub-steppe plant community in southern Utah, Van Vuren (1982) found that bison diets were composed of 93% grasses and sedges. Sedges also have been noted as common dietary items of several bison populations (Fuller 1966; Meagher 1973; Reynolds et al. 1978). In Yellowstone National Park, Wyoming, and in northern Canada, sedges constituted the highest proportion of bison diets in all seasons, with grasses second in importance. In northeastern Colorado, sedges were important to bison only during spring. In other bison herds located at Wood Buffalo National Park, Alberta (Soper 1941) and Elk Island National Park, Alberta (Holsworth 1960), bison fed on grasses in summer and sedges in winter. In some areas, forbs are seasonally important to foraging bison (Soper 1941; Nelson 1965; Banfield 1974; Wasser 1977). In semidesert range in southwestern Colorado, forbs were common food items during all seasons, but never exceeded 17% in any season (Wasser 1977). In Yellowstone National Park and in northern Canada, forbs were important to bison only during summer, whereas in northeastern Colorado, forbs were important dietary items during fall and winter. Bison in the Colorado National Monument, southwestern Colorado, primarily forage on grass in summer and browse in winter, and eat both in spring and fall (Wasser 1977). Unlike other populations, these bison used browse as the major source of food (67%) during winter. Browse was not eaten by bison on the shortgrass plains in northeastern Colorado and was of minor importance to bison in Yellowstone National Park and in northern Canada.

On the shortgrass plains of the Pawnee National Grasslands in Colorado, on which blue grama (*Bouteloua gracilis*) is the dominant species, Peden (1976) observed 36 plant species in the diets of bison, but only 11 contributed significantly to the total. Blue grama and buffalo grass (*Buchloe dactyloides*) were the most abundant plants in the habitat and also in the diet. A preference for western wheatgrass (*Agropyron smithii*) over blue grama was noted. Other commonly consumed species were red threeawn grass (*Aristida longiseta*), sun sedge (*Carex heliophila*), scarlet mallow (*Sphaeralcea coccinea*), sand dropseed (*Sporobolus cryprandrus*), and needle and thread (*Stipa comata*). Grasses were the main component of bison diets on the shortgrass plains, making up in excess of 79% of the diet in all seasons (Table 48.5). Sedges were important only in the spring, whereas forbs contributed from 3% to 9% of the diet during summer, fall, and winter.

On semidesert range in the Colorado National Monument, southwestern Colorado, Wasser (1977) reported strong selectivity by bison for preferred forages. The major plant communities in the study area were sagebrush (*Artemisia* spp.), Utah juniper (*Juniperus osteosperma*), mixed sagebrush and juniper, and saltbush (*Atriplex* sp.).

TABLE 48.5. Percentage composition of the diet of bison by forage class and season as averaged and summarized from nine studies in the United States and Canada

Herd Location ^a	Season and Forage Class ^b																							
	Winter						Spring						Summer						Fall					
	G	S+R	F	S	L	O	G	S+R	F	S	L	O	G	S+R	F	S	L	O	G	S+R	F	S	L	O
NE Col	87	T	9	—	—	—	79	16	T	—	—	—	88	1	3	—	—	—	89	—	9	—	—	—
SW Col	27	T	3	67	—	—	57	1	17	25	—	—	72	4	7	17	—	—	57	2	11	29	—	—
S Utah	—	—	—	—	—	—	—	—	—	—	—	—	96	3	1	—	—	—	—	—	—	—	—	—
YNP	34	65	T	1	—	—	46	50	3	T	—	—	32	59	6	2	—	—	30	69	T	T	—	—
N Can-PANP	34	59	—	—	—	7	35	65	—	—	—	—	26	73	—	—	—	1	17	63	—	—	—	20
N Can-SRL	36	63	—	1	—	—	16	81	1	2	—	—	24	59	8	8	—	—	21	71	4	2	—	—
N Can-MBS	2	96	—	2	—	—	6	68	—	26	—	—	11	53	2	28	6	—	32	15	4	12	37	—
Alaska	29	70	—	1	—	—	—	—	—	—	—	—	3	2	—	95	—	—	38	36	—	26	—	—

^aNE Col, Northeastern Colorado, Pawnee National Grasslands, shortgrass plains, after Peden (1976); SW Col, southwestern Colorado, Colorado National Monument, semidesert range, after Wasser (1977); S Utah, southern Utah, Henry Mountains, shrub-steppe plant community, after Van Vuren (1984b); YNP, Yellowstone National Park, forest with interspersed grass-sedge meadows, after Meagher (1973); N Can-PANP, northern Canada, Prince Albert National Park, Saskatchewyan, boreal aspen forest interspersed with sedge-grass meadows, after Fortin et al. (2002); N Can-SRL, northern Canada, Slave River Lowlands, Northwest Territories, boreal forest interspersed with sedge-grass meadows, after Reynolds et al. (1976); Reynolds et al. (1978); N Can-MBS, northern Canada, Mackenzie Bison Sanctuary, Northwest Territories, boreal forest and old glacial lake beds interspersed with wet sedge meadows and willow savannas, after Larter and Gates (1991); Alaska, Farewell herd, boreal forest river flood plains and dry glacial lake beds interspersed with grass-sedge meadows—winter diets, after Campbell and Hinkes (1983), summer and fall diets, after Waggoner and Hinkes (1986). T, Trace amount or <1%.

^bForage class: G, grass; S+R, sedge and rush; F, forbs; S, shrubs; L, lichen; O, other.

The most common plant species in the bison diet during most seasons was fourwing saltbush (*Atriplex canescens*), followed by needle and thread, which was important during cooler months. Sand dropseed and Galleta grass (*Hilaria jamesii*) were prominent in the diet in warmer seasons. Prickly pear cacti (*Opuntia* spp.) were among the 10 top forages during all seasons except summer (Wasser 1977). The only forbs used significantly during all seasons except winter were mallows (*Malva* spp.). Some of the most common plants in the habitat, cheatgrass (*Bromus tectorum*), Utah juniper, and big sagebrush (*Artemisia tridentata*), were the least preferred forages. Grasses contributed from a low of 27% of the diet in winter to a high of 72% of the diet in summer (Table 48.5). Shrubs were the major dietary component during winter at 67% and were the second most important dietary item in fall, spring, and summer at 29%, 25%, and 17%, respectively.

On a shrub-steppe plant community range in the Henry Mountains in southern Utah, Van Vuren (1982) reported summer diets of bison comprised 93% grasses and sedges, 5% forbs, and 1% browse. In another area on the west side of the mountains, where dominant shrubs in the habitat were big sagebrush, black sagebrush (*A. nova*), and snowberry (*Symphoricarpos* spp.) and the grasses were mainly native perennials, including bluegrass (*Poa* spp.), needlegrass (*Stipa* spp.), wheatgrass (*Agropyron* spp.), fescue (*Festuca* spp.), fringed brome (*Bromus ciliatus*), squirreltail (*Sitanion hystrix*), and june-grass (*Koeleria cristata*), bison diets comprised 99% grasses and sedges and 1% forbs (Table 48.5; Van Vuren 1984b). Grasses contributed 96% of the bison diet, with bluegrass (66%) the most important, followed by june-grass (13%), fescue (10%), fringed brome (3%), and wheatgrass (2%), whereas sedges contributed only 3% of the bison diet (Van Vuren 1984b). Total forbs contributed just 1% and shrubs were present only in a trace (<0.5%) amount. Grasses predominated in the summer diet of bison in the Henry Mountains.

In Yellowstone National Park, much of the habitat consists of lodgepole pine (*Pinus contorta*) forests. Interspersed throughout the area are meadows dominated by sedges and grasses. Sedges were the main bison forage in all seasons and grasses were the next most common forage (Meagher 1973). Sedge content in the diet varied from 50% in spring to a high of 69% in fall, whereas the grass content varied from 30% to 46% in fall and spring, respectively (Table 48.5). Minor quantities of forbs (6%) and browse (2%) were consumed, but this occurred mainly during summer.

In a Boreal Aspen Forest habitat in Prince Albert National Park in northern Saskatchewan, Fortin et al. (2002) observed that the bison diet was almost entirely composed of sedges and grasses, varying from the lowest of 80% of the fall diet to 100% of the spring diet (Table 48.5). The seven most abundant plant groups in the habitat were two sedge species, slough sedge and water sedge (*Carex aquatilis*); four species of grass, wheatgrass, northern reed grass, foxtail (*Hordeum jubatum*), and whitetop (*Scolochloa festucacea*); and one rush species, wire rush (*Juncus balticus*). These species represented 50–72% of the total biomass available throughout the year and contributed 81–99% of the bison diet (Fortin et al. 2002). Sedges were the most important dietary component to bison in all seasons, varying from the low of 59% of the winter diet to the high of 73% in summer (Table 48.5). Slough sedge was the major food item throughout the year, as it was highly selected for and used disproportionately to its availability (Fortin et al. 2002). Grasses were the second most important forage item, contributing from a low of 17% in the fall diet to a high of 35% in spring (Table 48.5). Fortin et al. (2002) concluded that bison dietary decisions were made in preference for rapid energy acquisition over long-term gains.

In the Northwest Territories, bison habitat along the Slave River Lowlands is within the Boreal Forest region of Canada, where white spruce (*Picea glauca*) forests separate vast open meadows supporting sedge and grass communities. Bison diets from this area contained 29 different plants, of which 12 were present in quantities exceeding 1% in any one season. Slough sedge was by far the most abundant plant in the diet, varying from 42% in winter to 77% in spring (Reynolds 1976). The second most common food was reed grass (*Calamagrostis* spp.), which varied from 15% of the diet in spring to 35% in winter. Slough sedge and reed grasses contributed >70% of the bison diet at all seasons (Reynolds

et al. 1978). Although slough sedge was the most abundant plant in the bison diet, it was second to reed grass in abundance in the habitat. Together, these two plants were the most abundant meadow plants in the Slave River Lowlands. Sedges and grasses collectively contributed in excess of 80% of bison diets in all seasons, varying from the low of 83% in summer to the high of 99% in winter (Table 48.5). Forbs and browse appeared to be of minor importance and were consumed in small amounts, mainly in summer and fall.

In the Boreal Forest habitat of the Mackenzie Bison Sanctuary in the Northwest Territories, Larter and Gates (1991) observed that seasonal bison diets varied. In winter, it was dominated by sedge (96–99%); in summer, it became a more diverse mixture of sedges, grasses, and shrubs. In fall, it became the most diverse, with lichen being a major component (34–41%). In wet meadow habitats, high-biomass stands of slough sedge and water sedge were the dominant plant species. In grass-sedge associations, other plant species were reed grass, wheatgrass, foxtail, reed canary grass (*Phalaris arundinacea*), rough hair grass (*Agrostis scabra*), and willows (Larter and Gates 1991). Sedges and grasses collectively contributed the major component of the bison diet in all seasons except fall, varying from the low of 47% in fall to the high of 98% of the winter diet (Table 48.5). Sedges were the most important dietary item throughout the year except during fall, when lichens and grass dominated the diet at 37% and 32%, respectively. Grasses were important to bison in fall (32%), less so in summer (11%), relatively unimportant during spring (6%), and almost nonexistent in winter (2%) (Table 48.5). The diet of the wood bison in the Mackenzie Bison Sanctuary was more diverse than the grass-dominant diets of southern plains bison (Peden 1976; Wasser 1977; Van Vuren 1984b) or of other northern Canadian herds of wood and plains bison (Reynolds et al. 1978; Fortin et al. 2002). These dietary differences basically reflect relative differences in forage availability in the various areas (Larter and Gates 1991). Shrubs contributed 26% and 28% of spring and summer diets, respectively (Table 48.5). This is similar to what is found for the Farewell herd in Alaska (Waggoner and Hinkes 1986), but differs from findings for Yellowstone National Park bison and other northern bison herds in Canada in the Slave River Lowlands (Reynolds et al. 1978) and in Prince Albert National Park (Fortin et al. 2002). However, the winter diet was similar to that of other populations of bison (Meagher 1973; Reynolds et al. 1978; Fortin et al. 2002).

In the northern Boreal Forest river flood plains habitat of Alaska, Campbell and Hinkes (1983) reported the winter diet of the Farewell plains bison herd as primarily sedges and rushes, and grasses (fescue), collectively constituting 99% (Table 48.5). Grass and sedge-dominated communities made up approximately 38% of the study area before a major fire, and the habitats being used by bison were dominated by bluejoint reed grass (*Calamagrostis canadensis*) and sedges, as well as other grasses and low-shrub-dominated communities. Range expansion was enhanced because of the increase in new sedge-grass areas created by the fire, which linked summer with prefire winter ranges. The summer diet of the Farewell bison herd was composed of 95% shrubs (Table 48.5). The fall diet from the river flood plains was 68% shrubs, whereas the fall diets from the dry lake beds and the burn area were dominated by sedges (74%) and grasses (75%), respectively (Waggoner and Hinkes 1986). Grasses and sedges were used heavily when available during migration movements from summering to wintering areas. In general, Alaskan plains bison diets who comprised mainly of three forage classes, grasses (38%), sedges and rushes (36%), and shrubs (26%) (Table 48.5).

ECOLOGY

Forage and Habitat Requirements. Bison, over most of their North American range, typically show strong selection for open grassland or meadow habitat types. Use of forested areas for escape cover, thermal cover, or other purposes such as calving also occurs to varying degrees. However, habitat selection by bison appears to be driven more by the interplay between their nutritional requirements and plant phenology, forage biomass, and snow depth (Larter and Gates 1991) than by predator avoidance or climatic condition. When these latter elements intensify,

temporary shifts in habitat selection often occur. In the Mackenzie Bison Sanctuary in northern Canada, wood bison consistently selected wet and mesic meadows that were dominated by key forage species, slough sedge, in association with other grasses and sedges (Larter and Gates 1991). During summer and winter, they selected habitats that yielded the greatest amount of protein, and habitat selection did not change between years (Larter and Gates 1991).

In Aspen Parklands habitat, bison have shown a preference in summer and fall for grazing in upland meadows despite relatively low pasture biomass and potential dry matter intake rates (Hudson and Frank 1987). On the Slave River Lowlands, Reynolds (1976) observed that foraging was done in open meadows, whereas loafing and ruminating occurred in forest habitat. During winter, bison in that northern habitat foraged in small, sheltered meadows and along river and creek beds. Such areas offered less severe snow conditions and tended to support preferred forage. Although forested habitats, especially coniferous types, were avoided during summer and winter in the Mackenzie Bison Sanctuary (Larter and Gates 1991), shifts to greater use of coniferous habitat during the fall are believed related more to food availability (greater biomass of lichen) than to factors such as rut, climate, or biting flies (Melton et al. 1989; Larter and Gates 1991). During fall, bison dispersed among all habitats at a time when forage quantity and quality became more homogeneous throughout these habitat types (Larter and Gates 1991).

The recent burn history of a landscape has a strong influence on bison habitat selection, although there is some variability in their response. In the Wichita Mountains Wildlife Refuge in southwestern Oklahoma, bison increased use of a portion of their annual range following a prescribed burn (Shaw and Carter 1990). In a tallgrass prairie in Oklahoma that was subjected to seasonally and spatially variable burning regimes, mixed groups of bison showed significantly more use of burned areas than unburned areas (Coppedge and Shaw 1998). However, bull groups exhibited significantly more use of unburned areas than burned areas. Positive response to burns on tallgrass prairie appear particularly marked during the summer season, when bison concentrate on warm-season, perennial C₄ grasses, but this response is less apparent during fall and winter, when bison concentrate on cool-season, C₃ grasses (Vinton et al. 1993). In Nebraska, bison significantly increased their use of burned areas during the growing season 1–3 years post-fire, but did not select for these areas during the nongrowing season (Biondini and Steuter 1998).

In Alaska, bison in the Farewell study area showed a marked shift in range use within 4–5 years following wildfire, which included areas that had been previously forested with open black spruce (*Picea mariana*), but which became dominated with grass and sedge communities after the fire (Campbell and Hinkes 1983). Interestingly, studies of bison diet within the Farewell herd showed relatively high use of shrubs during summer at higher elevation ranges where only browse was readily available (Waggoner and Hinkes 1986). Periodic range burning has been effectively used to enhance bison habitat in the Northwest Territories of Canada (Chowns et al. 1998).

In a study on the Blue Mountain Bison Ranch in Colorado from August through September, bison selected different sites for nocturnal grazing than for diurnal grazing (Hein and Preston 1998). In this study, nocturnal grazing accounted for 15% of the daily grazing pattern of the herd. Also, Hudson and Frank (1987) noted that a greater percentage of summer foraging occurred at night in Aspen Parklands habitat in central Alberta.

Bison generally are less selective in what they eat than are other ungulates under similar environmental conditions. In the Henry Mountains of southern Utah, bison selected similar forage to cattle, but tended to move more; did not overgraze preferred feeding areas; and made greater use of steep slopes (Nelson 1965; Van Vuren 1982). Diets of bison on the shortgrass plains of Colorado resembled cattle diets more than sheep diets in areas of light grazing (Peden 1972). Bison are less selective than cattle and are therefore better adapted to use herbage of the shortgrass prairie more fully (Peden et al. 1974). A study on the Konza Prairie Research Natural Area in Kansas showed that the ratio of cool-season to warm-season grasses (C₃:C₄) in the diet of all bison

groups changed as the seasonal availability changed (Post et al. 2001). Consumption of cool-season (C₃) grasses showed two peaks, the first in spring and the second in fall. In Yellowstone National Park, Wyoming, forage availability regulated bison feeding patterns within the preferred sedge and upland feeding sites (Meagher 1973). Bison were usually the least selective and cattle were the most selective during feeding trial experiments involving bison, yak, and cattle when provided sedge, grass, and alfalfa hays (Richmond et al. 1977). Bison have shown less grazing selectivity than cattle (Rice et al. 1974). In northern Canada, forage consumption by bison was not directly proportional to plant availability, indicating light to moderate feeding selection (Reynolds et al. 1978). Bison were superior to cattle in the digestion of all northern forages, including a greater ability to digest sedge hay, which resulted in superior performance (Hawley 1987). Therefore, bison are better adapted than cattle to use poorer quality rangeland forages and to survive harsh winter conditions and severe northern environments (Reynolds and Peden 1987; Hawley 1987).

In Alaska and northern Canada, although grasses and sedges were usually heavily selected for, dietary shifts to a high content of shrubs and lichens during summer and fall indicated the capability of bison to switch from a diet high in sedge when sedge biomass is scarce (Waggoner and Hinkes 1986; Larter and Gates 1991). It is apparent that where grasses and sedges are available in the habitat, they are selectively grazed by bison, and where they are sparse, browse may be substituted. Dietary shifts from grasses to sedges and back again within a habitat type usually are directly related to plant phenology. Bison generally may be considered as specialized grazers.

Effects of Bison on Habitat. It is likely that the vast historical bison herds had a significant effect on vegetation and soil nutrient regime within their traditional ranges through grazing, nutrient cycling, and sheer physical disturbance. Recent enclosure studies on migratory ungulates in Yellowstone National Park have shown the importance of ungulates in controlling soil nitrogen cycling (Frank and Groffman 1998; Tracy and Frank 1998). For specific details on the ability of bison to recycle nitrogen, see the section Physiology, Digestion and Nutrition.

Bison directly affect vegetation communities through grazing, urinating, defecating, trampling, rubbing, horning, and wallowing, and indirectly through incidental seed dispersal. These activities, in addition to climate and fire, help maintain grassland ecosystems on which bison and other species depend (Weaver and Clements 1938; Larson 1940; Axelrod 1985; Campbell et al. 1994; Coppedge and Shaw 1997). Larson (1940) observed that shortgrass vegetation thrived under moderately heavy grazing, unlike the taller bunch grasses such as sand dropseed and needle and thread.

Ungulate grazing on bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) in Yellowstone National Park results in compensatory growth following grazing, such that plants grazed in winter and spring have similar biomass as do the ungrazed plants (Merril et al. 1994). Response to grazing also included lower root biomass, increased foliar nitrogen levels, and alterations in soil nematode fauna. In a similar study of bison grazing effects on big bluestem (*Andropogon gerardii*) and switch grass (*Panicum virgatum*), compensatory increase in relative growth rate was observed in grazed tillers in the first year of grazing such that lost tissue was replaced by the end of the season (Vinton and Hartnett 1992). This response was enhanced on burned prairie for big bluestem, but unaffected for switch grass. At the same time, relative growth rates, mass, and survivorship of grazed big bluestem was lower than that of ungrazed individuals in the year following grazing.

Bison grazing patterns and selection for little bluestem (*Andropogon scoparius*) is affected by burn history and has potential to contribute to the decline of little bluestem under persistent grazing (Pfeiffer and Hartnett 1995). Following fire in tallgrass prairie dominated by little bluestem and big bluestem, bison increased their use of little bluestem threefold. In part, this related to removal of standing dead tillers associated with mature bunchgrass. Frequency of grazing on neighboring big bluestem was unaffected by fire (Pfeiffer and Hartnett 1995).

In studies of bison in relation to burn patterns and tallgrass prairie, Knapp et al. (1999) noted that bison grazing increased the spatial variation in tallgrass prairie in which fire tended to burn ungrazed patches. Preferential grazing of dominant species altered plant competition among grasses and forbs.

Recent field experiments with bison urine in South Dakota have demonstrated that aboveground biomass, root mass, and foliar nitrogen were higher on urine patches than off patches for Kentucky bluegrass (*Poa pratensis*) and little bluestem (Day and Detling 1990). Above-ground use by herbivores in this study was greater on urine patches than off urine patches.

Relative to cattle, bison exhibit habitat selection patterns that reinforce or otherwise help maintain habitat in a productive state. Studies by Wuerthner (1998) indicated that bison are less apt to re-graze a site during a single growing season, wander more, eat drier, rougher forage, and spend less time in riparian areas and wetlands. Such behavior likely reduces impact on native grasslands and riparian ecosystems.

Localized stands of trees, particularly those not tightly clumped, may be significantly affected by the horning and thrashing of bison during the rut and at other times of the year. McHugh (1958) estimated that 51% of the lodgepole pine in some areas of Yellowstone National Park had been horned by bison. Bison horning of vegetation in a tallgrass prairie landscape had its greatest effect on saplings and shrubs, as opposed to trees, and killed or severely damaged 4% of woody plants, caused moderate injury to 13%, and caused light injury to 12% (Coppedge and Shaw 1997). Such activity by bison and/or elk may inhibit succession of prairie to forest and thus serve to maintain grasslands (Moss 1932; Patten 1963; Meagher 1973).

Bison wallows support a characteristic vegetation distinct from that found on adjacent prairie and appear to be related to site morphology, soil texture, soil moisture, available phosphorous, and pH (Polley and Collins 1984). In central and southwestern Oklahoma, wallows were dominated by spike rush (*Eleocharis* spp.) (Polley and Collins 1984).

The thick fur on the head and forequarters of a bison is ideally suited for dispersal of awned, barbed, or sticky seed-bearing structures. The seed of buffalo grass, cockle burs (*Xanthium italicum*), and St. John's wort (*Hypericum perforatum*) readily adhere to bison fur. The dissemination of St. John's wort throughout the National Bison Range is believed to have been caused by bison (McHugh 1958).

Where bison trails or wallows are cut into steep hillsides, considerable water and wind erosion can occur (McHugh 1958; Capp 1964; Meagher 1973). Hillside trails can serve as drainage channels, effectively lowering the water table in upland areas and subsequently causing a change in the vegetation. Where trails cut near the top of steep sandy hills, erosion and slippage may produce barren areas.

Interspecific Relationships. For the most part, habitat niches of plains bison and moose do not overlap. However, in northwestern Canada, moose coexist with the majority of free-ranging wood bison herds, and sometimes at high densities. Whereas bison diets are largely dominated by grasses and/or sedges, they will forage on willows and other woody browse, particularly when more-preferred forage is of poor quality (Larter et al. 1994). Potential for forage competition with moose could occur under such circumstances. In Farewell, Alaska, bison spent more time browsing in shrublands when grasslands were unavailable (Waggoner and Hinkes 1986). Because of the difference in height, moose would be able to take advantage of taller browse than bison. In general, moose are primarily browsers and bison are primarily grazers and therefore are considered to be more complementary than competitive in feeding habits.

Bison and moose generally appear to tolerate each other. However, at Jackson Hole Wildlife Park, Wyoming, bison killed a 7-month-old moose calf soon after it had been introduced into the park (McHugh 1958). The intense aggression of bison toward other wildlife species observed at the Jackson Hole Wildlife Park may be more frequent than that normally occurring in the wild because of the semiconfined nature of the animals at the park.

In a study of ungulate habitat relationships at Wind Cave National Park, South Dakota, there was relatively little overlap in range use between bison and elk (Wydeven and Dahlgren 1985). At Elk Island National Park, Alberta, bison winter diet was strongly different than that of sympatric elk, white-tailed deer, and moose (Telfer and Cairns 1986). Compared with elk, winter bison diets included a much higher percentage of sedge (82% vs. 22%) and much lower percentage of browse (1% vs. 64%). Within aspen parkland habitat where bison and elk have overlapping range, bison forage cropping rates are higher than those of elk at an equivalent forage biomass, although both species spend similar amounts of time daily foraging (Hudson and Frank 1987).

In Jackson Hole Wildlife Park, McHugh (1958) considered bison at the top of the interspecific dominance hierarchy, followed by elk, mule deer, pronghorn antelope, moose, and white-tailed deer. Bison are usually dominant over elk, and McHugh (1958) noted that bison calves could displace six-point bull elk. However, at the edge of bison herds, five- and six-point bull elk could displace bison cows and yearling bulls. Aggression by bison reversed any elk dominance. Bison occasionally forced elk into deep snow in winter and chased them from feed in summer. The usually wary elk sometimes were caught and butted. Bison harass and kill elk calves in Jackson Hole Wildlife Park, Fort Niobrara National Wildlife Refuge, Wind Cave National Park, and Yellowstone National Park (Rush 1942; McHugh 1958; Mahan 1977). At the National Bison Range, Montana, a bottle-raised bull elk calf formed an attachment to two cow bison and, when mature, rounded up a herd of cow bison and bugled. On another occasion, a harem bull elk killed a yearling bison (McHugh 1958). At Yellowstone National Park, elk and bison have been reported within 10 m of each other despite their seeming intolerance. At Elk Island National Park and Yellowstone National Park, bison interfere with elk livetrapping programs, in part because bison are attracted to the high-quality hay bait lines used for trapping elk; elk will not enter traps when bison are nearby.

Bison and white-tailed deer at Colorado National Monument did not appear to compete for food (Capp 1964). Wydeven and Dahlgren (1985) observed relatively little range overlap between bison and mule deer. Winter diet of bison at Elk Island National Park included substantially less browse than did that of white-tailed deer (1% vs. 57%) and more herbage (99% vs. 43%) (Telfer and Cairns 1986). Bison charge and strike mule deer at Jackson Hole Wildlife Park and Yellowstone National Park (McHugh 1958).

There is potential for bison to compete with woodland caribou (*Rangifer tarandus*) on northern ranges. Dietary overlap has been documented within the Mackenzie Bison Sanctuary in northern Canada, where bison selectively feed on terrestrial lichen from August to November (Larter and Gates 1991). In southern Yukon, Fischer (2002) assessed the potential for exploitative competition between bison and woodland caribou in winter by determining resource selection and overlap in resource use across three spatial scales: the landscape, habitat, and feeding site. Additionally, bison and caribou diets were analyzed and overlap in forage species use was assessed. Bison and caribou used resources in a differential non-random and selective manner at all levels. At the level of the landscape, caribou used higher elevations and areas that were more rugged and further from water than bison. Similar trends were also evident at the habitat level. Bison selected for graminoid-dominated habitats and caribou selected for coniferous/shrub-dominated habitats. Overlap in resource use at feeding sites was also minimal, since bison foraged in areas with high graminoid abundance while caribou foraged in areas with high lichen abundance. The dietary overlap was less than 10%; lichens made up nearly 80% of caribou diets while over 80% of bison diets consisted of graminoids. Fischer (2002) concluded that the potential for exploitative competition between bison and caribou in the late winter was low.

In a study of niche overlap in Yellowstone National Park that examined a group of ungulates including bison and bighorn sheep (*Ovis canadensis*), bison and sheep diets were not significantly associated with each other (Singer and Norland 1994). Traditional bighorn sheep range in much of North America typically is located in terrain not associated with bison use. However, in northern British Columbia, bison

in summer will graze and browse in high-elevation, alpine and sub-alpine meadows as well as shrublands also used occasionally by Stone's sheep (*Ovis dalli stonei*). The two species occasionally comingle. Three instances of an older bighorn ram being associated with a bison bull were observed at the National Bison Range (McHugh 1958).

Pronghorn antelope are highly selective feeders (Schwartz et al. 1977), whereas bison are more flexible in choice of diet. Whereas pronghorn diets are 50–80% forbs, bison diets are usually <20% forbs (Peden 1972). In studies at Yellowstone National Park, bison and pronghorn antelope diets were not significantly associated with each other (Singer and Norland 1994). The theory that large and small ruminants will not compete with each other for food resources (Bell 1971) is further affirmed by similarity in sheep and pronghorn diets and their dissimilarity to bison diets (Peden 1972). Wydeven and Dahlgren (1985) suggested there was greater potential for competition between pronghorn and bison than between bison and either mule deer or elk. In a study of bison, pronghorn antelope, and prairie dog (*Cynomys* sp.) feeding relationships at Wind Cave National Park, bison preferentially grazed on graminoids located around the margins of prairie dog colonies; pronghorn focused on the forb-dominated central portions of prairie dog colonies (Krueger 1986).

In Wyoming, Bryant (1885) noted that pronghorns and deer would seek protection from wolves in bison herds. At Wind Cave National Park, pronghorn at times pass near or through bison herds unhindered. However, at the Jackson Hole Wildlife Park, bison disturbed a group of resting pronghorns when passing within 50 m (McHugh 1958). Bison occasionally charge pronghorns. McHugh (1958) observed a bison kill an 8-month-old pronghorn buck.

Bison diets more closely resemble those of cattle than those of sheep under light grazing conditions; however, the differences become less distinct under heavy grazing (Peden 1972). Diets of feral horses (*Equus caballus*) near Sundre, Alberta, had a higher sedge component than did diets of free-ranging cattle (Salter 1978). In this respect, feral horse diets show greater similarity to diets of northern bison than do cattle diets. Herbivores, however, appear to select for higher proportions of plant groups that are best digested (Peden et al. 1974). This may provide a mechanism whereby bison and other herbivores can avoid competition, particularly at low to moderate stocking rates. In the past, there seems to have been a reasonably good balance between bison and their forage supply, and competition with other species for food has not been a major factor limiting population growth (Longhurst 1961).

Draft horses at the Jackson Hole Wildlife Park were dominant over bison cows and yearlings at a salt lick during October; however, by March, they had lost some dominance (McHugh 1958). All bison exhibited dominance over a saddle horse. In Yellowstone National Park, the head animal keeper observed only one horse killed by bison in 23 years. Numerous instances of horses being killed or charged when used to pursue bison have been reported from other areas (McHugh 1958, 1972). Cattle ranged with bison during summer on a ranch in South Dakota and appeared to be compatible; the two species essentially ignored each other (Colman 1978).

In some regions, bison may form the prey base on which wolf populations depend, although this appears dependent in part on the abundance and diversity of alternate prey sources. In a study of wolf predation in northeastern British Columbia, Weaver and Haas (1998) found that bison constituted 26.7% of the prey biomass and 10.3% of the prey items in wolf diets. This compared with 32.9% and 34.7% for caribou, respectively, and 17.2% and 13.4% for moose. Within this study area, bison are among the more abundant prey species. Bison are, for the most part, indifferent to the presence of wolves until attacked (Fuller 1960; McHugh 1972). When a bison population decreases below a certain critical level, wolf predation—in the absence of alternate prey—may take more than the annual increment and effectively reduce the population. Bison may actively chase wolves (Smith et al. 1996) and defend their young from wolves, although the occurrence of this latter phenomenon appears difficult to predict (Carbyn 1998).

At Yellowstone National Park, coyotes stayed closer to bison in winter than in summer (McHugh 1958). These coyotes may have caught

small mammals that were trapped in snow craters made by feeding bison or they may have been waiting for scavenging opportunities. On two occasions, coyotes wandering into a herd of bison at the National Bison Range were horned and trampled to death (McHugh 1958).

The importance of scavenged or killed bison in the diets of grizzly bears is considerably reduced from what it likely was when the plains grizzly and large bison herds coexisted on the Great Plains, although bison are significant contributors to grizzly bear diets where these species still coexist. A radiotelemetry study of grizzly bear in Yellowstone revealed that 95% of the energy requirements of grizzly bears were being derived from the largest bodied ungulate species; scavenged adult bison made up 16% of that total (Mattson 1997). Winter-killed bison and other ungulates may be important food sources to bears in early spring after they emerge from dens (Meagher 1978). In Yellowstone National Park, three grizzly bears captured an elk calf within 213 m of a bison herd without causing alarm to the bison (McHugh 1958). On occasion, bison prove too large an adversary for grizzly bears and may kill their would-be predators (McHugh 1972).

The role of bison in black bear ecology can be expected to parallel that of grizzly bear where black bear and bison ranges overlap. During a wolf study from 1975 to 1978 in the Slave River Lowlands, Northwest Territories, observations of black bears following bison groups and feeding on bison carcasses during the calving and postcalving seasons were made, but no observations were made of black bears actually chasing, attacking, or killing bison (Van Camp 1987). Black bears are opportunistic scavengers and probably scavenge on bison carcasses when available.

Humans have hunted North American bison for more than 12,000 years (McHugh 1972). The ecological relationship between the two species has remained that of a classic predator and its prey for approximately 11,900 of those years. In this regard, an early pioneer stated that for the Indian, bison were “meat, drink, shoes, houses, fire, vessels, and their Master's whole substance” (McHugh 1972:4). Bison influenced the settlement of North America more than any other endemic species (Roe 1970) with the possible exception of beaver. Whereas aboriginal cultures spiritually embraced the bison, European pioneers inhabiting buffalo country often viewed them as “an insufferable nuisance” (McHugh 1972:xxii). It was this dichotomy that, in part, led to the disruption of what had been an ecological balance between humans and bison. In less than 100 years, an estimated 40–60 million North American bison had been reduced to just over 1000 animals (Hornaday 1889). Only the dedication of a few conservationists in Canada and the United States and the physical isolation of bison in the Mackenzie basin (Raup 1933) saved them from extinction.

Bison have a special attraction to and relationship with prairie dog (*Cynomys ludovicianus*) colonies. Colonies are preferentially grazed by bison and are used for grooming and wallowing. Part of the attraction for bison relates to the lack of extensive dead standing graminoids such that foraging is more efficient. Heavily grazed prairie dog colonies at Wind Cave National Park had lower plant biomass and were dominated by plants that had higher leaf nitrogen than plants outside the colony (Detling 1998). Bison at Wind Cave National Park showed particularly strong attraction to prairie dog colonies by midsummer. They tended to graze in portions of colonies that were <8 years old and rested in the oldest parts (>26 years old) of the colony (Coppock et al. 1983). These observations were consistent with those of Krueger (1986), who observed bison foraging efforts concentrated around the margins of prairie dog colonies. Following experimental 2-year exclusion of prairie dogs and bison from prairie dog colonies, Cid et al. (1991) observed a 32–36% increase in aboveground biomass (mostly graminoid), whereas species diversity, equitability, and dominance remained similar for all treatments.

In Theodore Roosevelt National Park, North Dakota, extensive use of prairie dog colonies by bison during the breeding season occurs (Radtke et al. 1999). In one instance, 273 bison aggregated on a prairie dog town. Krueger (1986) observed that bison activity appeared to reduce foraging time available for prairie dogs. Prairie dogs benefit as a result of bison keeping the vegetation at a more favorable structural level (Shaw 1998). To what other extent prairie dogs may benefit from

bison foraging is unclear, although potential mechanisms could include forage fertilizing and perhaps interference with predators.

Bison substantively shift their use from prairie dog colonies to recently burned areas where such an option exists (Coppock and Detling 1986). This phenomenon could be used as a management tool to mitigate negative impacts of bison on prairie dog colonies.

In a comparison of diet and distribution between bison and plains pocket gophers (*Geomys bursarius*) in north-central Nebraska, diets did not overlap. Highest pocket gopher activity was in forb patches, which appeared to be a direct response to bison activity (Steuter et al. 1995).

In a review of the close relationship between the brown-headed cowbird (*Molothrus ater*) and bison, Chace and Cruz (1998) suggested that cowbirds likely had a larger historical range and occupied a broader elevational range than at present. In turn, this effect could have influenced the intensity and extent of nest parasitism on high-elevation songbirds (Chace and Cruz 1998). Creation of small ephemeral wetlands through wallowing and attraction of insects to bison has likely had an attendant historical effect on avian species diversity and distribution within the prairie ecosystem where bison were common.

AGE ESTIMATION

Skinner and Kaisen (1947) developed a system of wear classification for bison teeth by recognizing six general age categories based on tooth wear and the sequence of molar eruption: immaturity, early adolescence, late adolescence, early maturity, full maturity, and old age. Fuller (1959) was able to identify five yearly age classes based on sequence of tooth eruption and replacement, and he could identify three general age classes based on tooth wear (young adult, adult, and aged). However, the precise age of animals older than 4 years could not be determined based on tooth eruption.

A more precise technique for determining the age of bison older than 4 years was developed by counting annual cementum layers in the roots of the fourth premolar (Novakowski 1965). In bison, cementum deposition on PM4 begins at age 4 years, making yearly age estimates possible after this. Cementum band counts using optical and scanning electron microscope examinations on the first mandibular molar were used to successfully determine the age of 20 wood bison (Haynes 1984). The first mandibular molar was selected for age determination because it is a large tooth, which is usually present even in weathered jaws; it is fully erupted and functional at 12 months of age, and thin layers of cementum are laid down annually on its roots (Haynes 1984). Although assessment of three classes of teeth—incisiforms, premolars, and molars—determined that all classes contained annuli in their cementum that accurately reflected age of the animal, premolar teeth provided the lowest standard deviation of cementum ages (± 1.04 years) and were considered to be best for age determination (Moffitt 1998). Premolars are more likely to remain attached to the alveolar bone after death because of their slightly more complex root system, which results in greater recovery of these teeth after an extended period post-death (Moffitt 1998).

Frison and Reher (1970) compared patterns of mandibular tooth eruption and wear with known-age samples to establish seven broad age categories for bison specimens collected from the Glenrock Jump in Wyoming: 0.5, 1.5, 2.5, 3.5, and 4.5 years, mature (5.5–9.5 years), and old age (10.5–13.5 years). Based on tooth eruption, the first five age categories for the Glenrock specimens could be distinctly classified with no overlap. Based on tooth wear, mature and old-age categories could be distinguished, but because of the subjective nature of wear classifications, definite ages could not be determined.

Age estimation from the postcranial elements of bison has always been difficult. Because of the need to estimate age and sex for such elements from archaeological sites, Duffield (1973) developed an age determination technique using a table showing ages associated with degree of epiphysal closure. It was possible to assign skeletal remains into yearly age categories up to 11 years using this table. However, precision depended on the degree of articulation of the elements examined (Duffield 1973). Fuller (1959) distinguished calf and yearling categories based on differences in body size and conformation.

ECONOMIC STATUS, MANAGEMENT, AND CONSERVATION

Current Status. Jennings (1978) estimated that there were approximately 65,000 plains bison in North America during the mid-1970s, with only a small proportion of those animals being free-ranging and wild. Most of these bison were confined in fenced areas of various sizes in parks, in nature preserves, and on private lands. By 1990, there were an estimated 90,000 plains bison in the United States, of which about 70,000 (78%) were in privately owned herds (National Buffalo Association 1990). In 2002, there were approximately 400,000–480,000 plains bison in the United States, of which about 385,000–465,000 (96%) were in privately owned herds. The total number of plains bison in Alberta, in Canada, and in North America, respectively, is estimated to be approximately 100,000–120,000, 200,000–240,000, and 600,000–720,000 animals (Gerald Hauer, Bison Specialist, Bison Centre of Excellence, pers. commun., 2002). Within North America, about 580,000–700,000, or 97% of the total number of plains bison, are held in privately owned herds. Only about 3% of the total number of continental plains bison are maintained in publicly owned and conservation-oriented herds. The distribution of public plains bison herds in North America is shown in Fig. 48.6. The origin, current status, conservation objectives, and management regime for each of these herds are presently under investigation by the World Conservation Union Bison Specialist Group.

Wood bison have achieved modest recovery and are no longer threatened by imminent extinction. However, the scope for further recovery in the wild in Canada is constrained by a variety of factors, of which the presence of diseased herds, habitat loss, and the increasing number of commercial bison ranches are the main limitations (Gates et al. 2001b). Reestablishment of additional herds within the original range of the subspecies in Canada and in Alaska will continue to play a key role in the conservation and recovery of wood bison. In addition, these initiatives will continue to contribute to ecological restoration and create opportunities for bison to play a major role in the culture and economies of northern peoples, as they have in the past.

Status of Wood Bison Recovery Herds in Canada. As of 2002, there were approximately 3154 wood bison in six free-ranging, disease-free herds in northwestern Canada (Table 48.6 and Fig. 48.7). There were 1029 in five captive breeding herds, three of which are public herds and two of which are privately owned herds with conservation objectives; and about 4495 in infected, or presumed infected, free-ranging herds in and around Wood Buffalo National Park (Tables 48.6 and 48.7). In addition, there are at least 500–700 wood bison on 45–60 private ranches in Canada, mainly in the Prairie provinces. However, privately owned herds are managed for commercial production and are not regarded as contributing to the Wood Bison Recovery Program unless they are directly linked to conservation projects. The number and size of privately owned herds is increasing rapidly, but this is driven mainly by commercial interests. Two reestablished wild herds, the Mackenzie and the Yukon herds, have exceeded the minimum individual population objective of 400 animals (as set by the Wood Bison Recovery Team) and are the only disease-free, free-ranging wood bison populations for which hunting is permitted.

Wood bison conservation and recovery herds are classified into four categories: public herds that are free-ranging and not exposed to or infected with bovine tuberculosis and brucellosis; captive breeding herds that are under public ownership or are being co-managed; captive breeding herds that are under private ownership, but are directly linked to the recovery program as conservation projects (Table 48.6); and public herds that are free-ranging and infected or presumed to be infected with bovine tuberculosis and/or brucellosis (Table 48.7). The status of the six public wood bison herds that are free-ranging and disease-free follows.

The Mackenzie population (Fig. 48.7), the first disease-free herd to be reestablished in the wild, was founded in 1963 with the transfer of 18 wood bison from Wood Buffalo National Park to the Fort Providence area west of Great Slave Lake, Northwest Territories (Gates and Larter 1990). The herd currently is about 2000 animals and is the largest of six disease-free wild populations (Table 48.6). Regulated hunting has been

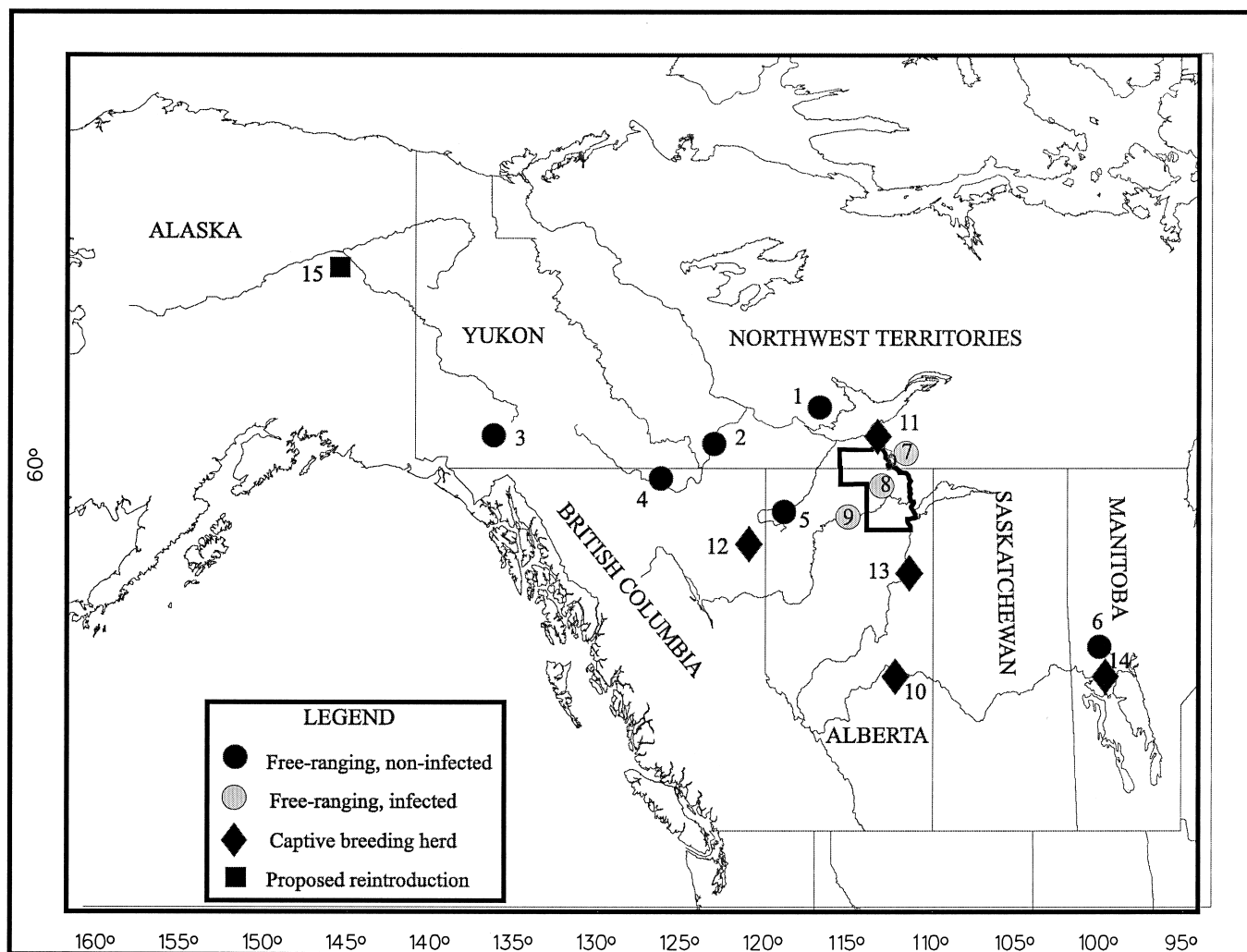


FIGURE 48.7. Distribution of free-ranging and captive breeding wood bison (*Bison bison athabasca*) herds in Canada and the location of a proposed reintroduction in Alaska. Numbers provide a cross-reference to the following list of herds and locations: 1, Mackenzie (2000); 2, Nahanni (200); 3, Yukon (530); 4, Nordquist (62); 5, Hay-Zama (262); 6, Chitek Lake (100); 7, Slave River Lowlands (518); 8, Wood Buffalo National Park (3870); 9, Caribou-Lower Peace (107) (Wentzel-Wabasca); 10, Elk Island National Park (350); 11, Hook Lake Recovery Project (132); 12, Etthithun Lake (49) (Note: now free-ranging); 13, Syncrude Canada Ltd. Beaver Creek Wood Bison Ranch (200); 14, Waterhen Wood Bison Ranches Ltd. (298); 15, Yukon Flats, Alaska (proposed).

permitted since 1988. All other reestablished, free-ranging, disease-free herds were founded with stock originating or derived from Elk Island National Park.

The Nahanni population (Fig. 48.7) was established in 1980, when 28 wood bison were directly released to the wild. It was supplemented with 12 bison in 1989 and 60 in 1998. The Nahanni herd is estimated to be approximately 200 (Table 48.6). It ranges in the Liard River drainage in the southwestern Northwest Territories and northeastern British Columbia. Hunting of this herd is not permitted in either jurisdiction.

The Yukon herd was established by seven independent releases for a total of 170 wood bison from 1986 through 1992. Most of the released bison were transferred from Elk Island National Park, with small numbers being transferred from the Moose Jaw Wild Animal Park in 1989 and the Toronto Zoo in 1992. The Aishihik herd free-ranging in the Yukon is about 530 (Fig. 48.7 and Table 48.6). Based on winter herd counts, annual calf recruitment from 1998 to 2003 has maintained a rate of 18–20%/year. Hunting (annual harvest of 70–90 animals) has been instituted as a management tool to limit the growth of the herd and maintain a population of approximately 500 (Government of Yukon 1998).

Wood bison were reintroduced into northeastern British Columbia in March 1995 to establish the Nordquist herd. Forty-nine were

transferred from Elk Island National Park to the Nordquist Flats area in the Upper Liard River Valley at a site approximately 80 km from the southern part of the Nahanni herd's range (Fig. 48.7). The present population is estimated at 62 animals (Table 48.6). The Nahanni and Nordquist herds eventually are expected to coalesce to establish a population of at least 400 bison. The management goals for wood bison in British Columbia are to reestablish additional herds through translocation, maintain separation from plains bison, maintain disease-free status, and permit populations to increase to a level sufficient to support nonconsumptive and consumptive use (Harper et al. 2000).

A project to reestablish the Hay-Zama wood bison herd in northwestern Alberta (Fig. 48.7) was initiated in 1981 in cooperation with the Dene Tha First Nation. A free-ranging herd was established in 1993 when 48 bison escaped prematurely from the fenced compound. An aerial survey (Morton 2003) estimated the population at 262 in winter 2002/2003 (Table 48.6). The Government of Alberta established a 36,000-km² management area in the northwest part of the province to protect the Hay-Zama wood bison herd because all other bison in the province are designated as "livestock" in the Alberta Wildlife Act. This management area has the potential to support at least 400 wood bison, but plans are to maintain the herd well below 400 animals until the northern bison disease issue is resolved.

TABLE 48.6. Status of public, free-ranging, disease-free wood bison herds in Canada, public and co-managed captive breeding herds, and privately owned herds that have conservation objectives

Location	Herd Type	Status	Year of Estimate	Source of Stock ^a	Year Established	Number Released ^b
Mackenzie	Free-ranging/public	2000	2000	NR	1963	18
Yukon	Free-ranging/public	530	2002	EINP	1986	170
Nahanni	Free-ranging/public	200	2002	EINP	1980	100
Chitek Lake	Free-ranging/public	100	2002	EINP	1991	22
Hay-Zama	Free-ranging/public	262	2003	EINP	1993	48
Nordquist	Free-ranging/public	62	2003	EINP	1995	49
Subtotal		3154				
Elk Island National Park	Captive/public	350	2002	NR	1965	21
Hook Lake Wood Bison Recovery Project	Captive/co-managed	132	2003	SRL	1996	62
Etthithun Lake	Captive/public	49	2003	EINP	1999	43
Subtotal		531				
Waterhen Wood Bison Ranches Ltd.	Private/conservation	298	2003	EINP	1984	34
Syncrude Canada Ltd./Beaver Creek Wood Bison Ranch	Private/conservation	200	2003	EINP	1993	30
Subtotal		498				
Total		4183				

^aNR, Nyarling River; EINP, Elk Island National Park; SRL, Slave River Lowlands.

^bNumber released to establish free-ranging herd or initial number to establish captive breeding herd.

A free-ranging herd of wood bison was established in the northern Interlake Region of Manitoba (Fig. 48.7) from a total of 22 wood bison released near Chitek Lake, north of the Waterhen Wood Bison Ranch, from 1991 to 1993. The population was estimated to be approximately 100 during winter 2002–2003 (Table 48.6). The Chitek Lake region has the potential to support 400–500 wood bison. The province of Manitoba has established a protected area for those wood bison and their habitat.

The status of the three captive breeding herds of wood bison that either are under public ownership or are co-managed for conservation and recovery follows.

The Elk Island National Park wood bison herd (Fig. 48.7) has played a key role in the recovery of wood bison in Canada, providing stock directly or indirectly for the establishment of five wild populations. The 2002 fall population was approximately 350 (Table 48.6). This semiwild herd is fenced in a 65-km² area, relies on natural forage, and interacts with its environment under natural conditions. However, this herd is not subjected to predation by wolves or any other large carnivores.

In 1991, the Deninu Kue' First Nation initiated a program to restore a disease-free herd of wood bison in the Hook Lake area of the eastern Slave River Lowlands, Northwest Territories. Specific objectives of the Hook Lake Wood Bison Recovery Project which was implemented in 1996 are to raise a disease-free herd of captive wood bison from salvaged Hook Lake calves, conserve genetic integrity, salvage disease-free wood bison from the wild Hook Lake herd, and use the captive herd as a source stock to establish a disease-free wild population (Nishi et al. 2001; Nishi et al. 2002a). The project involves three phases including

habitat renewal, propagation of a disease-free captive-breeding herd in Fort Resolution (Fig. 48.7), and eventual reestablishment of a disease-free herd in the wild (Gates et al. 1998; Nishi et al. 2001). By July 2001, 62 calves had been removed from the wild herd yielding a captive breeding herd of 58 founders plus another 50 captive-born (Nishi et al. 2002a). This has resulted in a captive breeding herd of at least 132 disease-free wood bison (Table 48.6). The number of founders used to establish the Hook Lake captive breeding herd represents more genetic diversity than two previous attempts to salvage wood bison genetics from Wood Buffalo National Park (Nishi et al. 2001).

In March 1999, 19 wood bison were transferred from Elk Island National Park to a fenced 850-ha enclosure in the Etthithun Lake area in northeastern British Columbia (Fig. 48.7). In February 2000, 24 additional wood bison were moved to the captive herd from Elk Island National Park. In January 2003, the total herd, including 7 calves, numbered 49 (Table 48.6). However, at press time, it was learned that the Etthithun Lake wood bison are no longer contained by fencing and constitute a new free-ranging herd.

The status of the two captive breeding herds that are privately owned, but have conservation objectives with direct linkages to the Wood Bison Recovery Program follows.

In 1984, Elk Island National Park provided founding stock for a wood bison ranch in the northern Interlake region of Manitoba (Fig. 48.7). In 1991 and 1993, 22 wood bison from this herd were used to establish a free-ranging herd in the Chitek Lake area. The Skownan First Nation manages the Waterhen Wood Bison Ranches Ltd. captive herd of approximately 298 animals (Table 48.6) as a commercial wood bison ranch.

The Syncrude Canada Ltd. herd was established in 1993 with 30 wood bison from Elk Island National Park to determine whether restored soil on reclaimed oil sands could support forage crops and a productive bison herd. Syncrude Canada Ltd. and the Fort McKay First Nation cooperatively manage the Beaver Creek Wood Bison Ranch herd of wood bison in fenced pastures encompassing 2.6 km² of oil sands reclamation property north of Fort McMurray (Fig. 48.7). This captive breeding herd presently numbers about 200 (Table 48.6). In the future, there is potential to convert 1800 ha of reclaimed oil sands lands to a mosaic of grassland, wetland, and shrubland habitats for maintenance of a commercial and/or conservation herd exceeding 400 animals.

Disease testing has confirmed that bison herds in the vicinity of Wood Buffalo National Park and the Slave River Lowlands have been exposed to or are infected with bovine tuberculosis and brucellosis, which were transferred with plains bison that were introduced from

TABLE 48.7. Status of public, free-ranging wood bison herds in Canada that are infected or presumed infected with bovine tuberculosis and brucellosis

Location	Herd Type	Status	Year of Estimate	Source of Stock
Slave River Lowlands	Free-ranging/public	518	2000	Indigenous
Wood Buffalo National Park	Free-ranging/public	3870	2002	Indigenous
Caribou-Lower Peace, Wentzel	Free-ranging/public	44	2002	Indigenous
Caribou-Lower Peace, Wabasca	Free-ranging/public	63	2002	Indigenous
Total		4495		

1044 HOOFED MAMMALS

Wainwright, Alberta, in the 1920s (Tessaro 1987). The status of the four public, free-ranging populations of bison that are infected or presumed to be infected with bovine tuberculosis and brucellosis follows.

In 1970, there were about 2500 bison on the Slave River Lowlands, Northwest Territories, adjacent to Wood Buffalo National Park. The Hook Lake herd on the east side of the Slave River (Fig. 48.7) declined from 1700 to about 200 by the late 1980s. Poor calf production, infection with bovine tuberculosis and brucellosis, wolf predation, and hunting contributed to this decline (Reynolds and Hawley 1987). In 2000, the Slave River Lowlands population, including both the east and west side of the Slave River, was estimated at 518 bison (Table 48.7).

The Wood Buffalo National Park wood bison population (Fig. 48.7) has continued to decline since the 1970s from at least 10,000 to a low of about 2200 in 2000. However, in winter 2002, a more intensive coverage aerial survey resulted in a minimum count of 3870 bison (Table 48.7) in Wood Buffalo National Park (Mark Bradley, Wood Buffalo National Park, pers. commun., 2003). The metapopulation of bison associated with Wood Buffalo National Park, which includes the Slave River Lowlands herds, is approximately 4300–4400 bison. It is infected with bovine tuberculosis and brucellosis (Joly and Messier 2001a, 2001b). The long-term viability of Wood Buffalo National Park subpopulations and the impact on wood bison recovery needs to be addressed. There is a requirement for a collaborative, multistakeholder planning process to develop a management plan that will lead to eradication of these bovine diseases and recovery of healthy increasing herds of wood bison in the Greater Wood Buffalo Region.

There is relatively little information concerning bison populations in the Caribou-Lower Peace region of Alberta adjacent to the southwest corner of Wood Buffalo National Park (Fig. 48.7). A Wentzel Lake bison herd ranges in the boundary area between Wood Buffalo National Park and Wentzel Lake, north of the Peace River. An estimate of the number of animals residing in the Wentzel area in winter 2002 was 44 (Table 48.7). During an aerial survey in March 2002, a minimum of 63 bison was counted in two herds located between the Mikkwa and Wabasca Rivers (Kim Morton, Alberta Sustainable Resource Development, pers. commun., 2003). These animals constitute a second bison population known as the Wabasca herd (Table 48.7). There is a need to assess the size and structure, the disease and genetic status, habitat use, and movement patterns of these two wild herds in the Caribou-Lower Peace region of Alberta.

Habitat Management. Expansion of resource extraction, forestry, and associated human activities in the boreal forests of northern Alberta and British Columbia present challenges and opportunities for wood bison recovery in these areas. Although habitat loss and degradation and increased hunting are likely to result from development activities, there is some potential for positive effects. For example, the Syncrude Canada Ltd. captive breeding herd was established on reclaimed grasslands in northeastern Alberta, and planting of forage species in oil and gas exploration right-of-ways in northeastern British Columbia was commissioned to enhance habitat for wood bison.

Disease Management. Two exotic diseases are problematic for wild bison conservation in North America. Bovine brucellosis and bovine tuberculosis are bacterial diseases originating in cattle. Bison are susceptible and the pathobiology of the infectious organisms is similar in cattle and bison. Free-ranging bison populations in and adjacent to Wood Buffalo National Park are infected with *Mycobacterium bovis*, the causative agent for tuberculosis. It was introduced in the region with the transfer of plains bison in the 1920s. Bison populations in northern Canada and those in Yellowstone and Grand Teton National Parks are infected with *Brucella abortus*, which causes the disease brucellosis. These pathogens are zoonoses, as they can cause disease in humans. In addition, they have been the subject of largely successful eradication programs in domestic livestock in Canada and the United States. Brucellosis in Yellowstone bison is of immediate concern to the cattle industry in Montana, Wyoming, and Idaho. The presence of tuberculosis and brucellosis in bison in the Greater Wood Buffalo Region is of concern for wood bison conservation (Tessaro 1986; Gates et al.

1992a, 1997, 2001c), the commercial bison industry, and the cattle industry in northern Canada. Proposals to eradicate these pathogens from bison have been the subject of significant controversy since the mid-1980s.

In December 2000, following several years of collaborative planning by the Greater Yellowstone Interagency Brucellosis Committee, the U.S. Department of the Interior National Park Service and the U.S. Department of Agriculture Animal and Plant Health Inspection Service and Forest Service signed a Record of Decision on a Joint Management Plan for bison in Yellowstone National Park and Montana (*Federal Register* 2001). This plan was designed to preserve the Yellowstone bison population and minimize the risk of transmission of brucellosis between bison and cattle, but was not designed to achieve disease eradication. The plan allows for limited use of public lands outside the park by bison during winter when cattle are not present. The potential for mixing of bison with cattle is reduced by hazing bison back into the park when possible. Bison that remain outside the park are subject to capture or removal and cattle are not allowed to return to public lands until a sufficient amount of time passes to ensure that bacteria are no longer viable on the range. In an area where there is a large degree of concern about bison leaving the park, bison may be captured and tested for antibodies to *B. abortus*, and seropositive bison may be slaughtered. The Joint Management Plan prescribes a spring bison population of up to 3000 animals be maintained. The signatory agencies have agreed to increase the use of nonlethal management measures should severe winter conditions result in a large removal for management purposes or a natural winter die-off. Cattle in areas north and west of Yellowstone National Park must be vaccinated against brucellosis. Vaccination of bison inside the park with a safe and effective vaccine delivered by remote injection is also prescribed. In addition, research initiatives are being undertaken in support of the management plan. Initiatives include development and testing of the efficacy and environmental safety of vaccines for use in bison and elk, pathobiology, histopathology, and epidemiology and population effects of brucellosis in bison, environmental persistence of *B. abortus* in tissues and contaminated ground, detection of *B. abortus* in tissues, the potential for transmission of the disease between ungulate species, and factors affecting seasonal movements and distribution of bison.

In Canada, tuberculosis and brucellosis are widespread among bison herds in the vicinity of Wood Buffalo National Park (Tessaro et al. 1990). All subpopulations within Wood Buffalo National Park are infected. Two herds in the Slave River Lowlands, adjacent to Wood Buffalo National Park, are infected with these two diseases (Broughton 1987). Evidence of disease was also detected in bison outside the southwest corner of Wood Buffalo National Park in the Caribou-Lower Peace region (Tessaro et al. 1990). The disease status in other small remnant herds reported to exist south of Wood Buffalo National Park has not been assessed (Gates et al. 2001c). Also, there is concern that livestock in the region are at risk of becoming infected. In 1985, Canada's national cattle herd was declared free of bovine brucellosis, and bovine tuberculosis had nearly been eliminated (Gates et al. 1997). Consequently, wildlife reservoirs of these two diseases became of increasing interest to the livestock industry and agencies responsible for regulating infectious animal diseases. These infected bison herds are seen as the last unregulated source for potential reinfection of cattle in Canada. Agricultural activity near the southwest corner of Wood Buffalo National Park has substantially expanded over the past 30 years. Not only are local farmers grazing cattle and bison in the area, but livestock is transported under subsidy to and from community grazing pastures in the region. In recent years, the commercial bison industry has rapidly expanded in northern Alberta, with an increase in the risk of infection through contact with wild bison from infected herds (Gates et al. 2001c). Free-ranging bison have been seen in a large area west and south of Wood Buffalo National Park and in the agricultural zone west of the park (Gainer 1985; Gates et al. 1992b, 2001c). Clearly, there is a need to better integrate conservation biology with agricultural livestock policy to develop management options and better address the unique conservation challenges that are presented by diseased, free-ranging bison populations in Northern Canada (Nishi et al. 2002b).

Unlike the Yellowstone Ecosystem, there are several healthy wild bison populations in northern Canada for which there is concern about the risk of infection (Gates et al. 2001b, 2001c). Two captive breeding herds of wood bison also have been established in the region. Among the free-ranging herds, the Mackenzie population is in closest proximity to the infected herds; about 100 km separates it from Wood Buffalo National Park. The Government of the Northwest Territories, in cooperation with Wood Buffalo National Park, established a buffer zone and ongoing surveillance program in 1987 between the disease-free Mackenzie herd and Wood Buffalo National Park to reduce the risk of disease transmission. The program attempts to exclude bison from the buffer zone through active surveillance and culling (Gates et al. 1992b). In northern Alberta, bison around Wood Buffalo National Park are not protected from hunting to encourage depopulation of the area and to reduce the risk of contact between healthy and infected bovine populations.

Although a collaborative research program has been completed in Wood Buffalo National Park to define the role of the diseases in bison population dynamics, there is presently no mechanism for developing a long-term approach to bison conservation and disease risk management. Research has been completed on the role of the two diseases in limiting population growth of northern bison (Joly and Messier 2001a, 2001b) and a disease risk assessment was completed by the Animal, Plant and Food Health Risk Assessment Network (1998). Gates et al. (2001c) compiled and mapped local ecological knowledge of bison in the Northwest Territories and Alberta, described community-based initiatives and interests, and calculated spatially explicit movement corridors through northern Alberta. They suggested that the information gained from this research provides a sufficient basis for initiating a planning process to define actions to deal with disease risk management and bison conservation. Gates et al. (2001c) recommended that a collaborative planning process be developed in which the interests of northern communities, the livestock industry, conservation groups, and government agencies are represented. They recommended implementing a process similar to the collaborative resource management process described by Wondolleck and Yaffee (2000), a stakeholder consensus decision-making process that involves the people who use the resources (affected interests) in developing decisions about those resources. Collaborative resource management is the most open and accessible process available for planning and decision making in natural resource management and has the potential to produce the most widely endorsed plan.

It is clear that any effective solution to the diseased bison problems in the Greater Yellowstone Ecosystem and northern Canada must satisfy interested parties who hold differing and often opposing points of view. There is no apparent easy solution to either situation. In our view, continued dialogue and collaborative planning should be accompanied by research aimed at addressing key information gaps while safeguarding values at risk such as the genetic and ecological value of infected bison populations as well as the disease-free status of free-ranging bison herds and livestock. Essential to this process will be the need for increased integration and collaboration among conservation biologists, veterinary practitioners, wildlife management authorities, the general public, and all affected stakeholders in a truly collaborative management planning process (Nishi et al. 2002b).

Emerging Issues. Chronic wasting disease (CWD), a form of spongiform encephalopathy, was first detected in North American wildlife in association with captive mule deer at a research facility run by the Colorado Division of Wildlife in 1967 (Madson 1998). The infective agent of CWD is a class of proteins now referred to as "prions," which can be transmitted where animals consume contaminated ruminant proteins in feed and possibly by other means (Prusiner 1995). This disease and its relatives such as scrapie, bovine spongiform encephalopathy, and the human variant, Creutzfeldt-Jakob disease, typically result in an incurable neuropathological condition resulting in death. Among North American wildlife, CWD has not been reported in bison, pronghorn, or bighorn sheep, but has been diagnosed in elk, mule deer, white-tailed

deer, and black-tailed deer (Williams and Young 1982; Spraker et al. 1997).

Conservation and Recovery Management. The bison was a keystone component of the North American plains and is considered to be a keystone species in tallgrass prairie (Knapp et al. 1999). Bison provided sustenance and the very "life blood" for aboriginal residents in North America and were the staple food for early explorers, fur traders, and many European settlers. The plains bison was nearly exterminated during the late 1800s because of indiscriminate killing resulting from market hunting for meat to satisfy the increasing population growth of European settlement and hide hunters for the fur trade. Threats to conservation and recovery of wild bison continue to exist even though bison numbers have significantly increased because of conservation and recovery efforts since the early 1900s as well as the rapid expansion of commercial bison production. Further recovery of bison as a wildlife species on public lands is limited by a variety of factors. These include habitat loss from agricultural development, urbanization, and other competitive intensive land uses; commercial bison production; loss of genetic diversity; bovine diseases; reintroduction difficulties; problems with maintaining genetic distinctness between subspecies; introgression of cattle DNA; and, in some instances, legislation, regulations, and policies that are inadequate for the long-term protection and conservation of bison (Boyd and Gates 2001). In general, there is a misconception that the North American bison as a wildlife species is secure and will survive in perpetuity.

Conservation Methods. In North America, bison management practices vary considerably, depending on the objectives of the individuals and agencies controlling the animals. Bison have been managed to preserve the species and subspecies, for commercial meat and commodities production in farming and ranching operations, as a game species of wildlife, as tourist attractions for nonconsumptive users, and for their historical significance. A variety of international, national, and local organizations and initiatives are involved with conservation and management of bison. A listing and brief description of the main organizations and initiatives follow.

THE WORLD CONSERVATION UNION/SPECIES SURVIVAL COMMISSION. The World Conservation Union (IUCN) was founded in 1948 and brings together more than 10,000 scientists and experts from 181 countries in a unique worldwide partnership. The IUCN mission is to influence, encourage, and assist societies throughout the world to conserve the integrity and diversity of nature. The Species Survival Commission (SSC), the largest of six commissions within the IUCN, cooperatively functions to provide information and recommendations on the status and conservation of species to managers, agencies, educational institutions, and others capable of implementing conservation actions. The Bison Specialist Group (BSG), which operates under the SSC, focuses specifically on bison conservation. There are two sections of the BSG, North America and Europe, each focusing on bison conservation in their respective jurisdictions and chaired by a regional co-chair. In 2002, the BSG, North America, commissioned a bison conservation status survey. This project is to review the conservation status of North American bison subspecies, the plains bison and the wood bison, and develop recommendations for enhancing bison conservation.

CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an international agreement between governments to ensure that international trade in specimens of wild animals and plants does not threaten their survival. No species protected by CITES has become extinct as a result of trade since the Convention was ratified, and its member parties now exceed 150. The species protected under CITES are listed in three appendices according to the degree of protection they need. In 1977, wood bison were placed on Appendix I, the highest level of protection. In June 1997, the subspecies was downlisted to Appendix II because of the absence of a threat from international trade, progress toward recovery in the wild, and the rapidly expanding ranching industry. In addition,

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there would be inherent problems with regulating exports and imports of wood bison and their products produced on commercial ranches if wood bison were to remain at the Appendix I level (Gates et al. 2001b). Plains bison are not on the CITES list.

COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a federal-provincial committee created in 1977 at the Conference of Federal, Provincial, and Territorial Government Wildlife Directors. This Canadian national committee, composed of scientific representatives from government as well as nongovernment scientific experts, operates at arm's length from governments and is responsible for assessing and classifying Canadian wildlife species that are suspected of being at risk based on the best available scientific, community and aboriginal traditional knowledge. With the proclamation into law of the Species at Risk Act in June 2003, COSEWIC has been established as a legal entity. Wood bison were recognized by COSEWIC as an endangered subspecies of Canadian wildlife in 1978 (Gates et al. 2001b). This status was changed to threatened in June 1988, based on recovery progress as reported in the COSEWIC status report (Wood Bison Recovery Team 1987). Plains bison are currently being assessed and therefore do not yet have a status designation by COSEWIC.

RECOVERY OF NATIONALLY ENDANGERED WILDLIFE. Canada launched a national recovery program in 1988 to rescue wildlife species at risk of extinction and to prevent other species from becoming at risk, named RENEW (the acronym for REcovery of Nationally Endangered Wildlife). This program involves federal, provincial, and territorial government agencies, wildlife management boards authorized by a land claims agreement, aboriginal organizations, other nongovernment organizations, and interested individuals working together for the recovery of endangered, threatened, or, where possible, extirpated species that have been designated by COSEWIC. The recovery process includes formation of national recovery teams, development of recovery strategies and action plans, cooperative recovery actions, and program evaluation. Wood bison is on the priority list for RENEW, and the National Wood Bison Recovery Plan was produced under its authority and direction (Gates et al. 2001b).

WOOD BISON RECOVERY PROGRAM. Wood bison probably were never as numerous as plains bison, although they inhabited a vast region in the boreal forest biome during the late Holocene. Most early observations of northern bison were recorded by explorers during expeditions throughout northern Canada in the late 1700s (Wood Bison Recovery Team 1987). The total population of wood bison in 1800 was about 168,000 animals, based on estimated carrying-capacity potential (Soper 1941). Wood bison were nearly eliminated from their remaining range in Canada during the late 1800s, coinciding with the rapid decline of plains bison between 1840 and 1900 (Raup 1933). By 1891, a population of only 300 wood bison remained in the wilderness region between Great Slave Lake and the Peace-Athabasca Delta (Ogilvie 1893). This population further declined to an estimated low of approximately 250 animals during 1896-1900 (Soper 1941). After 1900, wood bison occasionally were observed in parts of their original range, but numbers were insignificant except in the Slave River Lowlands and the area designated later as Wood Buffalo National Park (Gates et al. 1992a, 2001d). Heavy exploitation following the advent of the fur trade played a major role in the decline of wood bison in Canada (Gates et al. 1992a, 2001b).

Bison conservation efforts began in Canada in 1877 with passage of the Buffalo Protection Act (Hewitt 1921). However, this measure was largely ineffective because of lack of enforcement. The first police outpost was established along the Slave River in 1907, and six Buffalo Rangers were appointed in 1911 to patrol the wood bison range. The wood bison population began to increase slowly to approximately 500 by 1914 (Banfield and Novakowski 1960). By 1922, when Wood Buffalo National Park was established to save the wood bison from extinction and to protect their habitat, the total number was estimated at between 1500 and 2000 (Seibert 1925; Raup 1933; Soper 1941; Lothian 1979).

In 1905, the largest privately owned herd of plains bison in North America was threatened by the loss of grazing rights. Following negotiations between the Canadian government and the owner, 410 plains bison were purchased from the Pablo-Allard herd and shipped from northern Montana to Elk Island National Park, Alberta, in 1907 in a major conservation effort (Lothian 1981). On completion of the newly enclosed Buffalo Park at Wainwright, Alberta, in 1909, 325 plains bison from Elk Island, 218 plains bison from the original herd in Montana, and 77 plains bison from the exhibition herd in Banff were brought to Wainwright (Lothian 1981). Additional shipments over the next 5 years brought the total number of plains bison introduced at Wainwright to 748. In 1913, the Wainwright Buffalo Park herd had grown to 1188 plains bison, and by 1923 it had increased to 6780, where overcrowding caused range depletion. This led to a planned phased slaughter to control the herd, but the idea received such intense public criticism it was quickly abandoned, and a more publicly acceptable solution proposed to ship surplus plains bison north to the newly established Wood Buffalo National Park (Graham 1924). From 1925 to 1928, 6673 young plains bison were transported by rail from Wainwright to the Waterways railway terminus at Fort McMurray, Alberta, where they were then taken by barge down the Athabasca and Slave Rivers to Wood Buffalo National Park near Hay Camp (Lothian 1981). Plains bison were released at several sites along the west bank of the Slave River, south and north of Hay Camp (Fig. 48.8), into range already occupied by wood bison (Soper 1941). The total number of animals actually released into the Park was substantially lower than the number shipped, because of injuries and mortalities.

The proposed introduction of plains bison into wood bison range was challenged by the American Society of Mammalogists (Howell

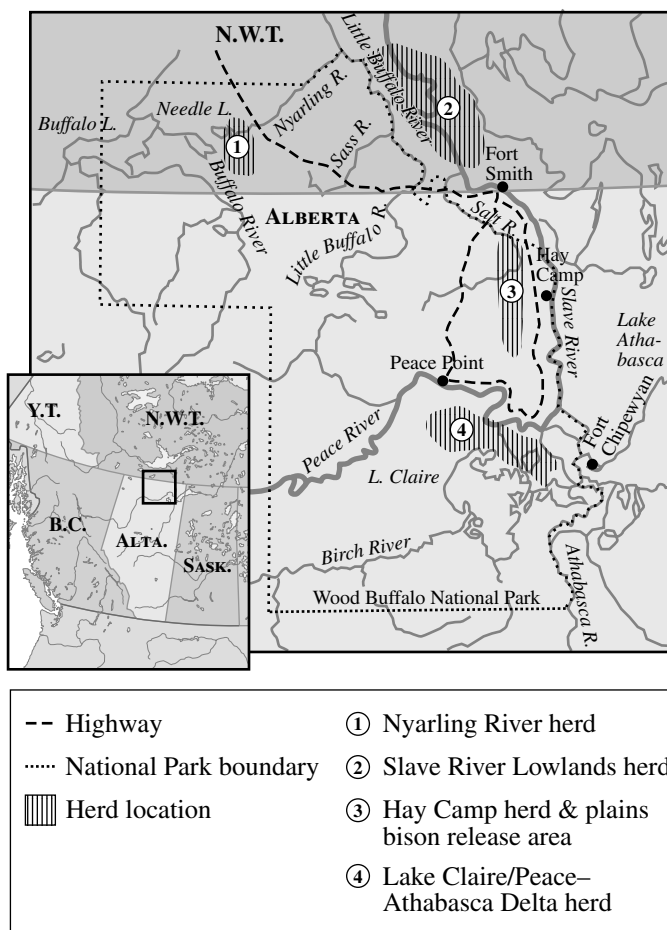


FIGURE 48.8. Distribution of bison (*Bison bison*) herds in the Greater Wood Buffalo National Park region in 1957 and the location of the Nyarling River wood bison (*Bison bison athabascae*) herd.

1925) and by individual biologists (Harper 1925; Saunders 1925). They believed interbreeding would result in the loss of both subspecies of bison, and wood bison would become infected with tuberculosis, which was known to be present in the Wainwright herd. The plains bison carried *Mycobacterium bovis* and *Brucella abortus*, the causative agents of bovine tuberculosis and brucellosis, respectively. The scientific challenges went unheeded and the Canadian government gave into public pressure some 78 years ago and proceeded with what turned out to be a serious conservation and biological mistake (Fuller 2002). Bison herds in the Greater Wood Buffalo Region remain infected to this day (Tessaro et al. 1990; Fuller 1991). The number of bison in Wood Buffalo National Park increased to an estimated 12,000 by 1934 (Soper 1941), and wolf control was used to maintain the population at this level until the late 1960s. In 1959, 5 bison collected from a herd of about 200 animals near the Nyarling River in the northwest corner of the Park (Fig. 48.8) were determined to be morphologically representative of wood bison (Banfield and Novakowski 1960). Despite some hybridization, Wood Buffalo National Park bison and herds founded with stock from the Nyarling River area remain genetically and morphologically distinguishable from plains bison (van Zyll de Jong et al. 1995; Wilson and Strobeck 1999) and warrant conservation as separate forms (Gates et al. 2001b; Wilson 2001; see the section Taxonomy).

Since 1960, there have been three major efforts to salvage wood bison from the Greater Wood Buffalo Region to establish disease-free captive breeding herds or wild populations. During the winter of 1963, 77 wood bison were captured in the Nyarling River and Buffalo Lake area in northwestern Wood Buffalo National Park (Fig. 48.8) to establish a captive-breeding herd near Fort Smith, Northwest Territories. After being tested for diseases, 19 of the captured wood bison were transported to a holding corral near Fort Smith, and in June 1963, 18 of these were transferred to establish the Mackenzie herd. The second salvage of wood bison was conducted again in northwestern Wood Buffalo National Park in 1965 and 21 animals were transferred to Elk Island National Park, Alberta. Unfortunately, the relocated wood bison carried bovine tuberculosis and brucellosis, but a rigorous management protocol involving isolation, quarantine of neonates, and elimination of all original stock managed to eradicate these diseases by 1971. The third salvage and recovery effort was initiated in 1996. Over a 3-year period, 62 newborn calves were captured from the Hook Lake herd in the Slave River Lowlands, Northwest Territories, maintained in enclosures near Fort Resolution, Northwest Territories, and treated prophylactically for exposure to tuberculosis and brucellosis (Gates et al. 1998; Nishi et al. 2001, 2002a). These bison are managed under quarantine as an experimental captive breeding herd, and the goal is to restore a disease-free population of wood bison in the Slave River Lowlands (Nishi et al. 2001).

The Wood Bison Recovery Team officially was established in 1988 under the Canadian initiative RENEW. In 1987, a recovery goal of four herds of 200 or more wood bison was established (Wood Bison Recovery Team 1987), which later was revised to four free-ranging populations of at least 400 each, presently the number believed to represent a minimum viable population (Gates et al. 2001b).

The Recovery Team completed a National Recovery Plan for wood bison in October 2001 with the ultimate goal of removing wood bison from the lists of species at risk (Gates et al. 2001b). Prescribed activities in the Recovery Plan are consistent with principles embraced in the World Conservation Strategy (International Union for Conservation of Nature and Natural Resources [IUCN] 1980), the World Conservation Strategy for Canada (Pollard and McKechnie 1986), guidelines established by the IUCN for reintroducing indigenous species to original range (IUCN 1987), and the Wildlife Policy for Canada (Environment Canada 1990). Three conservation principles endorsed by the Wood Bison Recovery Team that were embodied in the Plan are to preserve intraspecific diversity within the context of biodiversity conservation by continuing to manage wood and plains bison separately, to restore interactions between wood bison and their environment to allow for continued natural selection and evolution, and to promote recovery of either subspecies of bison in suitable habitat within its original geographic range and secure from factors that might threaten its long-term survival.

Issues and Challenges for Wood Bison Recovery. The presence of cattle diseases, tuberculosis and brucellosis, in bison herds in the Greater Wood Buffalo Region continues to be the major obstacle to further recovery of healthy populations in northern Canada (Fuller 1991; Gates et al. 1992a, 2001b). Total depopulation of Wood Buffalo National Park and replacement with disease free wood bison was recommended in 1990 by the Environmental Assessment Park (1990). However, as in 1923–25 this recommendation to slaughter and restock has received so much public opposition that definitive action has not yet taken place (Fuller 2002). We question, as does Fuller (2002), why the serious error made in 1923 must be repeated because there is no apparent logical reason for further delay. The risk of infection of the Mackenzie and Hay-Zama wood bison herds is significant and ways to mitigate disease risk for wild and domestic herds of bison in this region need to be implemented (Gates et al. 2001c). Wood bison are protected in northwestern Alberta in a wildlife management area that was designated in 1993. However, recovery in adjacent areas is constrained by the presence of disease-infected herds and by legislation that exempts bison from being managed as wildlife throughout the rest of the province (Gates et al. 2001d).

The bison ranching industry has grown rapidly in northwestern Canada, in terms of both the number of bison and the number of new ranches. Presence of captive and free-roaming plains bison within the historical range of wood bison creates an obstacle to implementation of the recovery plan. The existence of free-ranging wood bison adjacent to commercial bison operations is a potential conflict, creating a need for wildlife managers and the ranching industry to jointly address this issue.

Establishing additional free-ranging herds of wood bison within original range in Canada is a high conservation priority. The number of wood bison currently in herds that are subject to evolutionary selection in the wild is small relative to historical levels, and the degree to which existing herds can expand is limited by a variety of factors (Gates et al. 2001d). Furthermore, the risk of infection of several existing herds with cattle diseases remains high. The long-term conservation of wood bison and its full recovery require an increase in the number of wild herds. Availability of release sites where conflict with agriculture and urban activities are minimized is a major limiting factor to the establishment of new wild populations, although some habitat exists in northeastern British Columbia, central and northern Yukon, and the lower Mackenzie Valley in the Northwest Territories. In addition, extensive high-quality habitat for wood bison exists in Alaska (Berger et al. 1995).

The conservation of genetic resources is an important issue for wood bison conservation and recovery. The national captive breeding herd at Elk Island National Park is genetically less diverse than other wood bison populations, including the parent population in Wood Buffalo National Park (Wilson and Strobeck 1999; Wilson 2001). Studies of the Hook Lake Wood Bison Recovery Project indicate that a significant portion of the genetic variability from the parent population in the Slave River Lowlands has been successfully salvaged and is represented in the captive herd, one of the most genetically variable herds that has been salvaged from Wood Buffalo National Park (Nishi et al. 2001). However, the Hook Lake wood bison recovery herd, the Mackenzie herd, and the Elk Island National Park source herd of wood bison are all genetic less variable than the parent population in Wood Buffalo National Park (Nishi et al. 2001). Incorporating and maintaining as much genetic diversity as possible within existing and newly established herds is of paramount importance for successful recovery.

Hunting. Authorized hunting of bison occurs in several locations throughout North America. Harvest of bison by hunting combines meat production with recreation, which can generate considerable revenue through trophy fees. The demand for bison hunting opportunities far exceeds supply (National Buffalo Association 1990). Bison are hunted on public lands in three areas in the contiguous United States, four areas in Alaska, and in five areas in Canada.

The Henry Mountains, Utah, is home to the only free-roaming herd of plains bison in the 48 contiguous United States that is subject to regulated hunting. Over 400 buffalo roam the lower areas of

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the Henry Mountains in the winter and range in the higher regions during the summer. Permits are issued to hunt bison annually by the Utah Division of Wildlife Resources, with hunts usually occurring in October–December. The first sanctioned hunt was held in 1950, and the second occurred in 1960. Hunts have occurred annually with the exception of 4 years in the mid-1960s and early 1970s (National Buffalo Association 1990). Forty-two bull bison and hunter's choice bison permits were issued for the Henry Mountains in 2002.

A herd of approximately 450 plains bison is maintained on Antelope Island, where annual round-ups identify surplus animals for culling by live sale. However, a number of mature bulls that are designated as surplus are removed through a hunting program. An estimated 10 bulls/year may be available for hunting based on a population size of 450. In 1987, 15 mature bull permits were issued. In 1988, due to an increasing population, 22 cow permits were issued for an October hunt and 22 hunter-choice permits were issued for a November/December hunt (National Buffalo Association 1990).

Management hunts for bison were held during the 1980s and 1990s in areas of Montana adjacent to Yellowstone National Park. Montana's first bison hunt was held in 1986 for a total of 57 animals, most of which were taken from the Gardiner area (National Buffalo Association 1990). Hunts were staged to manage the risk of infection to domestic livestock with brucellosis carried by Yellowstone bison moving out of the park primarily during the winter. The hunts were highly controversial and were stopped in response to protests. Under a recent management plan (*Federal Register* 2001), the potential for mixing of bison with cattle outside the park is managed first by hazing bison back into the park. Bison remaining outside the park are then subject to capture and return to the park or lethal removal by management authorities. Public hunting is no longer permitted.

The Custer State Park plains bison herd originated from the transfer of 36 animals from the Scotty Philip herd (Pete Dupree herd) in 1914 with additional animals from the Pine Ridge Indian Reservation during the late 1940s, and later from Wind Cave National Park. The managed herd size at fall round-up is approximately 1400. This is reduced to about 950 after surplus animal removals in October for the annual live auction sale in November. In mid-December to mid-January, the removal of 8- to 10-year old bulls takes place through a 3-day guided trophy bull hunt with hunters selected through an application and draw process (National Buffalo Association 1990).

Plains bison are hunted in four different herds in Alaska. Permits are allocated through draws, and hunters are assigned specific hunting periods as determined by the order drawn. The largest population is located along the Delta River near Delta Junction. This herd was established in 1928 when 23 bison were translocated from the National Bison Range in Montana. By 1947, the herd had increased to 400. Hunting was initiated in 1951 and is used to limit the herd to a precalving population of 275–300. The Delta Junction herd is maintained at this level to manage the risk of damage to agricultural crops and to keep the herd within the carrying capacity of its summer range. Between 6000 and 11,000 people apply annually for permits to hunt the Delta herd. In the 2002/2003 hunting season, 70 bull permits and 65 cow permits were allocated.

Three other Alaskan populations were established with translocations from the Delta Junction herd. The Copper River herd was established in 1950 with 17 bison from the Delta herd. In 1999, it numbered 87; 12 hunting permits were let in 2002/2003. In 1962, 35 bison were transplanted from the Delta herd to the Chitina River drainage. Poor habitat and winter severity have limited the growth of this population and it remains at between 30 and 50. A small quota of two tags is allocated for this herd. The fourth Alaskan population was established near the western end of the Alaska Range along the south fork of the Koyukuk River in the Farewell Lake area. Introduced with releases in 1965 and 1968, the Farewell herd has grown to about 300. Forty either-sex permits were allocated in the 2002/2003 hunting season.

Bison hunting was first disallowed in Canada in 1877 with the passing of the federal Buffalo Protection Act. Hunting was reinstated in the mid-1950s in the Slave River Lowlands in the Northwest Territories. Regulated, outfitted hunts were permitted annually between 1956

and 1962, when an outbreak of anthrax forced a temporary closure of hunting. Between 1968 and 1977, sport hunters took an average of 123 bison/year during regulated seasons in the Slave River Lowlands. At the same time, hunting by General Hunting Licence (GHL) holders, which include eligible aboriginal residents and a few long-term nonaboriginal residents, had no season or quota limit. Between 1973 and 1976, the wood bison population in the Slave River Lowlands dramatically declined and sport hunting was closed in 1977, but hunting by GHL holders has remained unregulated, although voluntary restrictions were applied.

Regulated hunting for male bison was first permitted in the Mackenzie wood bison population beginning in 1988. In 2001, a quota of 47 permits was allocated among the residents of Fort Providence (20) and Rae-Edzo (3), a limited-entry draw for other eligible hunters in the Northwest Territories (15), and 9 permits were allocated to Fort Providence to provide outfitting and guiding services for nonresident bison hunters.

The Yukon Department of Renewable Resources first allowed wood bison hunting in 1997, when five permits were provided for Yukon residents. The 1998 management plan stipulates that the herd will be maintained at a size of 500 through special-permit hunting (Government of Yukon 1998). Ninety permits were issued in 2001–2002.

Regulated hunting of plains bison is allowed in northeastern British Columbia. The Pink Mountain herd was established in 1971 with the escape of captive plains bison from a ranch. The province assumed management authority for the herd in 1988. In February 2003, a total count survey resulted in 900 in the herd, which ranges in the Sikani Chief and Halfway River drainages. Five bull and 115 either-sex hunting permits were available for the 2002/2003 hunting season.

Free-ranging bison are found across northern Alberta. Bison hunting is not permitted in a special management zone that was established in northwestern Alberta to protect the reintroduced Hay-Zama wood bison population. Small herds and individual bison are found outside of this zone in areas near and adjacent to Wood Buffalo National Park. These bison are not recognized as wildlife under the Alberta Wildlife Act and are subject to unregulated hunting.

Nonconsumptive Use. Although difficult to evaluate, the direct and indirect human benefits derived from free-roaming bison herds should not be underestimated. The aesthetic value of bison also makes them a popular and valuable tourist attraction, especially in private and public zoos and parks. Grazing bison on public lands should make these areas more productive, and potentially would make them more attractive to public users.

Cultural and Ecological Revitalization. The Intertribal Bison Cooperative (ITBC) was initiated in the United States in 1990 to coordinate and assist tribes in returning bison to Indian country. The ITBC is a nonprofit tribal organization committed to reestablishing bison herds on Indian lands in a manner that promotes cultural enhancement, spiritual revitalization, ecological restoration, and economic development. The current membership of the ITBC is 51 tribes in 16 state regions, with an estimated collective herd of more than 8000 bison. Bison always have held great meaning for North American Indian people. Therefore, they feel reintroduction of healthy bison populations to tribal lands will help heal the spirit of both the Indian people and the bison.

The shortgrass expanse of the Great Plains, situated in the central United States between the Rocky Mountains on the West and the tallgrass prairies on the Midwest and South, is an already sparsely populated region, which is experiencing rapid depopulation as a result of a warming climate and cooling economy (Popper and Popper 1991). This situation has provided an opportunity for restoration of the Great Plains frontier by deprivatizing and reverting the most rural, environmentally fragile parts of the region to its native grasslands thereby creating a great "Buffalo Commons" as the world's largest historical preservation project (Popper and Popper 1991). Development of an operational strategy for a Buffalo Commons will require at least several decades to initiate and implement, whether it is governmentally assisted or privately induced on recently abandoned prairie lands. The Buffalo Commons land base could be greatly expanded from its present status

of national parks, grasslands, public grazing lands, wildlife refuges, and tribal lands as well as their state counterparts and many private and land conservancy holdings (Popper and Popper 1991).

Bison Farming. Bison farming is one of the fastest growing industries in agriculture. It is based mainly on consumer demand for healthy, lean, nutritious bison meat, which in North America is primarily destined for domestic markets. Bison producers exist in all 50 states, every Canadian province, and many countries around the world. Farms range in size from hobby herds of a few animals to major operations of 5000 or more head. Plains bison are unique among North American native ungulates in that they are generally not considered to be wildlife and, because of this status, commercial production of bison has been facilitated (Hawley 1989). The current legal classification of bison is important to the industry because regulations controlling the sale, slaughter, and transport of animals and the processing and sale of meat significantly differ between wildlife and domestic species (Hawley 1989). Bison can be processed in domestic animal abattoirs rather than requiring special facilities and regulations, a distinct advantage over wildlife species. Increasing interest in bison ranching has resulted in development of specialized handling facilities and the publication of specialty magazines. In 1978, the industry designed and published its first book on bison history and husbandry which was intended for use as a bison rancher's handbook (Jennings 1978). In 1990, this handbook was revised and updated into the Buffalo Producer's Guide to Management and Marketing (National Buffalo Association 1990), which was intended for use as a resource tool for bison farmers. Several organizations have been established throughout North America to support the industry. In the United States, the National Bison Association is the main organization whereas in Canada, the Canadian Bison Association is the national organization.

The National Bison Association is a nonprofit association of more than 2400 members from all 50 states and 16 foreign countries, which promotes the preservation, production, and marketing of bison. It is dedicated to the future of the industry and strives to better inform and educate its members and the general public about bison through its activities and services. The Canadian Bison Association provides services to more than 1400 bison producers across Canada as well as to any others involved in the industry.

Productive Advantages of Bison. Because of their intractable nature, cold-hardiness, and ability to digest poor-quality forages, bison appear to be most efficiently used as commercial meat animals under natural range conditions. The characteristics of bison that make them desirable as a source of meat primarily involve their ability to be productive under range conditions that are not optimal for cattle. One of the greatest assets of bison are their ability to graze native range throughout the year because of their cold weather resistance and ability to forage through deep snow (Hawley and Reynolds 1987; Hawley 1989). Furthermore, the superior digestion of low-quality forages allows bison to use range forage that would be considered marginal for cattle. Bison tend to be less selective grazers than cattle (Peden et al. 1974). This digestive difference can provide a production advantage to bison when feed quality is low (Hawley et al. 1981b), but this advantage may be reversed when feed quality is high (Hawley 1989). Although bison on range consume poorer quality forage than do cattle under similar conditions, they will readily consume grain and high-quality feeds (McHugh 1958, Peters 1958).

Feed requirements for bison are generally similar to those for cattle with the exception of a few important differences in relation to feed quality and intake (Hawley 1989). For example, bison usually eat less than cattle, especially during winter. Lower feed consumption may be an adaptive strategy to reduce growth and limit activity and intake at a time of year when forage is difficult to obtain and quality is low (Hawley et al. 1981a; Hawley 1987). In a minimum-input production system, this seasonal adjustment in intake by bison would serve to reduce feed costs during winter (Hawley 1989).

Bison can be raised under feedlot conditions, but this obviates some of the physiological productive advantages of bison over cattle. During the 1980s, there was a trend toward "finishing" bison on grain for 60–90 days to increase carcass fat and render bison meat more comparable to that of cattle (Hawley 1989). This may have enhanced

product attractiveness in the domestic market in the past, but more recently, this is considered counterproductive because the low-fat content of bison meat is desirable in marketing it as a health food. The primary marketing feature of bison meat is that it is a healthy and delicious alternative source of red meat that is lower in fat, calories, and cholesterol than beef, pork, or skinless chicken.

Crossbreeding. Crossbreeding bison with domestic cattle to take advantage of the hardiness of bison under adverse climatic and range conditions and the meat characteristics of domestic cattle dates back to the mid-eighteenth century (McHugh 1972). The government of Canada probably contributed one of the greatest sustained efforts of crossbreeding research experiments from 1916 to 1964, in which bison were crossed with Hereford, Angus, Shorthorn, and Holstein cattle. This work demonstrated that outstanding winter hardiness, as measured by hair coat density and performance of cattle–bison hybrids (cattalo) on winter range could be obtained by combining the two species (Peters 1978). However, major problems of hydromacy in domestic cows bred to bison bulls, mating indifference, and infertility of hybrid bulls developed (Hawley 1989). Hydromacy problems were alleviated by breeding bison cows to domestic bulls, but sterility problems of F₁ and F₂ bulls remained. Other disadvantages of cattalo to domestic cattle included lower calving frequencies, lower birth rates, and lower rates of post-weaning growth of hybrid calves under feedlot conditions (Peters 1958; Peters and Slen 1966; Hawley 1989). The major production advantage of hybrids was their winter hardiness (Smoliak and Peters 1955), but the disadvantages far outweighed the advantages and cattalo did not develop as an independent breed (Hawley 1989). More recently, beefalo, a mix of bison, Charolais, and Hereford, has renewed some interest in crossbreeding, but the genetic makeup and production advantages of beefalo have yet to be proven. Although the full potential of crossbreeding may not yet be realized, efforts so far have failed to produce a hybrid with outstanding production characteristics. It would appear that crossbreeding is probably not a viable production alternative (Hawley 1989).

Economics. Bison farming has been an active agricultural industry for several decades; however, it is still developing, which makes a meaningful economic evaluation difficult. Prices of stock and meat vary regionally and temporally (Hawley 1989). During the mid-1990s, animal prices were subject to a significant upward swing, especially for breeding stock, and the 1998 selling prices reflected that trend. Bull calves sold in the US\$600–800 range, yearling bulls sold in the US\$700–900 range, and 2-year old bulls averaged around US\$1100. For females, the prices increased to higher levels, where heifer calves sold in the price range of US\$2000, yearling heifers sold in the US\$2500–3000 range, and bred cows sold in the US\$3000–4000 range. The market is subject to a series of fluctuations, which can be quite severe, as experienced during 2002, when prices for breeding stock declined by up to 50%. At the Elk Island National Park annual live-sale in December 2001, male plains bison calves (33) averaged US\$155, yearling males (5) averaged US\$296, female calves (33) averaged US\$163, and yearling females (16) averaged US\$211 (Olson 2002). In February 2002, wood bison prices were somewhat higher than those of plains bison, but these prices were down nearly 50% from previous years. Male wood bison calves (27) averaged US\$591, 2-year-old males (7) averaged US\$1268, wood bison female calves (18) averaged US\$1940, yearling females (2) averaged US\$1640, and 2-year-old females (2) averaged US\$1800 (Olson 2002).

The commercial value of bison by-products (heads, robes, hides, wool, skulls, and horns) contributes significantly to the economic prospects of the industry and can provide considerable additional revenue compared with traditional livestock operations. There are markets in some areas of the United States for raw bison hides (US\$50–75), prime tanned hides (US\$400–800), and skulls of 2- or 3-year old bulls (US\$50–75) and 4+-year-old bulls (US\$75–125) (National Buffalo Association 1990). A limited market also exists for hooves, teeth, bones, tails, and bladders. Bison heads for display mounts have a limited market. Depending on size and quality, they are worth a few hundred dollars in an unprocessed state to thousands of dollars in a completed taxidermy mount.

Operating costs may be similar for bison and cattle under intensive farming production systems, but lower for bison under extensive ranching or less intensive farming systems (Hawley 1989). Capital investment for proper enclosures and handling facilities (exclusive of land) requires a greater initial expenditure for raising bison than for cattle in both types of production systems. Prime bison meat animals are bulls between 18 and 30 months of age, and the price of bison meat is generally 1.5–2 times that of the equivalent cuts of beef. Bison meat is a specialty product and will likely remain as such until supply is no longer limited. Bison meat is becoming more consistently available in the retail market. As production continues to increase, which will provide more stability in supply, the market for bison meat will likely increase. Demand is expected to exceed supply for many years to come (Hawley 1989).

The greatest potential for bison farming may be to complement cattle production rather than trying to replace it, because the greatest complement is derived by exploiting the environmental hardiness of bison (Hawley 1989). Bison are a suitable alternative on large areas of range that would be only marginal for cattle production because of severe winters, insect harassment, predation, and poor-quality forage (Hawley and Reynolds 1987). The primary constraints to the growth of the bison farming industry are the higher initial start-up costs and availability of breeding stock (Hawley 1989). The potential for growth and expansion of the bison farming industry is high, but will continue to be somewhat dependent on effective promotion.

RESEARCH NEEDS

Taxonomy and Genetics. The debate over the validity of bison subspecies in North America (Geist 1991; van Zyll de Jong et al. 1995) has the potential to result in genetic homogenization of wild bison if the distinction between these forms is denied as proposed by some authors (Bork et al. 1991; Geist 1991; Polziehn et al. 1996). The rapid development of molecular genetic techniques has led many investigators to regard these data as essential to conservation management, often to the exclusion of other data. Depending on the number and type of markers, there is a risk that molecular methods alone may not adequately define populations that merit separate management. Molecular methods that detect apparent reciprocal monophyly can be used to argue erroneously that morphologically or otherwise ecologically distinguishable populations should be managed as a unit. Natural or anthropogenic hybridization between closely related forms may further confound this problem, for example, the red wolf and coyotes (Nemecek 1996), wood bison \times plains bison (Wilson and Strobeck 1999), and bison \times cattle (Ward et al. 1999c).

Crandall et al. (2000) offered a method for diagnosing distinct populations, which emphasizes variation in phenotypes, allowing preservation of important adaptive characteristics and associated underlying genetic variation. The method incorporates both ecological and genetic exchangeability and considers whether each is recent or historical. There likely are sufficient available data to support this analysis for North American bison. In recognition of the pressure from taxonomic "lumpers," this pragmatic and conservative analysis is urgently needed for the species. A principle that should govern genetic management actions for the two forms of North American bison is preservation of the adaptive diversity of the species and the evolutionary processes that remain across its geographic range. A lack of evidence of nonexchangeability, either genetic or ecological (*sensu* Crandall et al. 2000), should not be used to promote homogenization or tampering with the gene pool of populations or to eliminate populations to reduce the geographic range of the species to make way for other uses of the land such as commercial bison production and other agricultural or industrial enterprises.

Diseases. Bovine tuberculosis and brucellosis remain the most important diseases of immediate concern for bison conservation because of their importance to human and domestic animal health and regulatory requirements for their control in both Canada (Gates et al. 1998) and the United States (Morrisette 2000). In addition, the effects of the diseases

on wild bison populations are of concern. The presence of both diseases, in synergism with wolf predation, may cause bison populations to exist at a low density relative to food carrying capacity (Joly and Messier 2001a). Management approaches that could either eliminate the diseases from wild bison or contain them within designated ranges without risk to disease-free bison or cattle populations remain problematic and further research is required. Approaches being studied include the development of vaccines (Roffe et al. 1999), improvements in the sensitivity and specificity of tests for disease (Lin et al. 1996), and salvage and veterinary treatment to establish disease-free herds (Gates et al. 1997) and mitigate the risk of spread of diseases from infected populations (Gates et al. 2001c; Bjornlie and Garrott 2001). Research on effective vaccines against brucellosis have been undertaken for the Yellowstone National Park herd (Roffe et al. 1999). This work is focused on efficacy in preventing infection with pathogenic field strains of *B. abortus* (Olsen et al. 1998) and biosafety of a new vaccine in the environment (Roffe et al. 1999; Cook et al. 2001). There was no published evidence of research on vaccine development for tuberculosis in bison. However, research is being undertaken to develop improved tests for detecting the presence of antibodies in bison (Joly and Messier 2001a).

Predator–Prey Dynamics. The recent reintroduction of wolves into the Yellowstone ecosystem has provided an opportunity to study in great detail the dynamics of a multiple-prey system and to add to knowledge gained from previous research on bison, other prey, and wolves in northern Canada (Carbyn and Trotter 1987; Van Camp 1987; Larter et al. 1994; Joly and Messier 2000). Research in Yellowstone National Park has shown that elk and bison female groups become more vigilant when sympatric with wolves (Laundre et al. 2001), wolves learn rapidly how to kill bison, and wolves prefer elk over bison (Smith et al. 2000). Wolves select bison calves over other classes and show a preference for weak individuals, including bulls (Smith et al. 2000). Carbyn (1983) found a similar pattern of prey selection within a guild of ungulates present in Riding Mountain National Park, Manitoba.

Although behavioral interactions among wolves and prey species are becoming better understood, less is known about the regulation by wolves of species within multiple-prey assemblages in which bison are represented. Messier (1996) demonstrated that for predation to be regulatory, there must be density dependence in both the functional (number of prey killed per wolf) and numerical responses of wolves to prey abundance, except when learning or prey switching is expressed as a sigmoidal functional response. In systems where wolves do not exhibit a numerical response to a particular species of prey, the relationship between prey density and predation rate can be inversely proportional and nonlinear (Dale et al. 1994; Messier 1996). This can cause the extirpation of a more highly preferred prey species in a guild, for example, woodland caribou in a moose–wolf system (Seip 1992). Indeed, Larter et al. (1994) found that although bison formed a larger proportion of the wolf diet because of their greater biomass, moose were the preferred prey species in the Mackenzie Bison range in the Northwest Territories. Furthermore, they suggested that woodland caribou may have declined substantially since bison were reintroduced in the study area.

Interactions between selectivity by wolves, relative and absolute abundance of each species, predation rate, and prey population dynamics is an important area of research. With its diversity of prey species, the Yellowstone ecosystem represents a unique opportunity to undertake research on predator–prey dynamics. Several interesting questions can be addressed in this system. What is the relationship between wolf density and ungulate biomass? Is the relationship between elk biomass and predation rate density dependent or will it be uncoupled if elk decline and bison become an increasing proportion of the wolves' diet? If the predation rate on bison increases as other species decline, will the relatively higher availability of bison lead to near extirpation of more preferred prey species? Will the system shift to a predominantly bison–wolf system? Will the numerical response of wolves to bison be linear if other prey species decline? The Yellowstone ecosystem offers a unique "laboratory" in which to answer these and many other questions regarding predators and prey.

ACKNOWLEDGMENTS

We gratefully acknowledge Environment Canada, Canadian Wildlife Service; the University of Calgary, Faculty of Environmental Design; and Tera Environmental Consultants Ltd. for supporting and encouraging us throughout the preparation of this chapter. We thank the biological and warden staff at Elk Island National Park for their assistance and cooperation; in particular, we are extremely grateful to Norm Cool and Wes Olson. We especially thank Greg Wilson for his helpful review comments on the manuscript, in particular, with the taxonomy and genetics sections. We are deeply indebted to Roberta McCarthy, Environment Canada Library, Downsview, Ontario, and Terri Fraser and Susan Blackman, Canadian Wildlife Service Librarians, Edmonton, Alberta, for their excellent and continuous library assistance and support. We thank Vi Jespersen, Canadian Wildlife Service, for electronic input of the initial draft manuscript. We further express our great appreciation of those many individuals, government agencies, and nongovernment organizations that have been involved with the conservation of both subspecies of the North American bison.

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